

**THE INFLUENCE OF HABITAT FRAGMENTATION ON
MARBLED MURRELET (*BRACHYRAMPHUS
MARMORATUS*) HABITAT QUALITY IN
SOUTHWESTERN BRITISH COLUMBIA**

by

Joshua M. Malt
B.Sc., University of Victoria, 2002

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

In the
Department
of
Biological Sciences

© Joshua M. Malt 2007

SIMON FRASER UNIVERSITY

Spring 2007

All rights reserved. This work may not be
reproduced in whole or in part, by photocopy
or other means, without permission of the author.

APPROVAL

Name: Joshua Malt
Degree: Master of Science

Title of Thesis:

The influence of habitat fragmentation on Marbled Murrelet (*Brachyramphus marmoratus*)
habitat quality in southwestern British Columbia

Examining Committee:

Chair: Dr. A. Beckenbach, Professor

Dr. R.C. Ydenberg, Professor, Senior Supervisor
Department of Biological Sciences, S.F.U.

Dr. D.B. Lank, Research Associate and Adjunct Professor
Department of Biological Sciences, S.F.U.

Dr. K.D. Rothley, Assistant Professor
School of Resource and Environmental Management, S.F.U.

Dr. A.E. Burger, Adjunct Associate Professor
Department of Biology, University of Victoria

Dr. J.M. Marzluff, Professor
Ecosystem Sciences Division, College of Forest Resources, University of Victoria
Public Examiner

4 April 2007
Date Approved



DECLARATION OF PARTIAL COPYRIGHT LICENCE

The author, whose copyright is declared on the title page of this work, has granted to Simon Fraser University the right to lend this thesis, project or extended essay to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users.

The author has further granted permission to Simon Fraser University to keep or make a digital copy for use in its circulating collection (currently available to the public at the "Institutional Repository" link of the SFU Library website <www.lib.sfu.ca> at: <<http://ir.lib.sfu.ca/handle/1892/112>>) and, without changing the content, to translate the thesis/project or extended essays, if technically possible, to any medium or format for the purpose of preservation of the digital work.

The author has further agreed that permission for multiple copying of this work for scholarly purposes may be granted by either the author or the Dean of Graduate Studies.

It is understood that copying or publication of this work for financial gain shall not be allowed without the author's written permission.

Permission for public performance, or limited permission for private scholarly use, of any multimedia materials forming part of this work, may have been granted by the author. This information may be found on the separately catalogued multimedia material and in the signed Partial Copyright Licence.

The original Partial Copyright Licence attesting to these terms, and signed by this author, may be found in the original bound copy of this work, retained in the Simon Fraser University Archive.

Simon Fraser University Library
Burnaby, BC, Canada



STATEMENT OF ETHICS APPROVAL

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

(a) Human research ethics approval from the Simon Fraser University Office of Research Ethics,

or

(b) Advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University;

or has conducted the research

(c) as a co-investigator, in a research project approved in advance,

or

(d) as a member of a course approved in advance for minimal risk human research, by the Office of Research Ethics.

A copy of the approval letter has been filed at the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, BC, Canada

ABSTRACT

I investigated the effects of habitat fragmentation on habitat quality on the marbled murrelet (*Brachyramphus marmoratus*), a threatened seabird that nests on mossy side branches in old-growth forests. I compared relative predation risk and nest-site availability between forest interior sites and three edge types: "hard" (recent clearcuts), "soft" (regenerating forest), and natural (i.e. riparian areas). Higher artificial nest disturbance from avian predators at edges relative to interiors occurred at hard, but not soft edges, suggesting that predation risk initially increases, but then decreases with time. Differences in moss abundance at anthropogenic edges relative to natural-edged patches provided evidence that fragmentation will reduce the availability of marbled murrelet nest-sites. Landscape-scale surveys of murrelet nest predators suggested that populations of common ravens and Steller's jays will increase with habitat fragmentation. To mitigate impacts on murrelet breeding success, I recommend that harvesting patterns minimize the ratio of hard edge to interior old-growth habitat.

Keywords: habitat fragmentation; edge effects; nest predation risk; habitat quality; marbled murrelets

ACKNOWLEDGEMENTS

Firstly, I would like to acknowledge all the generous financial support this project has received. During the first two years of my M.Sc. Thesis, I was supported by a NSERC Industrial Postgraduate Scholarship, and afterwards by a NSERC-CRD grant to my supervisor, David Lank. Research was funded by NSERC-CRD, British Columbia Forest Science Program, Canadian Forest Products Ltd., Timberwest Forest Corp., International Forest Products, Ltd., and Western Forest Products, Inc.

My gratitude to all the hard-working field crew that participated in this project, including Tom Ainsworth, Edward Spat, Shane Tillapaugh, Rocky Lis, and Camila Marcos. Special thanks to Shane “Dude-Man” Tillapaugh, for making every moment full of fun, and for his diligent attention to detail. Thanks to Tom Ainsworth for his commitment to the project, and for being a true friend. Thanks to my good friend Rocky, who had no problem taking orders from the “Yo-J”. Special thanks to John Deal, David Lindsay, and Wayne Wall for spatial data and logistical field support.

Thanks to my supervisor Dov Lank, for always having an open door and an open mind, and for believing in my ability to take on this large-scale project. Thanks to Kris Rothley for interesting conversations on spatial analyses, and for extremely useful help with developing management recommendations. Thanks to Alan Burger for his thorough comments on previous drafts of this thesis. Thanks to Ron Ydenberg for acting as my official senior supervisor. Thanks to Mai Yasue and Elsie Krebs for valuable comments on previous drafts. Thanks also to Elsie for many interesting conversations on ecological theory, and for her help in preparation for the first field season. Special thanks to Carl Schwartz and Laurie Ainsworth for statistical advice.

Finally, my gratitude to all the loved ones in my life, without whom this thesis would have little meaning. Special thanks to my parents, Lyon Malt and Pam Malt, who have always believed in my ability to achieve anything I set my mind to, and have given me the love and support to do so. Lastly, thank you, Gordon, for your last-minute proofreading, and for your ever-present love and support.

TABLE OF CONTENTS

Approval.....	ii
Abstract.....	iii
Acknowledgements	iv
Table of Contents	vi
List of Figures	viii
List of Tables	x
Thesis Summary	1
Chapter 1 Temporal dynamics of edge effects on nest predation risk on the Marbled Murrelet.....	8
1.1 Introduction	8
1.2 Methods	11
1.2.1 Study area	11
1.2.2 Site selection	12
1.2.3 Artificial nest experiment	13
1.2.4 Comparison with patterns at real nests	15
1.2.5 Predator surveys	16
1.2.6 Data analysis	17
1.3 Results	19
1.3.1 Artificial nest experiment	19
1.3.2 Comparison with patterns at real nests	20
1.3.3 Predator surveys	20
1.4 Discussion.....	21
1.4.1 Predation risk caused by avian nest predators.....	22
1.4.2 Corvid predator surveys	23
1.4.3 Squirrels as potential nest predators	24
1.4.4 Comparison with patterns at real nests	26
1.5 Management implications	28
1.6 Tables and Figures	30
Chapter 2 Effects of forest fragmentation on nest predator populations: landscape and patch-scale variation in predation risk on the Marbled Murrelet.....	40
2.1 Introduction	40
2.2 Methods	42
2.2.1 Study area	42
2.2.2 Landscape-scale predator surveys	42
2.2.3 Artificial nest study	43
2.2.4 Quantification of landscape structure	44
2.2.5 Data analysis	46
2.3 Results	49

2.3.1	Landscape-scale predator surveys	49
2.3.2	Artificial nest experiment	50
2.4	Discussion	51
2.4.1	Habitat fragmentation and predator populations	51
2.4.2	Landscape and patch-scale effects on predation risk	53
2.4.3	Cumulative predation risk	55
2.4.4	Comparisons to other landscape-scale studies	56
2.5	Management implications	57
2.6	Tables and Figures	59
Chapter 3 The effects of anthropogenic edges on marbled murrelet		
habitat availability: the influence of microclimate		68
3.1	Introduction	68
3.2	Methods	70
3.2.1	Study Areas	70
3.2.2	Microclimate sampling	71
3.2.3	Habitat Sampling	72
3.2.4	Data Analysis	72
3.3	Results	74
3.3.1	Microclimate Sampling	74
3.3.2	Habitat Sampling	74
3.4	Discussion	75
3.5	Management Implications	79
3.6	Tables and Figures	81
Literature Cited.....		88

LIST OF FIGURES

Figure 1.1. Location of the two study regions, Nimpkish Valley, and around Desolation Sound, Southwest British Columbia, Canada. Individual study sites are indicated by white circles. Dark shading indicates old-growth forest.	30
Figure 1.2. Examples of three different edge-types adjacent to old-growth forest patches in southwestern British Columbia, including a) hard, b) soft, and c) natural edges.	31
Figure 1.3. Common raven (<i>Corvus corax</i>) disturbing an artificial egg, captured by a motion-sensitive digital camera in the Nimpkish Valley, B.C.	32
Figure 1.4. 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 is pooled among Nimpkish Valley, and Desolation Sound, B.C.	34
Figure 1.5. 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.	35
Figure 1.6. Proportion of nests disturbed by squirrel predators (<i>Tamiasciurus</i> spp.) in edge and interior habitats at hard, soft and natural-edged sites for artificial eggs (a), and artificial nestlings (b). Data is pooled among Nimpkish Valley, and Desolation Sound, B.C.	36
Figure 1.7. Estimated logit detection of Steller’s jays at edges and interiors of hard and soft-edged sites around Desolation Sound, British Columbia.	38
Figure 1.8. Distribution of (a) Steller’s jays and (b) gray jay densities in gap, border, and forest margin habitats pooled among Desolation Sound, B.C., and the Nimpkish Valley, B.C.	39
Figure 2.1. Influence of (a) percent landscape in old-growth forest, (b) percent landscape in clearcuts, (c) percent landscape in regenerating forest, and (d) number of landscape old-growth patches, on mean detections of Steller’s jay in road transects in the Nimpkish Valley, British Columbia. The response variable in graphs (a-c) are plotted as residuals to take the other variables into account (i.e. detections in graph (a) are the residuals of the model including %Clearcuts and %Regenerating).	63
Figure 2.2. Influence of number of old-growth patches in the surrounding landscape on mean detections of common ravens in road transects in the Nimpkish Valley, British Columbia.	64
Figure 2.3. Influence of a) percent old-growth and b) number of old-growth patches of old-growth patches in the surrounding landscape on mean	

<p>detections of all predators combined (Steller's jays, gray jays, and common ravens), in road transects in the Nimpkish Valley, British Columbia. Detections in graph (a) are residuals accounting for percent clearcuts and percent regenerating forest in the landscape.</p>	65
<p>Figure 2.4. The influence of percent landscape old-growth on disturbances of artificial eggs by avian predators, at hard (a), soft (b), and natural-edged sites (c), in the Nimpkish Valley, British Columbia.....</p>	67
<p>Figure 3.1. Change with time of mean temperature (°C), at nest sites in patch edges and interiors, in the Nimpkish Valley, British Columbia. Regression lines are plotted separately for edge and interiors both early and late in the season (151-161, and 183-192 julian dates, respectively).....</p>	84
<p>Figure 3.2. Vapour Pressure Deficit (least-squared means \pm 95% confidence limits) of artificial nest sites in hard, soft, and natural-edged patches in the Nimpkish Valley, British Columbia (values include both edges and interiors). Different letters represent significant post-hoc tests at alpha = 0.05.....</p>	85
<p>Figure 3.3. (a) Density of marbled murrelet nest platforms per tree, and (b) density of trees with at least one nest platform, in plots at edges and interiors of patches with hard, soft, and natural edge-types, in the Nimpkish Valley and Desolation Sound, British Columbia. Values are least-squared means \pm 95% confidence limits, and different letters represent significant post-hoc tests at alpha = 0.05.</p>	86
<p>Figure 3.4. (a) Epiphyte thickness score and (b) epiphyte cover score of canopy trees in plots at patches with hard, soft, and natural edge-types, in the Nimpkish Valley and Desolation Sound, British Columbia (values include both edges and interiors). Values are least-squared means \pm 95% confidence limits, and different letters represent significant post-hoc tests at alpha = 0.05.</p>	87

LIST OF TABLES

Table 1.1. Significance levels of treatment effects for artificial nests disturbed by avian predators and squirrels around Desolation Sound and in the Nimpkish Valley, B.C.	33
Table 1.2. Significance levels of treatment effects for predator detections around Desolation Sound and the Nimpkish Valley, B.C.	37
Table 2.1. Description of landscape metric variables calculated from 1660 hectare (2.3 km radius) landscapes surrounding predator survey transects and artificial nest sites. Variables are classified according to their hypothesized effect type(s), including habitat loss ('Loss'), habitat fragmentation per se ('Fragmentation'), and matrix composition effects ('Matrix')	59
Table 2.2. The set of models used to rank alternative hypotheses of effects of landscape structure on corvid abundances. Models are divided into four groups representing different effect types, and are numbered for easy reference	60
Table 2.3. Ranking of linear regression models predicting the effects of landscape structure on the frequency of Steller's jay and common raven detections in the Nimpkish Valley, British Columbia, May-August, 2003-2005. Model number (#), number of estimated parameters (K), small sample Akaike's Information Criteria (AICc), difference between AICc of the model and that of the best model ($\Delta AICc$), and Akaike's weight (ω) are listed. Only the top set of models with a sum of weights of ≥ 0.95 were included. Models in bold are considered to have the most substantial support ($\Delta AICc \leq 2$)	61
Table 2.4. Mean values (\pm 95% confidence limits) and significance levels of fragmentation variables calculated from 1660 hectare (2.3 km radius) landscapes surrounding predator survey transects, in the Nimpkish Valley, British Columbia. Values of landscape variables were compared between landscapes where gray jays were detected and landscapes where gray jays were not detected	62
Table 2.5. Effects of patch and landscape variables on disturbance of artificial nests by avian predators (eggs) and squirrels (eggs and nestlings) in the Nimpkish Valley, B.C. Landscape variables are measured from 1660 hectare (2.3 km radius) landscapes surrounding each experimental nest site	66
Table 2.6. Effects of patch and landscape variables on disturbance of artificial nests by avian predators (eggs) and squirrels (eggs and nestlings) around Desolation Sound, B.C. Landscape variables are measured from 1660 hectare landscapes (2.3 km radius) surrounding each experimental nest site	66

Table 3.1. Significance of effects of microclimate variables in edge and interior plots in hard, soft, and natural-edged patches in the Nimpkish Valley, British Columbia.....	81
Table 3.2. Mean values (\pm 1 standard error) of microclimate variables between early (May 31 – June 10) and late (July 2 – July 11) sampling periods, and between edge and interior habitats in the Nimpkish Valley, B.C., 2007.....	82
Table 3.3. Significance of effects of habitat variables in edge and interior plots in hard, soft, and natural-edged patches in the Nimpkish Valley and around Desolation Sound, British Columbia.	83

THESIS SUMMARY

The loss and fragmentation of forest habitat is one of the strongest ways in which humans can impact natural ecosystems. As forests are harvested, habitat which provides food and breeding sites is removed. Forest fragmentation, defined as the "breaking apart" of continuous forest habitat into many smaller patches (Fahrig 1997), may impose additional impacts by reducing the quality of the remaining habitat fragments. This reduction in quality may result from the influence of the surrounding 'matrix' of converted habitat in which these habitat patches are embedded. For instance, the matrix may support larger populations of generalist nest predators which depredate the nests of birds in the forested patches (Andrén 1992). These predators can cause "edge effects" on nest predation, whereby predation rates at habitat edges are elevated relative to interiors (Andrén 1994, Paton 1994, Batáry and Báldi 2004). These effects may be particularly strong in the smaller patches created by forest fragmentation, which have a high proportion of edge per area of habitat. In addition to these patch-scale effects, elevated predation risk due to fragmentation can also occur at the landscape scale. For instance, increased corvid populations have been positively correlated with an increase in nest predation risk at the landscape scale (Andrén 1992, Luginbuhl et al. 2001), and edge effects can occur more often in fragmented landscapes relative to intact landscapes (Driscoll and Donovan 2004). As a consequence of these effects, habitat fragmentation may lead to population declines greater than those predicted from habitat loss alone (Andrén 1994).

Fragmentation may also reduce the quality of habitat patches because of abiotic edge effects. Edges often have higher temperature extremes, stronger wind speeds, and lower humidity levels relative to interior locations (Chen et al. 1995, Stewart and Mallik 2006). These microclimate gradients can lead to changes in the growth and survival of plant species at forest edges (Hylander et al. 2002, Hylander et al. 2005, Muir et al. 2006, Stewart and Mallik 2006). This can lead to a reduction in habitat availability for wildlife species that depend on plants that are sensitive to changes in microclimate. 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).

The ability of managers to make effective decisions regarding potential effects of habitat fragmentation depends on their ability to predict under what conditions negative fragmentation effects occur. This is hampered by the fact that fragmentation effects vary widely with both local and regional factors. An often cited example of this variation is that edge effects occur more commonly in forests of eastern North America than in western forests (Sisk and Battin 2002). In the east, the matrix is dominated by agricultural land which supports large populations of generalist predators who are able to elevate predation risk at habitat edges (Chalfoun et al. 2002). In contrast, nest predators in western forests are often more forest dependant, and therefore often decrease as forests are harvested (Tewksbury et al. 1998, De Santo and Willson 2001). However, the situation in western forests is likely more complex than it first appears. In contrast to the high-contrast permanently maintained agricultural edges in the east, western forests fragmented by silviculture consist of a dynamic mosaic of forest patches of different ages. Therefore, the contrast between habitat patches and the surrounding matrix is temporally dynamic in these landscapes, and will decrease with time as harvested forests undergo succession. This results in a continuum of edge-types from 'hard' edges

adjacent to recent clearcuts, to 'soft' edges adjacent to older, regenerating forests. This variability has the potential to influence the strength of both abiotic and biotic edge effects.

To summarize, although habitat fragmentation can strongly impact animal populations, the strength of these effects will depend on many factors at multiple spatial and temporal scales. It is therefore imperative that managers understand how fragmentation affects populations in the specific management context in which they are operating. This is especially true for threatened species for which there is little remaining habitat, and for which designation of high-quality habitat reserves is a priority. The marbled murrelet (*Brachyramphus marmoratus*) is exactly such a species. Marbled murrelets are seabirds (family Alcidae) who forage in near-shore marine habitats along the Pacific Coast from California to Alaska (McShane et al. 2004), and nest inland, predominantly on large, mossy branches in old-growth forests. Substantial harvesting of old-growth forest habitat has resulted in listing marbled murrelets as a protected species in both the United States south of Alaska and in Canada (CMMRT 2003, McShane et al. 2004). These listings were based in part on concerns that habitat loss will reduce the population size a given area can support (Burger 2001), but it is still uncertain how forest fragmentation per se will impact murrelet populations (Raphael et al. 2002). There is currently little consensus on how different edge-types affect the breeding success of the marbled murrelet, with inconsistent results among natural and artificial edges (Nelson and Hamer 1995, Manley and Nelson 1999, Bradley 2002). This issue is important 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 (Nelson and Hamer 1995, McShane et al. 2004, Zharikov et al. 2006). Also, while harvesting of old-growth habitat has already reduced the availability of potential murrelet habitat, microclimate edge effects may further reduce the availability of

nest sites in the remaining habitat. Developing a comprehensive understanding of potential effects of fragmentation on habitat quality will improve the ability of managers to design productive murrelet reserves, a process currently underway in coastal British Columbia.

The objective of this study was to understand how habitat fragmentation influences the quality of marbled murrelet nesting habitat. We addressed this question in a comprehensive manner, incorporating factors that are likely to influence both nest-site availability and reproductive success. First, we conducted an artificial nest experiment comparing an index of predation risk between edges and interiors at three different edge-types: 'hard' edges adjacent to recent clear-cuts, 'soft' edges next to regenerating stands, and natural edges next to large rivers or avalanche chutes (Chapter 1). We supplemented these data with surveys of potential predators in the same habitats to investigate the relationship between predator densities and predation risk. Secondly, we used a large-scale, multi-year dataset of predator surveys to assess how corvids respond to habitat fragmentation and matrix composition at the landscape scale (Chapter 2). We also examined whether fragmentation at the landscape scale helped to explain patterns of nest disturbance risk for our artificial nests. Finally, we examined abiotic edge effects, and how they may influence the availability of nesting sites for marbled murrelets (Chapter 3). This involved measuring microclimate variables and sampling indicators of potential nesting habitat between edges and interiors at the three edge-types.

Our patch level edge effects study indicated that edge effects on nest disturbance risk may vary by edge-type in western forests (Chapter 1). 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. In contrast, there was no significant difference in disturbance between edge and interior locations at natural

sites. This introduces a temporal component to variation in predation risk, suggesting that predation risk initially increases, but then decreases with time in these forests. Our survey data suggested that Steller's jays may be the source of this pattern, as their abundances were highest at hard edges. Young clearcuts may provide more foraging opportunities for these generalist predators compared to older, regenerating stands that have little understory and few complementary resources.

Both Steller's jays and common ravens increased with an increase in the number of old-growth patches in the landscape, a common index of habitat fragmentation (Chapter 2). This suggests that habitat fragmentation per se will lead to higher densities of these predators at the landscape scale. In addition, Steller's jays increased with decreasing amounts of old-growth in the landscape, suggesting that timber harvesting will benefit this species. Steller's jays declined with an increased proportion of the matrix in regenerating forest, suggesting that densities of this predator may decline as forests regenerate after initial harvesting. In contrast, gray jays appeared to be more forest dependent, and were more common in less fragmented landscapes, with more old-growth forest. Landscape-scale patterns of artificial nest disturbance risk were contrary to expectations, as disturbance risk increased with declining amounts of old-growth in the landscape at hard and natural-edged patches.

Our sampling of murrelet habitat indicated that habitat fragmentation has the potential to significantly reduce the availability of marbled murrelet nest sites. There were fewer trees with at least one potential platform ('platform trees') at edges relative to interiors, with the highest numbers of platform trees in the interiors of natural-edged patches. Similarly, the density of potential nesting platforms was highest in natural-edged patches. Mean temperatures were higher at edges relative to interiors early in the season, and vapour pressure deficit was lower in natural patches relative to soft-edged patches. These patterns suggest that microclimate edge effects caused reduced

growth and survival these of mosses at anthropogenic edges, resulting in a decreased availability of marbled murrelet nest sites.

This study addressed the effects of habitat fragmentation on marbled murrelet habitat quality using a comprehensive, multi-scaled approach. As such, our results have specific relevance to the design of reserves that sustain productive murrelet populations. The majority of our results suggest that designating larger reserves of murrelet habitat will positively influence habitat quality by maximizing nest-site availability and reproductive success. Therefore, we recommend the creation of large, circular reserves that will minimize the edge/area of murrelet habitat patches. This will minimize the amount of habitat subjected to elevated predation risk and reduced nest-site availability. In the short term, the local prevalence of hard edge will be reduced. In the long-term, the amount of suitable habitat in these patches will increase, as hard edges regenerate into less dangerous soft edges. Where possible, these reserves should contain suitable natural edges such as streams channels and avalanche chutes. This will allow access for murrelets to a large number of potential nest sites that are not subject to microclimate edge effects or elevated predation risk. Designation of reserves is an important component to marbled murrelet management, but managers must ultimately manage at the landscape scale over the long-term. This will require adaptation to continually changing conditions. At the landscape scale, managers should maintain habitat mosaics that keep densities of generalist predators such as Steller's jays and common ravens low. These landscapes should consist of fewer and larger patches of old-growth, surrounded by older stands of regenerating forest. Finally, harvesting in areas adjacent to reserves should proceed in stages, such that the amount of hard edge adjacent at any given time is minimized.

Our ability to make management recommendations informed by our results is constrained by uncertainty regarding the role of forest dependent species as murrelet

nest predators. For instance, patch level disturbance risk suggested that the addition of squirrels 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. Neither predator has been observed preying on marbled murrelet nests, but both are suspected predators. This issue must be resolved in order to move forward with well-informed murrelet habitat management, because management recommendations will differ significantly depending on the strength of their contribution to nest predation. In the meantime, we must utilize our existing knowledge regarding abiotic and biotic fragmentation effects on marbled murrelet habitat quality. These data suggest that maintaining large patches of old-growth in a matrix of regenerating forest will minimize patch-scale edge effects, provide a high availability of nest sites, and maintain low densities of generalist nest predators in the landscape.

CHAPTER 1

TEMPORAL DYNAMICS OF EDGE EFFECTS ON NEST PREDATION RISK ON THE MARBLED MURRELET

1.1 Introduction

Loss and fragmentation of forest habitat are major factors contributing to population declines of forest birds worldwide (Wilcove 1985, Robinson et al. 1995, Batáry and Báldi 2004). 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, Paton 1994, Batáry and Báldi 2004). 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 on edges due to less nests site cover (Ratti and Reese 1988). This can cause reduced reproductive success in small habitat fragments, which contain a higher proportion of edge area compared to large 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 adequately quantify the amount of productive habitat available across landscapes, and to properly assess the demographic consequences of different management strategies.

It is essential that managers understand the factors that influence variation in edge effects, as this phenomenon appears to vary widely with respect to both local and regional factors (Andrén 1994, 1995, Lahiti 2001, Batáry and Báldi 2004). The level of structural contrast between habitat patches and the surrounding matrix is a factor that may play a central role in determining the strength and direction of edge effects (Andrén 1995, Suarez et al. 1997, Marzluff and Restani 1999, Rodewald and Yahner 2001, Chalfoun et al. 2002). 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 clear-cut regeneration (Sisk and Battin 2002). In forests which are predominantly fragmented by forestry, such as forests of western North America, edge effects may therefore change with time as forests undergo succession. Thus, our understanding of fragmentation effects requires knowledge on how edge effects may change over time, and how the combination of edge effects at different edge-types impact populations 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 (McShane et al. 2004). Substantial harvesting of old-growth forest habitat has resulted in listing marbled murrelets as a protected species in both the United States south of Alaska and in Canada (CMMRT 2003, McShane et al. 2004). These listings were based in part on concerns that habitat loss will reduce the population size a given area can support (Burger 2001), but it is still uncertain how forest fragmentation per se will impact murrelet populations (Raphael et al. 2002). Despite clear management benefits associated with this knowledge, there is currently little consensus on how different edge-types affect the breeding success of the marbled

murrelet, with inconsistent results among natural and artificial edges (Nelson and Hamer 1995, Manley and Nelson 1999, Bradley 2002). This issue is important 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 (Nelson and Hamer 1995, McShane et al. 2004, Zharikov et al. 2006). Developing a more comprehensive understanding of variation in predation risk among different edge-types will improve the ability of managers to design productive murrelet reserves, a process currently underway in coastal British Columbia.

We used artificial nests with nest cameras to provide estimates of relative predation risk in edge and interior locations at three edge-types used by marbled murrelets. This experimental approach allowed us to maximize our 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 will not necessarily be equal across all habitats. Our combined approach provides a comprehensive picture of variation in predation risk, while allowing us to assess the efficacy of using predator surveys as a management tool to predict this risk.

1.2 Methods

1.2.1 Study area

This study was carried out in two regions of coastal south-western 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)(Figure 1.1), from June to August in 2005 and 2004, respectively. Both regions contain large breeding populations of marbled murrelets (Bradley et al. 2004, Harper and Schroeder 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*) amabilis 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*).

1.2.2 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.). We selected 34 sites in Nimpkish and 18 sites around Desolation Sound (Figure 1.1), that were adjacent to one of three types of forest gaps, and that had sufficient amounts of old growth forest to establish interior treatments. 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 clear-cuts (5-11 years old), “Soft-edged” sites next to regenerating stands (17-39 years old), and “Natural-edged” sites next to large rivers or avalanche chutes (Figure 1.2). 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 least 150 m from any other forest openings. Mean distance (± 1 SE) from experimental edge was 9.5 ± 1.1 m for edge nests, and 232.5 ± 3.2 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 ± 1.85 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. ≥ 15 m above the ground and ≥ 18 cm in diameter)(Burger and Bahn 2004). Nest platforms were 25.8 ± 0.5 m above the ground, with diameters of 27.9 ± 1.7 cm, and had $55.4 \pm 1.5\%$ vertical cover. Nest trees were 36.0 ± 0.6 m high, had diameters at breast height of 101.3 ± 4.6 cm, and had 13.7 ± 0.9 suitable murrelet nests platforms per tree.

1.2.3 Artificial nest experiment

Our artificial nest design was modelled after similar studies conducted in Washington and Oregon (Marzluff et al. 2000, Luginbuhl et al. 2001, Raphael et al. 2002, Marzluff and Neatherlin 2006). 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. To minimize the presence of any human scent, all artificial nest contents were stored in bark mulch for at least 12 hours 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, California) and infrared sensors that detected movement of objects differing in temperature from their surroundings (Pixcontroller® Inc., Export, Pennsylvania). It took approximately 4 seconds to power up and initialize the cameras following motion detection, thus many nest visitors left prior to picture taking. Cameras were painted "forest green" to limit their conspicuousness, and mounted on the tree trunks approximately 1.5 meters directly above all 136 nests in Nimpkish. Predator photos refined our identification of marks left on eggs and in interpreting probable predators based on nestling remains. This calibration assisted identification, where cameras were not used (Desolation Sound), and in cases in Nimpkish where nests were disturbed, but the camera did not capture the predator.

We have designed our artificial nest experiment to minimize bias associated with this method. While we acknowledge that absolute predation rates may differ between

real and artificial nests (Major and Kendal 1996, Thompson III 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 in actual predation risk on real marbled murrelet nests. This requires that our artificial nests sample the same suite of predators that 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.), whose role as nest predators is suspected (Luginbuhl et al. 2001, Bradley and Marzluff 2003). 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). We were unable to distinguish between avian species (i.e. Steller's jays versus gray jays) because cameras only captured a fraction of predators that disturbed nests, and we were unable to distinguish predator marks on eggs or nestling remains to the species level. We therefore separated our analyses between avian and mammalian predator disturbances. Mice (*Peromyscus* spp.) were excluded because we assumed that murrelet adults and nestlings would be better able to defend against this rodent compared to larger-bodied squirrels. This provided a conservative measure of disturbance risk caused by mammals, whose role as murrelet nest predators has not been confirmed (Nelson 1997). However, we acknowledge the possibility of mice as predators of nestlings, as they have been observed forcing pigeons off nest branches (Bradley and Marzluff 2003).

Separation of nest disturbances by predator type enhanced our ability to provide realistic estimates of predation risk on marbled murrelet nests, and allowed us to assess the relative contributions of these predators to the observed patterns of this risk.

Because of low nesting densities and the high cost of finding real murrelet nests, it is very difficult to obtain an adequate sample of real nests to investigate variation on 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.

1.2.4 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 (Manley 1999, Tranquilla et al. 2003, Bradley et al. 2004, Zharikov et al. 2006). Because most nests around Desolation Sound could not be accessed from the ground, the precision of real nest locations (+/- 100 meters) was not sufficient for accurate classification of many real nests as “edge” or “interior”, which requires a precision +/- 50 meters. Therefore, we were only able to compare the effect of sites’ edge-type on nest fates between real and artificial nests.

We used the breeding success criteria of Bradley et al. (2004) and Zharikov et al. (2006), who classified nests as either active (successful) or failed during the “mid-chick rearing period”. This was determined with radio telemetry data, because many nests were inaccessible from the ground, and direct determination of reproductive success was not possible. From this sample of known “success”, we selected real nests that were within 250 meters 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 meters, 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 78 real nests: 12, 6, and 60 nests at hard, soft and natural edges, respectively. These were compared to 40 artificial nests: 16, 7, and 17 nests at

hard, soft and natural edges, respectively. This sample is a subset of the larger sample of nests used to assess predation risk in Desolation Sound, because we excluded any nests that had more than one edge-type within a 250 meter radius. Also note that 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 during the “mid-chick rearing period” were a result of predation. Some of these failures may have been due to other causes such as nest abandonment, but nest failure is nonetheless a reasonable proxy of predation risk, as 70% of known nest failures from California to Alaska were due to predation (Manley and Nelson 1999).

1.2.5 Predator surveys

We established two parallel transects of 4 point-count stations with 50 m radii at 18 of our experimental nest sites in Nimpkish, and at 6 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 meters into the forest interior, at least 150m from any other edge. Station centres were 150m apart, so that distances between 2 adjacent detection radii were 50 meters. Sampling periods at each station were 10 minutes 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 meter 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).

1.2.6 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 (4 cases).

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-type, or nest-type (egg/nestling) predicted nest disturbance of simulated nests using three different models: disturbances by all predators combined (avian and squirrels), avian predators only, and squirrels 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 ($\chi^2_1 = 23.70$, $p < 0.0001$), 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 disturbances to run the full model for each nest-type, so we kept this dataset 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 on the same site.

Independent contrasts were conducted for the edge-proximity by edge-type interaction of avian disturbances (the only significant interaction in all models tested). Similar Generalized Linear Models were used to compare the fates of experimental and real nests (binomial probability distributions and logit link functions), using the Genmod procedure SAS® version 9.1 (SAS, 2003). 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).

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. For all models, we present score statistics for type 3 Generalized Estimating Equations, with non-significant interaction terms removed from the model at $\alpha = 0.10$. We used a contingency chi-square 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.

1.3 Results

1.3.1 Artificial nest experiment

Fifty-nine of 136 nests (43%), and 23 of 66 nests (35%) were disturbed in Nimpkish and around Desolation Sound, respectively. We were able to classify most nest visits as either avian or mammalian (85% and 83% in Nimpkish and at Desolation Sound, respectively). 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*), a common raven (Figure 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, 68% of identifiable predator visits were avian species, 24% were red squirrels, and 8% of nests were targeted by both. At Desolation Sound, 68% of identifiable disturbances were caused by avian predators and the remaining (32%) by squirrels.

Disturbances were higher at edges relative to interiors for avian predators and squirrels combined ($\chi^2_1 = 5.14$, $P = 0.023$) (Table 1.1), suggesting detrimental edge effects at all three edge-types. The estimate of dispersion after fitting this model was 1.003, indicating a good fit between the predicted and observed variance of the model, and suggesting no significant spatial autocorrelation within sites.

Disturbance of eggs by avian predators between edge and interior locations was dependent upon edge-type (edge-proximity x edge-type interaction: $\chi^2_2 = 9.64$, $P = 0.008$)(Figures 1.4 and 1.5), suggesting that edge effects varied by edge-type. Independent contrasts showed that detrimental edge effects (higher disturbance at edges relative to interiors) at hard sites differed significantly from the opposite trend found at soft sites ($\chi^2_1 = 8.34$, $P = 0.004$), and the lack of edge effects at natural-edged sites ($\chi^2_1 = 4.51$, $p = 0.034$)(Figure 1.5). Soft and natural-edged sites did not differ from each other in avian egg disturbances ($\chi^2_1 = 1.89$, $P = 0.169$).

Squirrels disturbed eggs more often than nestlings ($\chi^2_1 = 4.60$, $P = 0.032$)(Table 1.1), and disturbed significantly more nests at edges than interiors at all three edge-types ($\chi^2_1 = 6.30$, $P = 0.012$)(Figures 1.6).

1.3.2 Comparison with patterns at real nests

There was no significant difference in its fates between real and experimental nests ($\chi^2_1 = 0.90$, $P = 0.343$), or between sites of different edge-types ($\chi^2_1 = 0.42$, $P = 0.811$). More importantly with respect to validation of edge-treatment effects from experimental nests, the effect of edge-type on nest fate was independent of study type ($\chi^2_2 = 1.08$, $P = 0.583$), suggesting that treatment patterns were not significantly different between experimental and real nests.

1.3.3 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 1.2). This effect differed among edge-types however, occurring only at hard-edged sites, and not at soft-edged sites (edge-proximity x edge-type interaction: $\chi^2_1 = 4.31$, $P = 0.038$)(Figure 1.7). There were

no significant treatment effects on Steller's jay observations in the Nimpkish Valley. Likewise, there were no significant treatment effects on gray jay observations in the Nimpkish Valley (Table 1.2).

There was a marginally significant difference between Douglas squirrels observed at edges relative to interiors around Desolation Sound ($\chi^2_1 = 3.55$, $P = 0.060$) (Table 1.2). In the Nimpkish Valley, the effect of edge-proximity on red squirrel detections was dependent on the edge-type involved (edge-proximity x edge-type interaction: $\chi^2_1 = 5.50$, $P = 0.064$). 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 ($\chi^2_2 = 8.52$, $P = 0.014$) (Figure 1.8). 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 (Figure 8a). In contrast, gray jays were observed infrequently, and were never observed in gaps of any kind (Figure 8b).

1.4 Discussion

Understanding variation in edge effects at different edge-types is an essential component of effective management of wildlife populations in landscapes fragmented by industrial forestry. Using the marbled murrelet as a model species, we have documented variation in the strength and direction of edge effects on nest disturbance risk at different ecologically relevant edge-types. Our carefully designed artificial nest experiment was therefore able to provide information on spatial variation in predation

risk in old-growth forests of coastal British Columbia that has hitherto been difficult to obtain for nesting marbled murrelets.

1.4.1 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 novel result introduces a temporal component to variation in predation risk in forests fragmented by silviculture. The predation risk at individual clear-cut 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 in forests fragmented by silviculture? Nest predation rates in each of these habitats will be directly related to the amount 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 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. Indeed, 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 not 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 (Andr n 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).

1.4.2 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. Around 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. Detection rates of Steller's jays were also higher at edges relative to interiors of hard-edged sites in

Nimpkish (with little differences in edge/interior locations at soft or natural-edged sites), but high variability in the data resulted in no statistically significant trends. Because of these patterns, and the fact that Steller's jays consistently used clear-cut gaps, we suspect that Steller's jays were the main drivers of nest disturbance risk in this system, as we observed them to consistently use clear-cut gaps. In contrast, gray jays never left the forest edge to enter clear-cuts 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 (Andr n 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 berries to make up a substantial portion of Steller's jay's diet (Masselink 2001, Vigallon and Marzluff 2005).

1.4.3 Squirrels as potential nest predators

Because Steller's jays and other corvids are known nest predators of marbled murrelets (Nelson and Hamer 1995, McShane et al. 2004, Peery et al. 2004b), we assume that our avian disturbance data is the most representative index of relative predation risk. However, if squirrels 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 and avian disturbances resulted in elevated predation risk at edges of all three edge-types.

Thus, the addition of squirrels to the predator community could strengthen detrimental edge effects at hard sites, and cause detrimental edge effects at soft and natural sites which wouldn't 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. 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 results that squirrels 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). Squirrel 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 squirrels 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 an unattended egg off the nest platform (Bloxtton and Raphael 2006). Given that squirrels prey on small vertebrates (Sullivan 1991, O'Donoghue 1994), it is plausible that they could depredate a young murrelet nestling. In laboratory experiments, northern flying squirrels consistently attempted to prey on eggs and nestlings (Bradley and Marzluff 2003). Unlike corvid predators, however, they probably are unable to flush an incubating parent off the nest. Consequently, squirrels

would only have an opportunity to depredate murrelet eggs when they are left unattended. Although squirrels have the potential to depredate murrelet nestlings and influence patterns of nest predation risk, they likely make up a lesser component of predation risk than avian predators, which disturbed the majority of the nests in this study.

1.4.4 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. Patterns of nest fates between sites of different edge-types were not significantly different from those observed at real nests at sites of comparable edge-types and elevation, which provides some validation for this approach. One important distinction between our artificial eggs and real murrelet nests is that our nests did not contain an incubating adult. This may cause our absolute nest disturbance rates to be elevated relative to real murrelet nests, but it should not influence our interpretations regarding *relative* predation risk between habitat treatments. This point is supported by the fact that we were able to distinguish between predator types relevant to marbled murrelet nest predation risk. Moreover, video footage has documented that both murrelet adults and nestlings are able to defend against Steller's jays, but that Steller's jays can easily depredate unattended eggs (Hébert and Golightly 2006). The same study documented that egg neglect by murrelets can be common early in the incubation period (9/27 adults missed 1-4 days of incubation)(Hébert and Golightly 2006). Thus, it appears that murrelets will be most susceptible to predation by jays during periods of egg neglect, or when nestlings are young. 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.

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. At the landscape scale around Desolation Sound, active nests were closer to hard-edge clearcuts, and farther from 'fuzzy-edge' (soft) clearcuts, than were failed nests (Zharikov et al. 2006). However, these results are at the scale of kilometres, and therefore are not directly comparable to our findings, which demonstrated edge effects on predation risk within 250 meters.

Two previous analyses of the data collected at Desolation Sound suggest that nests near to natural edges had higher nesting success relative to interior sites (Bradley 2002, Zharikov et al. 2006), while our data show no difference in predation risk between edge and interiors of natural sites. It is possible that factors such as breeder experience may be a more important determinant of reproductive success than predation risk at natural edges. Birds in this population that initiated breeding earlier had higher reproductive success, possibly because these birds were more experienced (Bradley 2002). If experienced breeders preferentially nest near natural edges because of a high availability of accessible nest sites (Manley 1999, Rodway and Regehr 2002), these sites may be associated with higher reproductive success, irrespective of the level of predation risk found there.

Future studies need to combine artificial nest experiments with observations of parental behaviour and nesting preferences of real nests at different edge-types. This will help us to better understand how different factors influence the relationship between predation risk and reproductive success. This will allow us to determine under which conditions our estimates of predation risk need to be refined to better predict habitat-specific variation in reproductive success.

1.5 Management implications

Our results provide evidence that marbled murrelet nest predators such as Steller's jays can cause elevated predation risk at edges and potentially negative consequences for nesting success depending on edge type. Moreover, the magnitude of such effects may change over time due to successional processes subsequent to harvesting. This paints a complex picture of landscape-scale fragmentation effects. We must consider not just whether or not edges exist in potential nesting habitat, but also the type of edges. Also, it would be inappropriate to evaluate the effect of a disturbance on marbled murrelet demographics at a snapshot in time immediately after the disturbance. Instead, managers must plan for the long-term, because the effects of harvesting will change over time. Evaluating the influence of such effects on the growth rate of murrelet populations will require evaluation of the combined impacts of different edge-types across the entire landscape over time. Habitat managers and forestry companies will need to incorporate timber supply modelling with population modelling to accomplish this goal.

This study has clear implications for the design of productive marbled murrelet reserves. This study predicts that new, hard edges will have the strongest negative impact on murrelet demography. This finding supports recommendations made by the Canadian Marbled Murrelet Recovery Team (CMMRT 2003), who suggest that hard edges be treated as less suitable habitat, whereas natural edges should be considered to be equal in suitability relative to forest interiors. 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

landscapes that have been highly fragmented in the past, larger patches of habitat may not be available. Managers may wish to create reserves that will reclaim previously lost nesting habitat by allowing recruitment of second growth forest into old-growth murrelet habitat. In this context, large reserves containing mostly regenerating forest could be established around smaller "cores" of existing old-growth habitat. This will maintain current soft edges and minimize predation risk around existing old-growth patches. Also, as the second-growth trees mature, this will result in larger old-growth patches as the buffers begin to resemble the core. Harvesting in areas adjacent to reserves 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. Using these guidelines to establish reserves where murrelets are known to nest will help to sustain healthy populations of murrelets. However, it is important to note that reserves alone are not sufficient to manage populations over the long-term. Managers must be able to adapt harvesting plans and reserve designations to changing landscape conditions. 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.

1.6 Tables and Figures

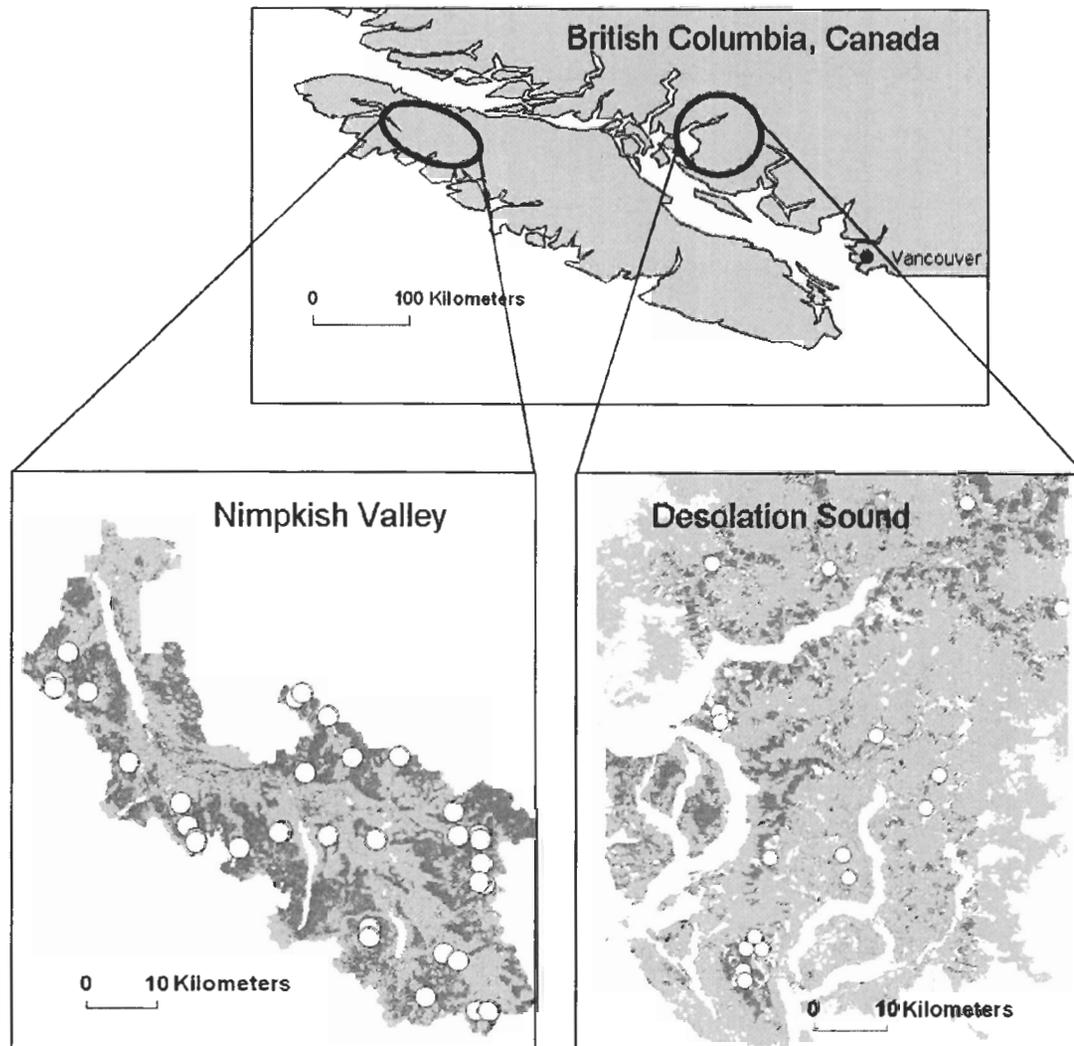


Figure 1.1. Location of the two study regions, Nimpkish Valley, and around Desolation Sound, Southwest British Columbia, Canada. Individual study sites are indicated by white circles. Dark shading indicates old-growth forest.

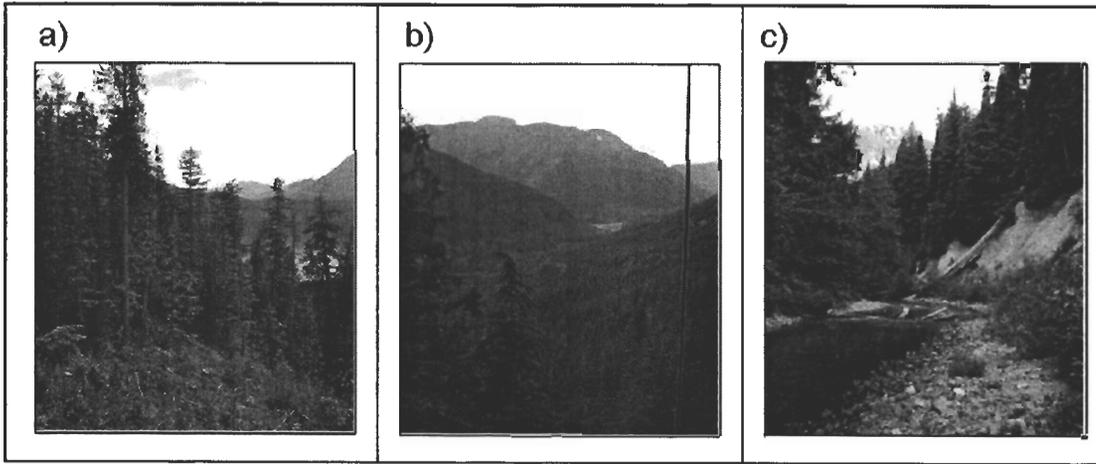


Figure 1.2. Examples of three different edge-types adjacent to old-growth forest patches in southwestern British Columbia, including a) hard, b) soft, and c) natural edges.



Figure 1.3. Common raven (*Corvus corax*) disturbing an artificial egg, captured by a motion-sensitive digital camera in the Nimpkish Valley, B.C.

Table 1.1. Significance levels of treatment effects for artificial nests disturbed by avian predators and squirrels around Desolation Sound and in the Nimpkish Valley, B.C.

Effect	df	X²	P
<i>Avian & Squirrels</i>			
Region	1	0.03	.862
Edge proximity	1	5.14	.023
Nest-type	1	23.70	<.0001
Edge-type	2	5.16	.076
<i>Avian predators (Eggs)</i>			
Region	1	2.87	.090
Edge proximity	1	0.09	.766
Edge-type	2	9.04	.011
Edge proximity x Edge-type	2	9.64	.008
<i>Squirrels (all Nest-types)</i>			
Region	1	0.76	.382
Edge proximity	1	6.30	.012
Nest-type	1	4.60	.032
Edge-type	2	2.98	.225

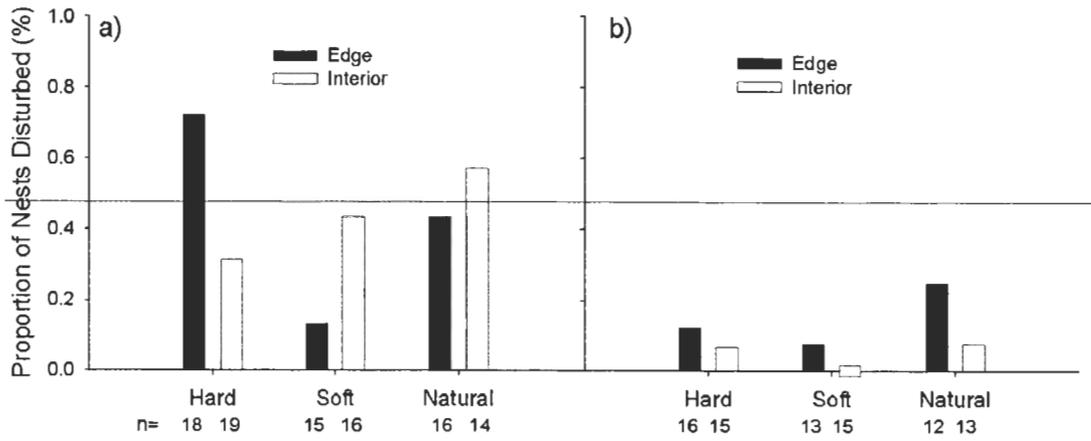


Figure 1.4. Proportion of nests disturbed by avian predators in edge and interior habitats at hard, soft and natural-edged sites for artificial eggs (a), and artificial nestlings (b). Data is pooled among Nimpkish Valley, and Desolation Sound, B.C.

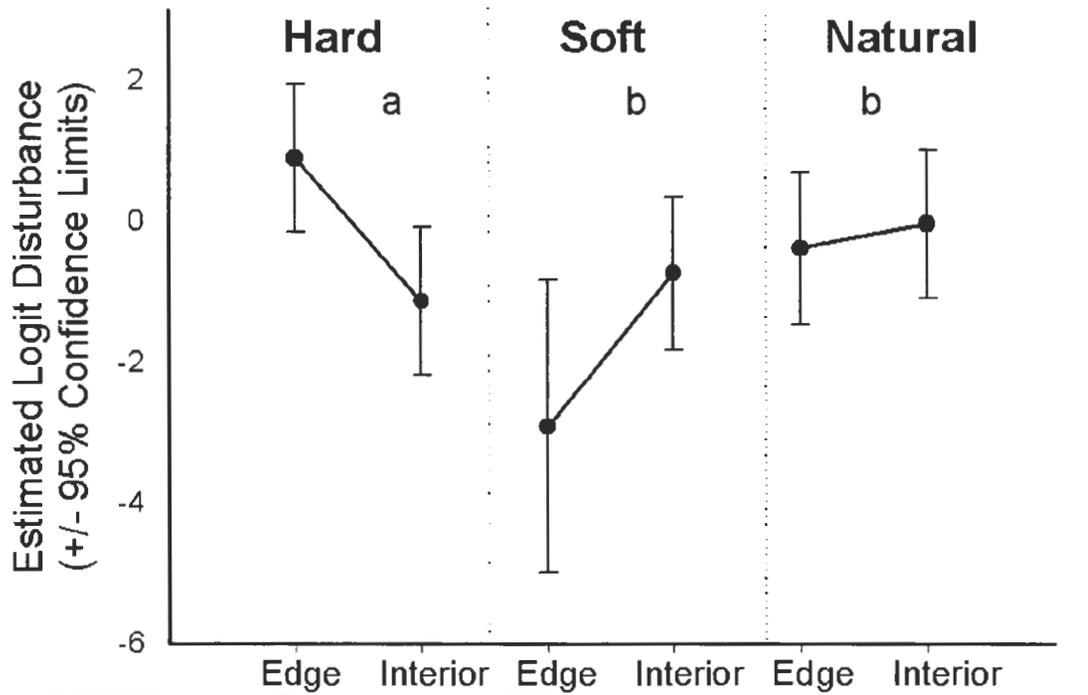


Figure 1.5. Estimated logit egg disturbance by avian predators in edge and interior habitats at hard, soft and natural-edged sites. Lower-case letters indicate significance of independent contrasts of the location by edge-type interaction.

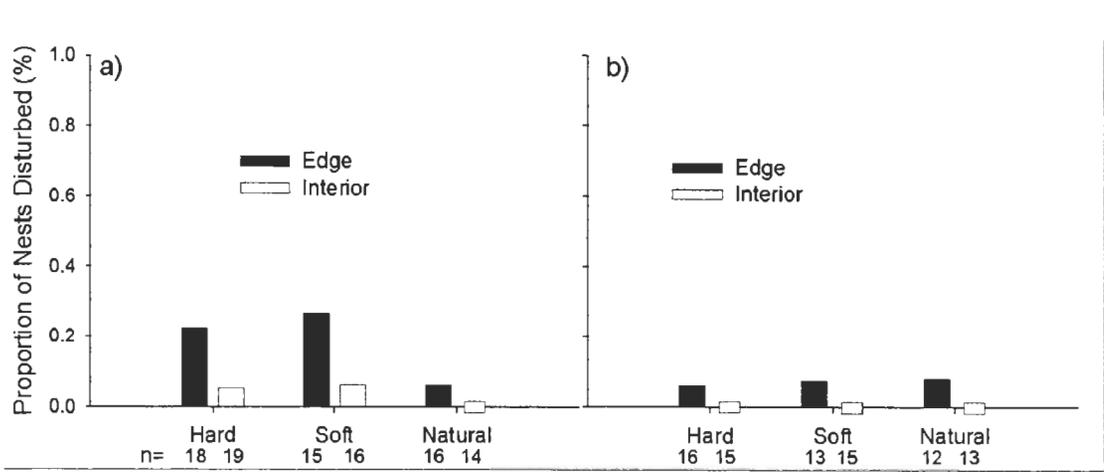


Figure 1.6. Proportion of nests disturbed by squirrel predators (*Tamiasciurus* spp.) in edge and interior habitats at hard, soft and natural-edged sites for artificial eggs (a), and artificial nestlings (b). Data is pooled among Nimpkish Valley, and Desolation Sound, B.C..

Table 1.2. Significance levels of treatment effects for predator detections around Desolation Sound and the Nimpkish Valley, B.C.

Effect	df	X²	P
<i>Steller's jays</i>			
<i>Desolation Sound</i>			
Edge proximity	1	3.87	0.049
Edge-type	1	0.79	0.372
Edge proximity x Edge-type	1	4.31	0.038
<i>Nimpkish Valley</i>			
Edge proximity	1	0.47	0.491
Edge-type	2	2.39	0.303
Edge proximity x Edge-type	2	0.97	0.616
<i>Gray jays¹</i>			
<i>Nimpkish Valley</i>			
Edge proximity	1	0.10	0.747
Edge-type	2	3.22	0.200
Edge proximity x Edge-type	2	0.40	0.820
<i>Squirrels</i>			
<i>Desolation Sound (T. douglasii)</i>			
Edge proximity	1	3.55	0.060
Edge-type	1	0.13	0.715
Edge proximity x Edge-type	1	2.20	0.138
<i>Nimpkish Valley (T. hudsonicus)</i>			
Edge proximity	1	0.66	0.417
Edge-type	2	1.36	0.508
Edge proximity x Edge-type	2	5.50	0.064

¹ There were insufficient observations of gray jays to conduct this analysis in Desolation Sound

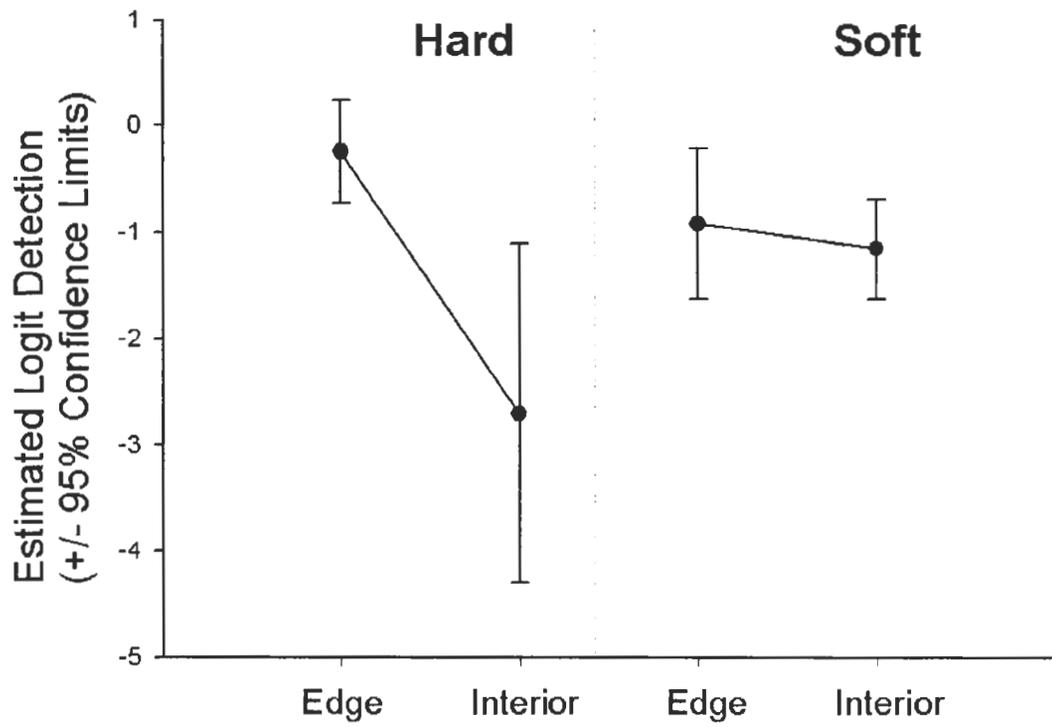


Figure 1.7. Estimated logit detection of Steller's jays at edges and interiors of hard and soft-edged sites around Desolation Sound, British Columbia.

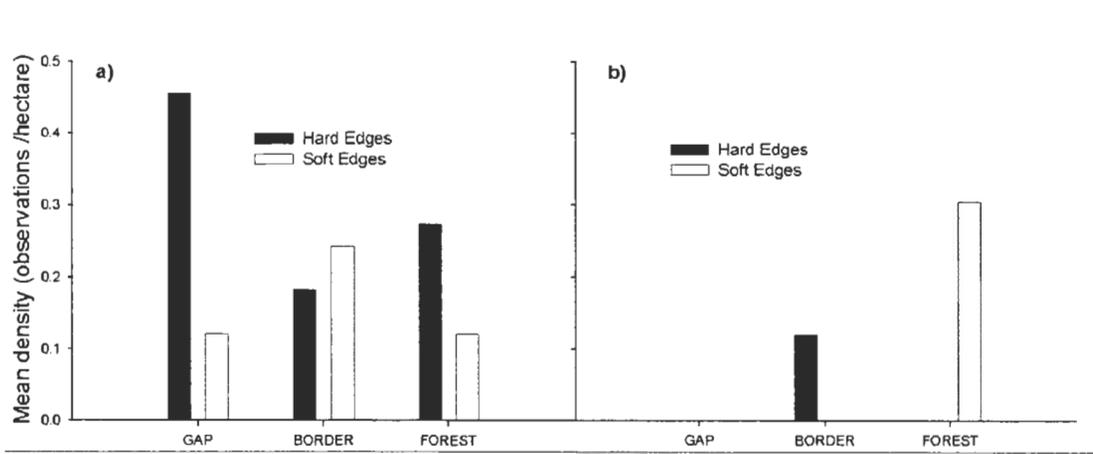


Figure 1.8. Distribution of (a) Steller's jays and (b) gray jay densities in gap, border, and forest margin habitats pooled among Desolation Sound, B.C., and the Nimpkish Valley, B.C.

CHAPTER 2

EFFECTS OF FOREST FRAGMENTATION ON NEST PREDATOR POPULATIONS: LANDSCAPE AND PATCH-SCALE VARIATION IN PREDATION RISK ON THE MARBLED MURRELET

2.1 Introduction

The loss and fragmentation of forests has the potential to strongly influence populations of forest birds. As forests are harvested, habitat is typically fragmented into many patches, resulting in a reduction in patch sizes and an increase in edge habitat (Fahrig 1997, Raphael et al. 2002). In addition, fragmented landscapes may support high densities of generalist nest predators such as corvids (i.e. crows, ravens, and jays) because the converted habitat provides access to additional resources (Andrén 1992). Increased corvid populations have been positively correlated with an increase in nest predation risk at the landscape scale (Andrén 1992, Luginbuhl et al. 2001), in small patches (Wilcove 1985) and at edges relative to interiors ("edge effects") (Andrén 1994, Paton 1994, Batáry and Báldi 2004). Therefore, rates of nest failure may increase as forest cover declines, causing some populations in highly fragmented landscapes to be unable to sustain themselves (Donovan et al. 1995, Robinson et al. 1995, Lloyd et al. 2005).

However, effects of fragmentation have shown to be conditional upon a complex set of factors at multiple scales (Andrén 1994, Marzluff and Restani 1999, Lahiti 2001, Rodewald 2002, Driscoll and Donovan 2004, Ries et al. 2004). Much of this complexity results from variation in the composition of the local predator community. For instance,

while generalist corvid predators may benefit from habitat fragmentation, forest-dependent predators (such as squirrels or forest birds) may actually decrease as forests are harvested (Tewksbury et al. 1998, De Santo and Willson 2001). In landscapes where forest-dependent predators dominate, predation risk may therefore decrease with increased habitat harvesting. Moreover, these predators may respond to fragmentation differently at patch and landscape scales, producing unexpected trends in landscapes where both generalist and intrinsic predators are present (Hannon and Cotterill 1998, Tewksbury et al. 2006). Finally, the composition of the habitat matrix (the modified habitat in which patches are embedded) may have a significant influence on how different predator species responded to fragmentation (Rodewald and Yahner 2001, Rodewald 2003). For example, generalist nest predators are often more abundant in landscapes fragmented by agriculture compared to those fragmented by silviculture (Chalfoun et al. 2002).

Understanding the combined effects of these different processes is essential in order to effectively manage habitat to sustain populations of forest breeding birds. While many studies have investigated the relationship between forest fragmentation and nest predation risk, few have studied these effects simultaneously at different scales (Driscoll and Donovan 2004, Tewksbury et al. 2006). Here, we investigate the potential influence of habitat fragmentation on predation risk on the threatened marbled murrelet (*Brachyramphus marmoratus*), using surveys to assess the landscape-level responses of potential nest predators, and artificial nests to assess patch-level variation in artificial nest disturbance risk.

The marbled murrelet is a threatened seabird which nests predominately on the mossy limbs of old-growth trees (McShane et al. 2004), and is therefore sensitive to the loss of old-growth forest habitat (Burger 2001, Burger et al. 2004). 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. 2004b). Other factors such as food availability may also influence reproduction (Peery et al. 2004b, Becker et al. 2007). The aim of this research was to assess how habitat fragmentation influences potential marbled murrelet predators, and how this affects predation risk at both patch and landscape scales. This information can be used by habitat managers and to design reserves and plan forest harvesting regimes that provide the sufficient amounts of quality habitat to sustain productive populations of marbled murrelets.

2.2 Methods

2.2.1 Study area

This study was conducted 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), in south-western British Columbia, Canada. Both regions have known breeding populations of marbled murrelets (Bradley et al. 2004, Harper and Schroeder 2004). Meteorological and ecological descriptions of these two regions are described in Chapter 1.

2.2.2 Landscape-scale predator surveys

Landscape-scale surveys of corvid species were conducted along 17 road-transects in Nimpkish in May and June, 2003-2005. Survey data of corvid species were provided by Canadian Forest Products Inc., and collected by Manning, Cooper and Associates, a resource management consulting firm. Surveys were conducted by

experienced field biologists, including: Paul Levesque (R.P.Bio.), Michael Shepard (R.P.Bio.), Suzanne Beauchesne (R.P.Bio.), and Paul Chytky (B.A.). Road-transects were selected from maps in ArcView 3.2 to represent the variation in forest structural stages and forest types present in the study area. Surveys were restricted to mainline roads to ensure accessibility over the three years of data collection. While surveying from roads may bias detection against forest interior species, this method is well suited for detection of generalist corvid species such as Steller's jays (*Cyanocitta stelleri*) and common ravens (*Corvus corax*). Each transect consisted of 10 point-count stations, each of which were surveyed three times per year, and conducted from sunrise until four hours post-sunrise (Ralph et al. 1995). Two transects were surveyed during each morning survey period (sunrise - four hours post sunrise), and the order in which they were surveyed was alternated systematically to minimize any detection bias associated with time of day. The sequence of point-count stations within transects was also alternated between each visit. Surveyors recorded all birds seen or heard for five minutes, and documented observation type (aural or visual), distance (>75m or <75m), as well as weather conditions at time of survey.

2.2.3 Artificial nest study

We established simulated marbled murrelet eggs and nestlings in suitable nest platforms at 34 sites in Nimpkish and at 18 sites around Desolation Sound. A full description of artificial nest construction, set-up, and justification is provided in Chapter 1. Briefly, at each site, one of each nest type was set up within 50 meters of the forest edge ('edge' nests)(Paton 1994), and in the patch interior at least 150 meters from any other forest opening ('interior' nests). Mean distance (± 1 SE) from experimental edge was 9.5 ± 1.1 m and 232.5 ± 2.2 m, for edge and interior nests, respectively. Each site

was selected for one of three different edge-types: “hard” edges were located adjacent to recent clear-cuts (5-11 years old), “soft” edges next to regenerating stands (17-39 years old), and “natural” edges next to large rivers or avalanche chutes. At all nests in Nimpkish, we established weatherproof automatic nest cameras to identify predators disturbing simulated nests. We also compared pictures and nest remains to determine predator identities where cameras were not used (Desolation Sound) or where predators were missed (Chapter 1). This allowed us to focus on predator types that are relevant to marbled murrelets when estimating of spatial variation in relative predation risk. However, cameras only captured a fraction of the predators that disturbed nests, and we were unable to identify predator marks or nestling remains to the species level. Therefore, we separated our analysis between the broader categories of avian and mammalian predator disturbances.

2.2.4 Quantification of landscape structure

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 25m² in ArcView 3.3 (ESRI Inc., Redlands, CA, USA). Each cell was assigned one of five distinct cover types: 1) young clearcuts (0-20 years), 2) regenerating forest (21-40 years old), 3) immature forest (41-140 years old), 4) old-growth forest (>141 years), and 5) water bodies such as large rivers, lakes, and ocean. Although old-growth forest is typically defined as > 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, Waterhouse et al. 2002). In

addition, our 'old-growth' cover type contained very little forest younger than 250 years (i.e. 96% was >250 years and 4% was 141-250 years in Nimpkish). In Nimpkish only, the 'young clearcuts' cover type included small amounts of young forest that were created by natural disturbances. Landscapes around Desolation Sound had the additional cover types of alpine areas (above the tree line), and 'brush and burn', a cover type resulting from industrial harvesting practices. We did not include variables such as tree species composition, small streams, or roads in our digital maps, as we did not believe these variables characterize fragmentation at the landscape scale as perceived by nest predators or breeding murrelets. We decided a priori to focus our analyses on young clearcuts, regenerating forest, and old-growth forest, as these structural stages appear to be the most relevant in predicting nest-site selection, artificial nest disturbance risk, and putative reproductive success of marbled murrelets (Zharikov et al. *in press*, Chapter 1). The relative proportions of these different cover types are determined by past and present forestry harvesting practices and therefore are relevant to long-term habitat management for marbled murrelets in coastal British Columbia.

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. *in press*), and is within the range of other landscape-scale fragmentation studies (Donovan et al. 1997, Lloyd et al. 2005). We decided a priori on a set of 10 landscape metrics that were most relevant to our questions in this study (see Table 2.1 for descriptions). We calculated all landscape metrics in the program FRAGSTATS (McGarigal et al. 2002). The percentage of core area in the landscape (old-growth area corrected for edge effects) was initially included, but was removed because it was very

highly correlated with percent landscape in old-growth ($R^2 = 0.99$, $P < 0.0001$), and therefore redundant.

2.2.5 Data analysis

2.2.5.1 Landscape-scale predator surveys

We calculated mean number of detections in each of the 17 transects for Steller's jays, common ravens, and gray jays, for each of the three years. We used least-square linear regression models to test for the effects of landscape structure on abundances of Steller's jays and common ravens (SAS 2003). There were insufficient gray jay detections (only detected in 5/17 transects) to run multivariate linear regression models. Therefore, we compared fragmentation variables in transects where gray jays were detected to transects where they were absent, using single factor ANOVAs (proc GLM, SAS 2003).

We tested for year effects by running models of %Old-growth, year of survey, and their interaction, for both Steller's jays and common ravens. Year had no significant effects on the abundance of Steller's jays ($F_2 = 0.38$, $P = 0.687$), and a marginally significant effect for ravens ($F_2 = 2.88$, $P = 0.066$). However, any effect of year was consistent across variation in %Old-growth for both Steller's jays ($F_2 = 0.12$, $P = 0.884$) and common ravens ($F_2 = 1.82$, $P = 0.174$). Therefore, we pooled the data by year in all subsequent analyses to minimize concerns regarding temporal autocorrelation.

We developed a set of 18 a priori models representing alternative hypotheses of potential effects of landscape structure on Steller's jays or common raven abundances, and ranked them using an information-theoretic approach. We grouped models into four distinct groups representing different general hypotheses regarding the effects of

landscape structure on corvid abundances: habitat loss alone, habitat fragmentation per se, habitat loss assuming matrix effects, and all effects combined (habitat loss and fragmentation, assuming matrix effects) (Table 2.2). We calculated Akaike's Information Criterion for small sample sizes (AICc), and the difference between AICc for the *ith* model and the model with the lowest AICc ($\Delta AICc$). We considered models with $\Delta AICc \leq 2$ to have the most substantial support (Burnham and Anderson 2002). We also tested for the effects of %Old-growth and Patch Density on all corvid predators combined (sum of mean detections of Steller's jays, common ravens, and gray jays for each transect), using univariate linear regression models. Finally, we tested for correlations between important independent variables from our top models with other closely related independent variables.

2.2.5.2 Artificial nest experiment

We tested for the influence of patch and landscape-level factors on nest disturbance (yes/no) using generalized linear models with binomial error distributions and logit link-functions in SAS[®] version 9.1 (SAS 2003). We specified a nested function to represent the fact that each site was nested within an edge-type. Models included combinations of the categorical patch-scale variables edge proximity (edge vs. interior), edge-type (hard, soft, and natural), and the landscape-scale covariates %Old-growth, Patch diversity, Patch density, Edge density, Patch size, and Contrast-weighted edge, (Table 2.1). Landscape variables assuming matrix effects were not included, because inclusion of edge-type tested for these effects at the patch scale.

Our initial model contained the entire dataset pooled by region to test for variation in patterns of nest disturbance between Nimpkish and Desolation Sound. Because Nimpkish had significantly more %Old-growth ($62.1 \pm 3.8\%$) than Desolation

Sound (37.3 ± 2.8 ; $F_1 = 27.7$, $P < 0.0001$), we excluded sites with very high (Nimpkish) and very low (Desolation Sound) amounts of old-growth to allow comparability between regions. Under this model, there were more disturbances in Nimpkish than around Desolation Sound ($X^2_1=3.78$, $P=0.052$), and the effect of Patch diversity was dependent on region ($X^2_1=4.24$, $P = 0.039$). Therefore, we separated all subsequent analyses between the two regions.

We were unable to run a global multivariate model of all patch and landscape-level effects predicting nest disturbance, because of the limited variation provided by our binary response variable (disturbed/ not disturbed). Instead, we ran a series of exploratory models, each of which included the patch-scale effects (edge proximity and edge-type), and one of the landscape covariates (see Table 2.1), to determine which fragmentation variables significantly predicted nest disturbance. We ran these models separately for avian disturbances of eggs, and squirrel disturbances of both eggs and nestlings (see Chapter 1). %Old-growth and Patch diversity were the only significant covariates for the Nimpkish analysis of avian egg disturbance, so these were the only landscape variables that we included in this model. For the Nimpkish analysis of squirrel disturbances, and both Desolation Sound analyses, we were only able to include one landscape variable (%Old-growth), due to computational errors associated with including too many effects (see above). For these final models, we sequentially removed non-significant interaction terms at $\alpha = 0.10$.

We tested for spatial autocorrelation in nest disturbances because of concern regarding spatial overlap between some of our landscapes. Spatial autocorrelation can result in a lack of independence among error components of field data, thereby increasing the chances of committing a type 1 error (Legendre and Legendre 1988). In our case, the disturbances of neighbouring nests may be spatially autocorrelated due to

overlap with a home range of corvid predators. We assessed the dispersion after model fitting (estimated by Deviance) to test for overdispersion, which is an indication of spatial autocorrelation (SAS 2003). If the deviance is near 1, this indicates that the data are neither overdispersed nor underdispersed (SAS 2003). We also attempted to test for spatial autocorrelation *between* sites by adding a random side effect to the models, and examining the posterior estimates (i.e. the probability of disturbance given the other effects in the model). When plotted on maps, these estimates can be examined for spatial autocorrelation to determine if the statistical methods need to be modified.

2.3 Results

2.3.1 Landscape-scale predator surveys

The top models of landscape variables predicting Steller's jays abundance included: 1) %Old-growth, %Clearcuts, and %Regenerating, and 2) Patch Density (Table 2.3). Under the first model, %Old-growth, %Clearcuts, and %Regenerating were all negatively related to Steller's jay abundance when accounting for the other effects in the model (Figure 2.1a-c). Under the second model, Patch Density was positively related to Steller's jay abundance (Figure 2.1d). The top model predicting common raven abundance included Patch Density only (Table 2.3), which was positively related to raven abundance (Figure 2.2). Landscapes surrounding transects where gray jays were detected had significantly more %Old-growth, larger Patch Sizes, less Clearcut Edge, and lower Patch Diversity, compared to transects where gray jays were not detected (Table 2.4). There was a significant negative relationship between %Old-growth and all predators combined ($R^2 = 0.73$, $F_{16,1} = 17.24$, $P < 0.001$), and a significant

positive relationship between Patch Density and all predators combined ($R^2 = 0.70$, $F_{16,1} = 14.17$, $P = 0.002$) (Figure 2.3).

%Old-growth was significantly positively correlated with Patch Size ($R^2 = 0.84$, $P < 0.0001$), and negatively correlated with %Regenerating ($R^2 = 0.25$, $P < 0.040$), but not %Clearcuts ($R^2 < 0.01$, $P = 0.715$). Patch Density was negatively correlated with Patch Size ($R^2 = 0.72$, $P < 0.0001$), and positively correlated with Patch diversity ($R^2 = 0.61$, $P = 0.0002$).

2.3.2 Artificial nest experiment

The deviance of our model was 1.25, suggesting negligible spatial autocorrelation within sites. However, because of the low variation in our binary response variable (see above), we were unable to estimate random site effects to assess spatial autocorrelation between sites. This suggests the main effects of our model accounted for most of the variation present. We therefore assumed that our treatment effects were more important predictors of nest disturbance fates than was spatial location, and that our probability of committing a type I error due to spatial autocorrelation was low.

In Nimpkish, the effect of %Old-growth on disturbance was dependent upon the edge-type of the site ($X^2_2 = 6.82$, $P=0.033$) (Table 2.5). Controlling for other effects, there was a significant positive relationship between %Old-growth and disturbance risk at hard and natural-edged sites, but not at soft-edged sites (Figure 2.4). The effect of Patch Diversity was also dependent upon edge-type ($X^2_2 = 6.32$, $P=0.043$). %Old-growth and Patch Diversity were highly inversely correlated in Nimpkish ($F_1=760.59$, $P < 0.0001$, $R^2= 0.93$), but not at Desolation Sound ($F_1 = 0.44$, $P = 0.514$, $R^2 = 0.03$).

Patch-level effects at Nimpkish were consistent with trends from a previous analysis of the pooled data set which also included Desolation Sound (Chapter 1). Overall, disturbance rates varied by edge-type ($X^2_2 = 6.58$, $P = 0.037$) (Table 2.5), with the highest level of disturbances at hard-edged sites. The edge proximity patterns of disturbance of eggs by avian predators appears dependent on edge-type ($X^2_2 = 5.15$, $P = 0.076$), with higher disturbance rates at edges relative to interiors at hard-edges, in contrast to the opposite trends found at soft ($X^2_1 = 4.45$, $P = 0.035$), and natural-edged sites ($X^2_1 = 3.74$, $P = 0.053$; post hoc tests).

In Nimpkish, disturbances by red squirrels were not significantly influenced by %Old-growth ($X^2_1 = 0.12$, $P = 0.733$) (Table 2.5). At the patch scale, the number of squirrel disturbances varied significantly among edge-types, ($X^2_2 = 6.91$, $P = 0.032$) with the highest rates of nest disturbance at soft-edged sites. Around Desolation Sound, there were no significant landscape or patch-scale effects of either avian or squirrel predators on artificial nests (Table 2.6).

2.4 Discussion

2.4.1 Habitat fragmentation and predator populations

Our results indicate that corvid populations respond significantly to both the loss and fragmentation of old-growth forests in south-western British Columbia. Both Steller's jays and common raven detections increased with increasing density of old-growth patches. The density of habitat patches is a useful indicator of fragmentation per se, as the number of patches in a landscape will increase as continuous habitat is 'broken' apart into many smaller fragments (Fahrig 1997). Therefore, these results suggest that habitat fragmentation per se will benefit both Steller's jays and common ravens.

Increasing detections of Steller's jays with declining old-growth forest in the landscape, controlling for other variables, suggests that population densities of this corvid will initially increase as forests are harvested. Higher populations of Steller's jays and common ravens can have negative implications for marbled murrelet reproduction, as both species are known predators of murrelet nests (Singer et al. 1991, Nelson and Hamer 1995, Manley 1999). Because nest predation appears to be responsible for the majority of nests failures in marbled murrelets (McShane et al. 2004), harvesting and fragmentation of old-growth habitat may reduce reproductive success per nesting attempt. This could cause populations in highly fragmented landscapes to be unable to replace themselves (i.e. population 'sinks') (Pulliam 1988, Peery et al. 2006).

A positive association of corvids with the number of old-growth patches in the landscape is consistent with Marzluff et al. (2004), who found that Steller's jays preferentially utilized areas with a high number of land-cover patches. Steller's jays appear to preferentially forage along habitat edges (De Santo and Willson 2001, Masselink 2001, Marzluff et al. 2004, Vigallon and Marzluff 2005), likely because the use of these areas facilitates access to resources on both sides of the edge (Ries and Sisk 2004). For instance, riparian and clearcut edges with high amounts of shrub vegetation may provide an abundance of insect and berry prey, while forest interiors provide nesting and caching sites (Masselink 2001, Vigallon and Marzluff 2005). Landscapes with a high density of old-growth patches also had lower mean patch sizes and more patch-type diversity in this study. Therefore, a large number of small patches, embedded in a matrix of many other habitat types, likely provide an abundance of foraging opportunities for generalist predators such as Steller's jays and common ravens.

In contrast to Steller's jays, who appear to respond to both habitat fragmentation and matrix composition, common ravens only responded to the density of old-growth patches (i.e. fragmentation per se). Common ravens have home ranges that are ca. 20 times the size of Steller's jay's home ranges (Marzluff and Neatherlin 2006). Therefore, it is likely that ravens' perception of the landscape is more 'coarse-grained' than that of Steller's jays. For instance, Steller's jays may respond to fragmentation and habitat loss at the landscape scale (i.e. within kilometres), as well as fine-scale variation in cover types at the patch scale. In contrast, ravens may respond to habitat fragmentation at an even larger landscape scale (i.e. within tens of kilometers), but not respond to finer scale variation in cover types at the scale we measured them.

2.4.2 Landscape and patch-scale effects on predation risk

For Steller's jays, our results indicate that in addition to the amount of habitat fragmentation, the composition of the matrix resulting from fragmentation also has an important influence on populations. When accounting for the amount of old-growth forest and young clearcuts at the landscape scale, Steller's jays declined with increasing proportions of regenerating forest (21-40 years). For a given level of old-growth fragmentation, the density of Steller's jays in the landscape may therefore decline as forests regenerate after initial harvesting. This result is consistent with the patch scale effects found in Chapter 1, where disturbance risk on artificial nests was lowest at soft edges. This also supports the idea that edge effects on predation risk may be temporally dynamic in western landscapes.

Other studies have also found that forests of simple structure (i.e. regenerating, even-aged stands) are associated with small corvid populations (Raphael et al. 2002). Lower densities of Steller's jays in these areas is likely a result of the low availability of

resources in regenerating forests, which have a closed canopy and little understory vegetation (Franklin et al. 2002). The apparent strong negative effect of regenerating forest on Steller's jays could cause old growth patches embedded in this matrix type to be "buffered" from changes in predation risk in the surrounding landscape. This may explain why the amount of old growth forest in the surrounding landscape had no influence on avian disturbance rates of artificial eggs at soft-edged sites.

At the landscape scale, nest disturbance rates increased with the amount of old-growth forest surrounding artificial nests at hard and natural-edged patches. This trend appears to contradict our general finding of declining predator populations with increasing old-growth cover (Figure 2.3a). However, gray jays could be driving this pattern, as landscapes in which gray jays were detected had more old-growth, larger patches, and less clearcut edge compared to landscapes where they were not detected. Other researchers have also found gray jays to be more abundant in intact landscapes (Raphael et al. 2002). Although gray jays may frequently use habitat at the edge of forests, they rarely leave forested patches to move into other habitats (Ibarzabal and Desrochers 2004).

In contrast to gray jays, both Steller's jays and common ravens were less abundant in more intact landscapes. However, lower predator densities in the overall landscape do not necessarily mean that predation risk in all patches will be lower, because predators may be distributed unevenly. For instance, if Steller's jays prefer clearcuts for foraging (Masselink 2001), they may maintain relatively high densities at the few clearcuts available in relatively intact landscapes. This also could explain why Steller's jays appear to respond positively to hard edges at the patch scale (Chapter 1), but not to the proportion of clearcuts at the landscape scale (this study). Therefore, the amount and configuration of old-growth and regenerating forest may determine predator

population densities at the landscape scale, whereas the response of individuals to resource patchiness may determine their distribution at the patch scale.

2.4.3 Cumulative predation risk

Our results suggest that habitat loss and fragmentation will increase the total density of corvid predators in the landscape. Mean detections of all predators combined increased with decreasing amounts of landscape old-growth, and increasing density of old-growth patches. This suggests that both habitat loss and habitat fragmentation per se will increase landscape-level predation risk. However, summing predator detections in this manner assumes equal contribution of each predator to predation risk. This approach is problematic, as the relative strength of each predator's contribution to predation risk will vary with factors such as body size, habitat use, and foraging behaviour. A more meaningful approach would be to 'weight' the abundances of each predator species according to their contribution to predation risk. This could be accomplished with video observations detailing success rates of predation attempts by different predators at murrelet nests.

The relative detectability of each predator species is also an important consideration when assessing cumulative predation risk. Although gray jays were detected only rarely, they may be more abundant in this region than the surveys suggest. In the same study region, we detected gray jays frequently in patch level predator surveys (Chapter 1). Similarly, (Bryant 1994) detected gray jays more often than Steller's jays during point-count surveys on northern Vancouver Island. Therefore, it is possible that the density of gray jays was underestimated relative to the other corvid species. This may have occurred because survey transects were located on roads, where detection of forest species such as gray jays may be more difficult. Gray jays

may be more important in this system compared to other areas where murrelets nest such as Clayoquot Sound, where gray jays are rarely observed (Rodway and Regehr 2002). Gray jays have never been observed depredating murrelet nests, but their role as nest predators is suspected (Nelson 1997). Gray jays could contribute to regional differences in predation risk patterns depending on their presence in the landscape. Thus, determining their contribution to predation risk is essential for effective management of marbled murrelets.

We detected no significant effects of landscape structure on nest disturbance rates around Desolation Sound. This was likely due to lower statistical power available to detect trends around Desolation Sound, which had a smaller sample size relative to Nimpkish. However, in general, there was significantly more old-growth, as well as more avian nest disturbances, in Nimpkish compared to Desolation Sound. This suggests that our landscape-scale result of higher overall predation risk with more old-growth in Nimpkish may be generalizable to the regional scale. This experiment needs to be replicated with sufficient power in other regions with varying amounts of old-growth cover, to determine if these results can be applied elsewhere.

2.4.4 Comparisons to other landscape-scale studies

Comparison of our results to other landscape-scale murrelet studies allows us to address the interrelationships among predation risk, habitat selection, and reproductive fitness. Murrelets have higher audio-visual occupancy rates (Meyer and Miller 2002, Meyer et al. 2002), and higher marine radar counts (Burger 2001, Burger et al. 2004) in landscapes with more old-growth habitat. Our survey data suggest that Steller's jays and common ravens will be relatively rare in these landscapes. Therefore, intact landscapes of old-growth forest may represent optimal habitat for murrelets, due to an

abundance of nest sites and fewer generalist predators. The caveat here is that if forest-dependent predators such as gray jays and squirrels are important predators on murrelet nests, predation risk in these areas may be higher than predicted from Steller's jays and ravens alone.

2.5 Management implications

We found evidence for increased populations of Steller's jays and common raven predators with increased landscape habitat loss and fragmentation. These data also suggest that Steller's jays not only respond to the amount of habitat fragmentation, but also to the type of fragmentation via the composition of the matrix. Finally, this study supports the existence of complex relationships between habitat fragmentation and nest predation risk, whereby different predators respond to fragmentation in different ways.

Increased populations of generalist predators that are known to prey on murrelet nests have clear implications for marbled murrelet habitat management. Our results suggest that in addition to habitat loss alone, habitat fragmentation per se will also initially result in increased populations of these predators. Therefore, in order to keep populations of Steller's jays and common ravens low, extensive areas of high contrast edge surrounding many small and medium-sized patches of old-growth should be avoided. Instead, a landscape consisting of fewer and larger patches of old-growth, surrounded by regenerating forest, may be substantially less deleterious with regard to predation-induced edge effects. A negative association of Steller's jays with regenerating forest is consistent with the idea that predation risk in western forests is temporally dynamic, and may decline with time (Chapter 1). We therefore support the allocation of "buffers" of regenerating forest around "cores" of old-growth murrelet

habitat. This will also provide the opportunity to create larger reserves in the long-term, if managers allow these buffers to recruit into marbled murrelet habitat.

Increasing overall predation risk with increasing old-growth habitat in the landscape suggest complex predator community dynamics, where predation risk is the combined result of responses to fragmentation at multiple scales. In light of this complexity, we recommend the use of a precautionary approach to murrelet habitat management. We do not recommend extensive harvesting to reduce predation risk, because patch level edge effects are still predicted to occur in both intact and fragmented landscapes. In addition, increased risk in unfragmented landscapes may be driven by gray jays, whose role as a predator of marbled murrelet nests has not been confirmed. It would therefore be premature to attempt to decreased predation risk by harvesting, especially because this strategy would result in increases in populations of both Steller's jays and common ravens. Understanding the role of forest-dependent predators such as squirrels or gray jays is essential, as management recommendations will differ widely depending on the strength of their contribution to murrelet nest predation. This issue must be addressed in order to move forward with well-informed murrelet habitat management. In the meantime, we recommend a precautionary approach, where large patches of old-growth forest in a matrix dominated by regenerating forest limit Steller's jays and common raven populations.

2.6 Tables and Figures

Table 2.1. Description of landscape metric variables calculated from 1660 hectare (2.3 km radius) landscapes surrounding predator survey transects and artificial nest sites. Variables are classified according to their hypothesized effect type(s), including habitat loss ('Loss'), habitat fragmentation per se ('Fragmentation'), and matrix composition effects ('Matrix').

Variable Name	Description	Effect type
%Old-growth	Percent in old-growth forest (>140 years)	Loss
%Clearcuts	Percent in clearcuts (0-20 years)	Loss, Matrix
%Regenerating	Percent in regenerating forest (21-40 years)	Loss, Matrix
Patch Density	Number of old-growth patches per area (#/ha)	Fragmentation
Patch Size	Mean patch size per area (ha)	Fragmentation
Old Edge	Length of old-growth edge per area (m/ha)	Fragmentation
Clearcut Edge	Length of clearcut edge per area (m/ha)	Fragmentation, Matrix
Regenerating Edge	Length of regenerating forest edge per area (m/ha)	Fragmentation, Matrix
Contrast-Edge	Length of old-growth edge per area, corrected for the relative contrast between patches for each edge-type (m/ha)	Fragmentation, Matrix
Patch Diversity	Diversity of patch types, using Simpsons' Diversity Index ¹ . Indicates the probability that two randomly selected patches will be of a different type. Ranges from 0 (no diversity) to 1 (maximum diversity)	Fragmentation, Matrix

¹(Simpson 1949)

Table 2.2. The set of models used to rank alternative hypotheses of effects of landscape structure on corvid abundances. Models are divided into four groups representing different effect types, and are numbered for easy reference.

Hypothesis Group	#	Models
Habitat loss	1	%Old-growth
Fragmentation per se	2	Old Edge
	3	Patch Size
	4	Patch Size + Old Edge
	5	Patch Density
Habitat loss assuming matrix effects	6	%Clearcuts
	7	%Regenerating
	8	%Old-growth + %Clearcuts + %Regenerating
Habitat loss and fragmentation, assuming matrix effects	9	Clearcut Edge
	10	Regenerating Edge
	11	Contrast Edge
	12	Old Edge + Clearcut edge+ Regenerating Edge
	13	Patch Diversity
	14	Patch Density + Patch Diversity
	15	%Old-growth + %Clearcuts + %Regenerating + Contrast Edge
	16	%Old-growth + Old Edge + Clearcut Edge + Regenerating Edge
	17	%Old-growth + Patch Size + Old Edge
	18	%Old-growth + Patch Density + Patch Diversity

Table 2.3. Ranking of linear regression models predicting the effects of landscape structure on the frequency of Steller's jay and common raven detections in the Nimpkish Valley, British Columbia, May-August, 2003-2005. Model number (#), number of estimated parameters (K), small sample Akaike's Information Criteria (AICc), difference between AICc of the model and that of the best model ($\Delta AICc$), and Akaike's weight (ω) are listed. Only the top set of models with a sum of weights of ≥ 0.95 were included. Models in bold are considered to have the most substantial support ($\Delta AICc \leq 2$)

#	Model	K	AICc	$\Delta AICc$	ω
<i>Steller's jays</i>					
8	%Old-growth + %Clearcuts + %Regenerating	5	47.61	0.00	0.35
5	Patch Density	3	48.28	0.67	0.25
3	Patch Size	3	50.54	2.93	0.08
14	Patch Density + Patch Diversity	4	51.24	3.63	0.06
1	%Old-growth	3	51.31	3.70	0.06
12	Old Edge + Clearcut Edge + Regenerating Edge	5	51.49	3.88	0.05
15	%Old-growth + %Clearcuts + %Regenerating + Contrast Edge	6	51.83	4.22	0.04
16	%Old-growth + Old Edge + Clearcut Edge + Regenerating Edge	6	52.38	4.78	0.03
4	Patch Size + Old Edge	4	52.75	5.15	0.03
13	Patch Diversity	3	54.18	6.57	0.01
<i>Common ravens</i>					
5	Patch Density	3	-22.15	0.00	0.55
14	Patch Density + Patch Diversity	4	-18.84	3.31	0.10
1	%Old-growth	3	-18.80	3.35	0.10
13	Patch Diversity	3	-18.61	3.54	0.09
3	Patch Size	3	-17.00	5.15	0.04
11	Contrast Edge	3	-16.56	5.59	0.03
10	Regenerating Edge	3	-15.17	6.98	0.02
18	%Old-growth + Patch Density + Patch Diversity	5	-14.90	7.26	0.02

Table 2.4. Mean values (\pm 95% confidence limits) and significance levels of fragmentation variables calculated from 1660 hectare (2.3 km radius) landscapes surrounding predator survey transects, in the Nimpkish Valley, British Columbia. Values of landscape variables were compared between landscapes where gray jays were detected and landscapes where gray jays were not detected.

Variable	gray jays detected	gray jays not detected	DF	F	P
%Old-growth	50.89 \pm 14.87	31.53 \pm 9.60	1	5.44	0.034
%Clearcuts	26.20 \pm 5.98	22.51 \pm 3.86	1	1.22	0.286
%Regenerating	13.21 \pm 13.76	18.34 \pm 8.88	1	0.54	0.475
Patch Density	1.02 \pm 0.48	1.73 \pm 0.31	1	7.09	0.018
Patch Size	61.98 \pm 23.25	22.00 \pm 15.01	1	9.48	0.008
Old Edge	35.54 \pm 6.52	32.75 \pm 4.21	1	0.59	0.456
Clearcut Edge	28.62 \pm 6.08	37.60 \pm 3.92	1	7.00	0.018
Regenerating Edge	14.18 \pm 13.25	24.36 \pm 8.55	1	1.90	0.189
Contrast- Edge	27.28 \pm 6.12	22.94 \pm 3.95	1	1.61	0.224
Patch Diversity	0.61 \pm 0.08	0.72 \pm 0.05	1	5.65	0.031

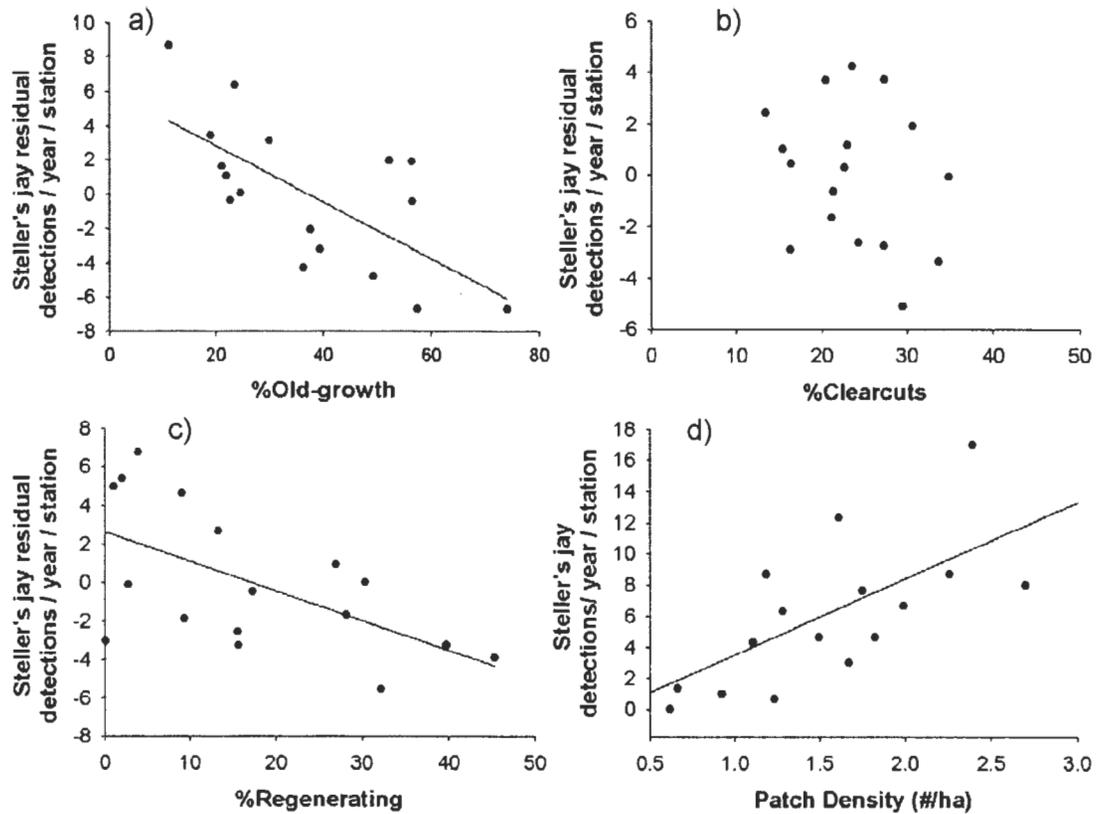


Figure 2.1. Influence of (a) percent landscape in old-growth forest, (b) percent landscape in clearcuts, (c) percent landscape in regenerating forest, and (d) number of landscape old-growth patches, on mean detections of Steller's jay in road transects in the Nimpkish Valley, British Columbia. The response variable in graphs (a-c) are plotted as residuals to take the other variables into account (i.e. detections in graph (a) are the residuals of the model including %Clearcuts and %Regenerating).

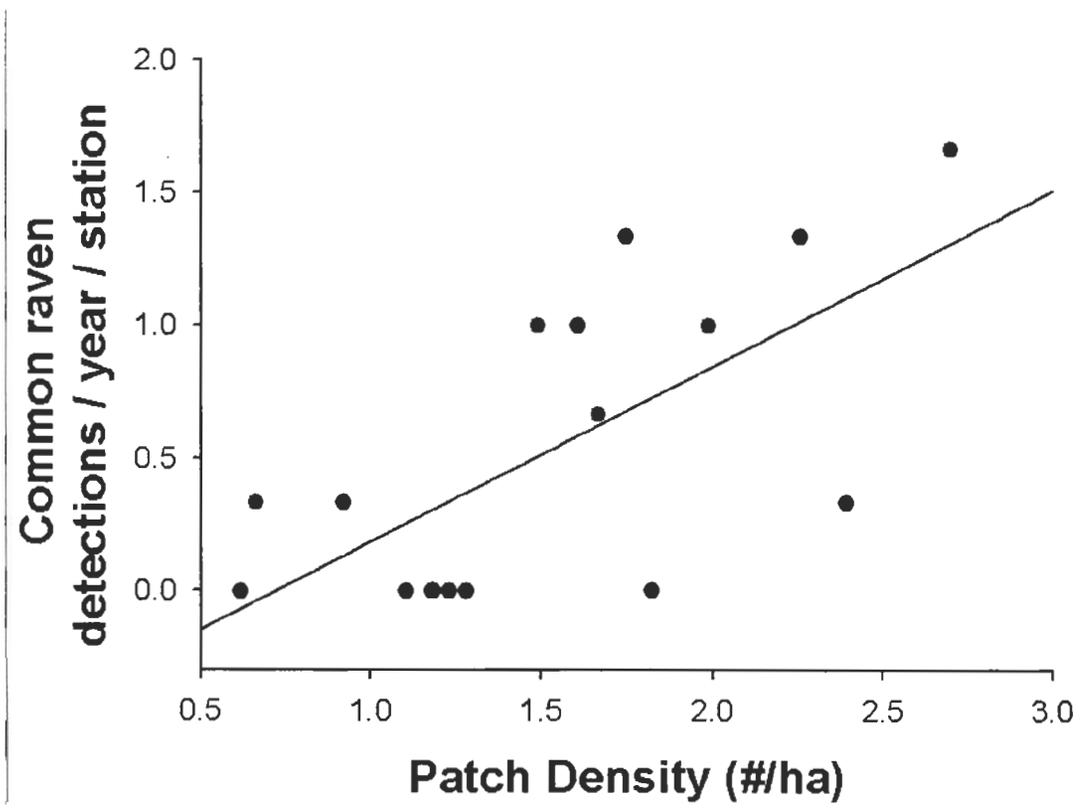


Figure 2.2. Influence of number of old-growth patches in the surrounding landscape on mean detections of common ravens in road transects in the Nimpkish Valley, British Columbia.

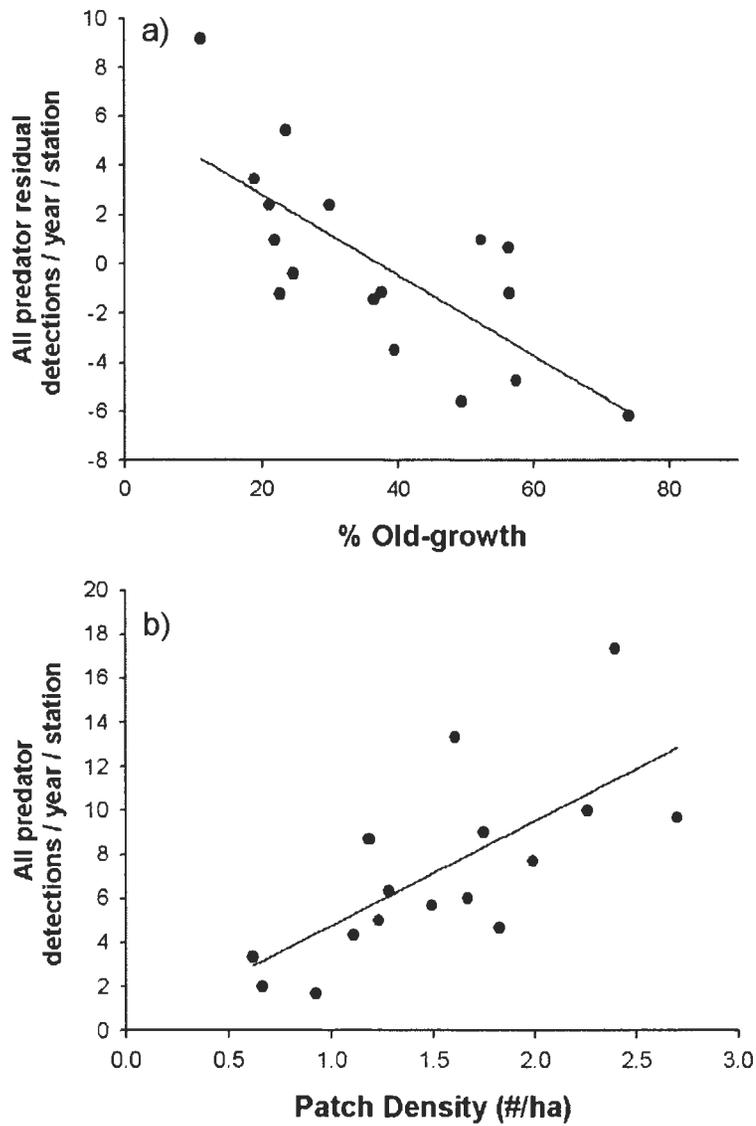


Figure 2.3. Influence of a) percent old-growth and b) number of old-growth patches of old-growth patches in the surrounding landscape on mean detections of all predators combined (Steller's jays, gray jays, and common ravens), in road transects in the Nimpkish Valley, British Columbia. Detections in graph (a) are residuals accounting for percent clearcuts and percent regenerating forest in the landscape.

Table 2.5. Effects of patch and landscape variables on disturbance of artificial nests by avian predators (eggs) and squirrels (eggs and nestlings) in the Nimpkish Valley, B.C. Landscape variables are measured from 1660 hectare (2.3 km radius) landscapes surrounding each experimental nest site.

Effect	DF	X²	P
Avian predators (eggs)			
Edge proximity	1	0.63	0.427
Edge-type	2	6.58	0.037
Edge proximity x Edge-type	2	5.15	0.076
%Old-growth	1	0.01	0.928
Patch Diversity	1	0.51	0.473
%Old-growth x Edge-type	2	6.82	0.033
Patch Diversity x Edge-type	2	6.32	0.043
Squirrels (eggs and nestlings)			
Edge proximity	1	2.07	0.149
Edge-type	2	6.91	0.032
Nest-type	1	<0.00	0.961
%Old-growth	1	0.12	0.733

Table 2.6. Effects of patch and landscape variables on disturbance of artificial nests by avian predators (eggs) and squirrels (eggs and nestlings) around Desolation Sound, B.C. Landscape variables are measured from 1660 hectare landscapes (2.3 km radius) surrounding each experimental nest site.

Effect	DF	X²	P
Avian predators (eggs)			
Edge proximity	1	1.54	0.214
Edge-type	2	2.23	0.327
%Old-growth	1	0.94	0.333
Squirrels (eggs and nestlings)			
Edge proximity	1	2.51	0.113
Edge-type	2	0.28	0.869
Nest-type	1	2.03	0.154
%Old-growth	1	0.04	0.834

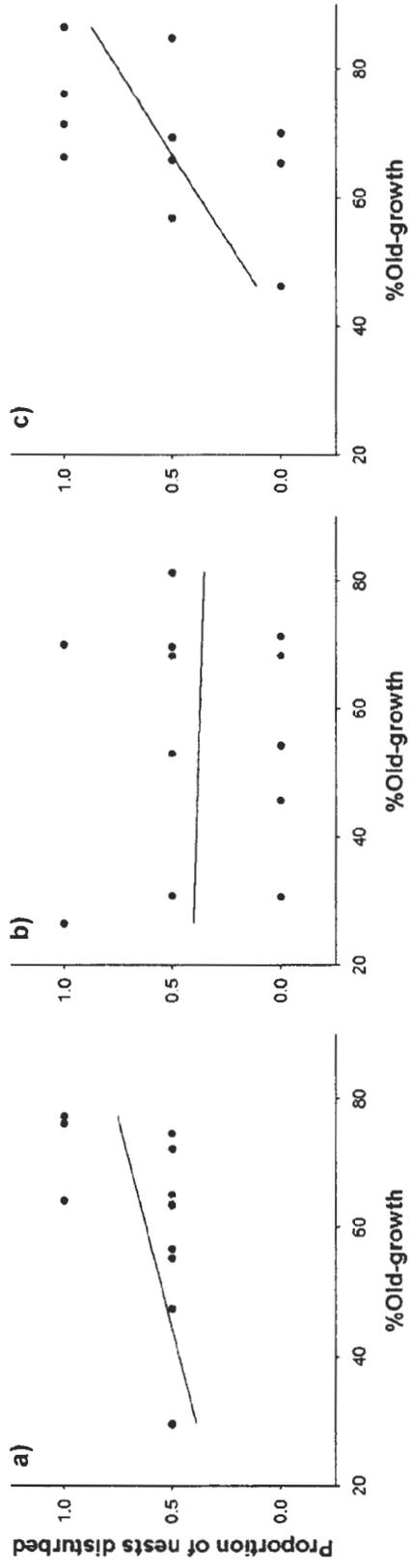


Figure 2.4. The influence of percent landscape old-growth on disturbances of artificial eggs by avian predators, at hard (a), soft (b), and natural-edged sites (c), in the Nimpkish Valley, British Columbia.

CHAPTER 3

THE EFFECTS OF ANTHROPOGENIC EDGES ON MARBLED MURRELET HABITAT AVAILABILITY: THE INFLUENCE OF MICROCLIMATE

3.1 Introduction

Forest harvesting creates artificial edges between cleared areas and the remaining forest, exposing forest biota to an altered environment. As a result, edges often have higher temperature extremes, stronger wind speeds, and lower humidity levels relative to interior locations (Chen et al. 1995, Stewart and Mallik 2006). In both temperate and boreal forests, these microclimate gradients, or "edge effects", can lead to changes in the growth, vitality, survival and reproduction of species at forest edges (Hylander et al. 2002, Hylander et al. 2005, Muir et al. 2006, Stewart and Mallik 2006). Ultimately, these effects can cause changes to forest structure and species composition at edges relative to interiors of forests (Harper et al. 2005).

Poikilohydric species such as mosses and lichens, which lack mechanisms to reduce water loss, may be particularly susceptible to these changes in microclimate (Busby et al. 1978). In particular, increased air temperature and decreased relative humidity have been shown to decrease the abundance of mosses at habitat edges (Hylander et al. 2002, Hylander 2005, Stewart and Mallik 2006). This can cause decreased species richness of bryophytes in small habitat fragments (Fenton and Frego 2005, Hylander et al. 2005). Epiphytic mosses growing in tree canopies may be particularly sensitive to microclimate edge effects, as they are more exposed to storm events and other extremes in microclimate (Esseen 2006).

Bryophytes contribute to forest biodiversity, influence ecosystem processes, and provide habitat for both invertebrate and vertebrate species (Glime 1978, Longton 1990, Bates 1992, Jonsson 1997). Therefore, it is important for habitat managers to understand the impacts of anthropogenic edges on mosses. However, edge effects on microclimate vary with respect to many factors, and associated plant responses will be complex (Murcia 1995, Chen et al. 1999). One factor of particular interest to habitat managers is the structural contrast between habitat patches, which may influence both the magnitude and extent of edge effects (Harper et al. 2005). For instance, edge effects may decline with time after harvesting, as clearcuts regenerate and patch contrast lessens (Matlack 1993, Harper et al. 2005). Patch contrast at natural edges may also be lower than fresh anthropogenic edges. This can result in weaker edge effects at forest/riparian ecotones compared to those at clearcut boundaries (Stewart and Mallik 2006).

The marbled murrelet, a threatened seabird that nests in old-growth forests adjacent to the North Pacific coastline, may be particularly susceptible to decreased bryophyte abundance from microclimate edge effects. Murrelets do not construct their own nests, but instead typically lay a single egg on "nest platforms" formed by epiphytic moss growth on wide branches of old-growth trees (McShane et al. 2004). Accordingly, murrelets prefer trees and forest patches with prolific moss growth, which provide an abundance of potential nest sites to choose from (Burger 2002). The loss of old growth forest is considered a major factor limiting habitat availability and contributing to murrelet population declines throughout its range (Burger 2002, Raphael et al. 2002, McShane et al. 2004, Raphael 2006). Habitat fragmentation and microclimate edge effects have the potential to further decrease habitat availability, by reducing the abundance of potential murrelet nest sites in the remaining patches. It is therefore imperative that habitat

managers understand how anthropogenic edges influence murrelet habitat. This knowledge will help managers to effectively design and maintain reserves to sustain murrelet populations.

While many studies have investigated microclimate edge effects on bryophytes on the forest floor (Fenton and Frego 2005, Hylander 2005, Stewart and Mallik 2006), fewer have studied microclimate effects on epiphytic mosses in the forest canopy (Muir et al. 2006). Here, we measured microclimate variables at potential marbled murrelet nest sites in edges and interior locations of the forest canopy in southern British Columbia. These were combined with estimates of nest site abundance to investigate the potential influence of edges on murrelet habitat availability. We replicated this design across artificial and natural edge-types representing different levels of patch contrast and years since harvest to determine how edge effects differ between these different edge-types and change over time.

3.2 Methods

3.2.1 Study Areas

This study was conducted in southwestern British Columbia, at 18 sites around Desolation Sound in 2004 (50° 05' N, 124° 40' W), and at 34 sites in the Nimpkish Valley ('Nimpkish') on Northern Vancouver Island ('50° 12' N 126° 37' W). This research was part of a broader study investigating spatial variation in predation risk using artificial nests (Chapter 1). Mean summer temperatures (April-August) at Nimpkish are 13.4°C, and 14.8°C around Desolation Sound. Cumulative precipitation is 300 mm in Nimpkish, and 290 mm around Desolation Sound. For a full description of the study areas, please refer to Chapter 1. Each site consisted of approximately 20 hectares of old growth forest

(>140 years old). At each site, two trees with potential nest platforms were selected at edge and interior locations. Potential nest platforms were defined as limbs that were \geq 15 m above the ground and \geq 18 cm in diameter, including epiphytes (Burger and Bahn 2004). Edge habitat was defined as forest within 50 meters of the edge of interest (Paton 1994), and interior habitat was at least 150 m from any other forest openings. Our sites were selected to fall into three edge-types, including "hard" edges (5-11 years since harvesting), "soft" edges (17-39 years), and natural edges formed by rivers or avalanches.

3.2.2 Microclimate sampling

We sampled microclimate variables in the canopies of old-growth trees at 32 sites in Nimpkish in 2005. This included 11 sites at hard edges, 11 at soft edges, and 10 at natural edges. We randomly selected one of the two trees climbed at both the edge and the interior of the site, and placed a datalogger underneath the nest platforms used for our artificial nests. We used HOBO[®] Temperature/Humidity dataloggers at 25 sites (Onset Computer Corp. Bourne, MA), and ibuttons[®] at seven sites (Maxim/Dallas, Sunnyvale, CA). HOBO[®] dataloggers sampled temperature, dew point, and absolute humidity, and relative humidity, whereas ibuttons[®] sampled temperature only. Sites were set-up with dataloggers between May 31 and June 10, and between July 2 and July 11, for a duration of approximately two weeks each, during which microclimate variables were sampled every 15 minutes. Sampling was initiated at 6:00 p.m. the day of set-up, and stopped at 6:00 a.m. the day of takedown. Samplings of sites of the three different edge-types were distributed throughout the sampling periods to minimize any seasonal bias.

3.2.3 Habitat Sampling

Habitat features pertaining to marbled murrelet nest-site availability were sampled in edge and interior plots at 18 sites around Desolation Sound in 2004 and at 31 sites in Nimpkish in 2005. We randomly selected the location of center points for our 25 meter radius plots, which were established in both edge and interior habitats at each site. Within each plot, 10 "canopy trees" (≥ 10 cm in diameter or reaching upper canopy layer) were selected using random bearings and distances from the plot center. The sample of distances that were drawn from were corrected for area. For instance, there were fewer distances available to choose from near the plot perimeter relative to the plot center. This is because the "O" representing distances farther from the plot center samples more area than the "O" of distances near the plot center. For each canopy tree, tree species, tree height and diameter at breast height (DBH) were recorded. The number of potential marbled murrelet nest platforms for each canopy tree was also recorded, which was defined as structures ≥ 18 cm in diameter (including mosses), and ≥ 15 meters from the ground. The percent epiphyte cover on tree limbs of each canopy tree was scored from zero to four (0= none; 1= trace; 2= 1-33%; 3= 34-66%; 4= 67-100%)(Burger and Bahn 2004). The thickness of these epiphytes was scored from zero to three (0=absent; 1=sparse; 2=intermediate; 3= thick mats). Within each plot, we counted the total number of canopy trees with at least one potential murrelet platform.

3.2.4 Data Analysis

Mean temperature, maximum temperature, minimum temperature, and relative humidity were calculated as the averaged values of all samples during the ca. two-week exposure period for each edge/interior location of each site. Vapour pressure deficit

(VPD) was calculated from the mean temperature and mean relative humidity for each sampling location, using the following formula:

$$\text{VPD} = (6.1078) [\exp(17.269T / 237.3 + T)] (1 - \text{RH})$$

where T is the temperature in degrees Celsius, RH is the relative humidity as a decimal, and VPD is expressed in hPa (from Fenton and Frego, 2005). VPD represents the difference between the saturation vapour pressure and the actual vapour pressure in the air at a given temperature. As VPD approaches zero, vapour in the air approaches saturation. 'Platform density' was defined as the mean number of platforms per canopy tree sampled in each plot. 'Platform tree density' was the number of canopy trees with at least one platform, corrected for plot area if a portion of the plot was outside of forest.

We ran mixed general linear models in PROC MIXED in SAS® version 9.1 (SAS 2003) to test for the effects of edge proximity (edge/interior), region (Nimpkish/Desolation Sound), and the patches' edge-type (hard/soft/natural) on mean microclimate and habitat variables for each plot. Julian date was included as a covariate in all analyses. We used a split-plot design, where edge-proximity was the subplot factor (fixed effect), and site the main plot factor, nested within region and edge-type (random effects). We sequentially removed non-significant interaction terms, only retaining those there were significant at this $\alpha = 0.10$. We conducted Tukey post-hoc tests to investigate the contrasts between levels of significant variables.

Although not directly related to our main questions, we investigated the effect of edge orientation on habitat and microclimate variables for plots and nest trees at patch edges only (excluding interior sites). We wished to test for these effects because of their importance in other studies of microclimate edge effects (Chen et al. 1995, Hylander 2005), and the possibility that they may co-vary with the main effects in our models. For all edge nests, we classified the orientation of the edge to the nearest cardinal direction

(North, South, East, and West). We ran models with a split-plot design (see above) with orientation, edge-type, julian date, and the interaction between orientation and edge-type, for all habitat and microclimate variables. For all tests, the effects of orientation or orientation by edge-type interactions were non-significant (all tests $P > 0.20$), suggesting that edge orientation does not significantly influence habitat or microclimate in this system. We therefore did not include edge orientation in any of our final models.

3.3 Results

3.3.1 Microclimate Sampling

The effect of edge proximity on the mean temperature at artificial nest sites was dependent on date ($F_{30,1} = 8.00$, $P = 0.008$)(Table 3.1). Mean temperature was higher at edges relative to interiors early in the season, but not later (Table 3.2, Figure 3.1). Similarly, minimum temperature was higher at edges relative to interiors early in the season (Table 3.1). VPD was significantly higher at soft edge patches relative to either hard or natural edge patches ($F_{21,2} = 13.11$, $P < 0.001$)(Table 3.1, Figure 3.2). All microclimate variables changed significantly between the early and late sampling periods, including: increases in mean temperature, maximum temperature, minimum temperature, and relative humidity; and a decrease in VPD (Table 3.2).

3.3.2 Habitat Sampling

Platform density was higher at natural-edged patches relative to other edge-types ($F_{47,2} = 4.39$, $P = 0.018$) (Table 3.2, Figure 3.3). However, this effect appeared to be dependent on the edge-proximity of the plot ($F_{46,2} = 2.47$, $P = 0.096$), as natural-edged sites had substantially higher platform density compared to other edge-types, and

natural interiors had significantly higher platform densities than did hard edges (post-hoc tests; Figure 3.3a). Platform tree density was lower in edge plots than in interior plots ($F_{48,1} = 6.63$, $P = 0.013$) (Table 3.2). The edge-type of the patch had a significant effect on platform tree density ($F_{47,2} = 4.87$, $P = 0.012$), as there was a significant difference between natural and hard-edged patches, but not between natural and soft-edged patches (Figure 3.3b). In addition, natural interiors had significantly higher platform tree densities relative to any of the other habitats (Figure 3.3b; post-hoc tests)

There was a significant effect of edge-type on epiphyte thickness score ($F_{47,2} = 4.72$, $P = 0.014$), with significantly higher epiphyte thickness at natural-edged patches relative to other edge-types (Figure 3.4a). Epiphyte thickness scores were significantly higher in Nimpkish plots relative to Desolation Sound plots ($F_{47,1} = 4.79$, $P = 0.034$). There was a non-significant trend of higher epiphyte cover scores in patch interiors relative to edges ($F_{48,1} = 3.24$, $P = 0.078$) (Table 3.3). There was also a trend towards an effect of edge-type on epiphyte cover ($F_{47,2} = 2.97$, $P = 0.061$) (Figure 3.4b).

3.4 Discussion

Our results demonstrate significant anthropogenic edge effects on microclimate and epiphyte biomass in old-growth forests of south-western British Columbia. Habitat edges had higher temperatures than interiors early in the season, and there were fewer trees with suitable marbled murrelet nest platforms at edges relative to interiors. This suggests that the creation of artificial edges by forest fragmentation will have negative consequences for bryophyte growth and survival in these landscapes, and potentially negatively affect the availability of murrelet habitat. Other researchers in temperate and boreal forests have found similar edge effects on microclimate, including higher temperatures, higher vapor pressure deficit, and lower humidity levels at edges relative

to interior habitats (Chen et al. 1995, Stewart and Mallik 2006). In turn, this has been related to reduced growth, vitality, and survival of mosses at habitat edges (Hylander et al. 2002, Hylander 2005, Stewart and Mallik 2006). Bryophyte growth is directly correlated with the amount of time mosses are wet (Busby et al. 1978). Therefore, higher temperatures and reduced VPD at edges may have reduced the growth rates of canopy mosses, thereby decreasing their abundance over time. Additionally, increased exposure to weather events such as strong winds may cause damage and removal of canopy epiphytes, further decreasing moss abundance at edges (Esseen 2006). Finally, edges often have lower tree densities due to higher mortality rates (Chen et al. 1992), which could reduce the availability of substrate for epiphyte establishment.

We found little difference in microclimate and habitat variables between hard and soft-edged patches. For instance, there were no significant differences in platform density, platform tree density, epiphyte cover, or epiphyte thickness between hard and soft patches. This was contrary to our expectations, because edges with less patch contrast (such as soft edges in this study) are predicted to have weaker edge effects relative to higher-contrast edges (Harper et al. 2005). However, unlike eastern forests, regenerating edges in western forests do not develop a "sidewall" of vegetation that may act to limit edge effects (Matlack 1993). Indeed, VPD was actually higher in patches bordering older regenerating forests (soft edges) compared to those bordering young, 'hard' clearcuts. Therefore, edge effects may persist longer after anthropogenic edge creation in western forests. However, we only measured effects at two discrete time intervals after harvesting, and therefore this study provides incomplete information on how these effects change with time. For instance, we have no knowledge of how edge effects changed in the intermediate years between hard and soft edges (i.e, 11-20 years post-harvest). Similarly, we do not know at what stage of forest regeneration

microclimate and habitat conditions at anthropogenic edges are restored to forest interior levels. These data would help habitat managers mitigate the effects of anthropogenic edges on murrelet nest site availability over the long-term.

Although microclimate and habitat edge effects were present at natural edges, patches with these edge-types appeared to be less affected compared to patches surrounded by anthropogenic edges. For instance, natural patches had the highest levels of platform density, platform tree density, and epiphyte thickness, as well as lower VPD relative to soft patches. Rodway and Regehr (2002) also found high levels of murrelet habitat indicators close to stream channels. As discussed above, higher humidity levels (i.e. lower VPD) found at natural edges likely increase the amount of time mosses are wet, resulting in increased growth rates. Also, the smaller forest openings present at these edge-types likely limit damage caused by exposure to extreme weather. This is consistent with Stewart and Mallik (2006), who documented stronger edge effects on microclimate at clear-cut edges compared to the forest/riparian ecotone. Murrelets use watercourses as inland flyways (Peery et al. 2004a), their nesting behaviour is positively associated with stream channels (Rodway and Regehr 2002), and they nest closer to streams than expected by chance at the landscape scale (Zharikov et al. 2006). Therefore, natural edges such as streams may constitute preferred habitat for murrelets, due to the abundance of potential nest sites found there.

Although we documented significant differences in microclimate variables between our habitat treatments, the absolute differences of these measurements were relatively small. For instance, while mean temperatures were significantly higher at edges relative to interiors early in the season, the value of this difference was less than 1° C. It is possible that extremes in microclimate that are more likely to impact mosses occur later in the season (i.e. we did not sample in August). This is supported by the

fact that both mean and maximum temperatures increased, and VPD decreased, from early to late in the season. Our placement of dataloggers underneath artificial nests may have also influenced our ability to detect extremes in microclimate. In particular, microclimate conditions below the nests might not have reached the same extremes as conditions above the nest, where mosses are exposed to direct solar radiation. Perhaps placing data loggers in these locations would have sampled a more representative range of conditions that may influence bryophyte growth and survival.

The habitat variables we measured are directly related to stand-level forest characteristics selected by marbled murrelets. For instance, Burger and Bahn (2004) documented positive relationships between platform density and epiphyte thickness with occupied detections of murrelets (Burger and Bahn 2004). Others have documented thicker moss depth, more platform trees, and higher platform density in nest plots compared to plots with no known nests (Nelson and Wilson 1999, Burger 2002). However, the essential question here is: are these differences in habitat availability large enough to have real impacts on marbled murrelets? The largest difference in platform tree density we documented was between approximately 57 platform trees/ha in natural interiors and 23 platform trees/ha at hard edges (Figure 3). In comparison, estimates of marbled murrelet nesting densities range from 0.11 nests per hectare (Conroy et al. 2002) to 0.9 nests per hectare in this area (Hamer and Meekins 1999).

Thus, based on habitat availability alone, it appears that even the low density of platform trees at hard edges could readily provide sufficient habitat for nesting murrelets. However, high habitat availability does not necessarily equate to high habitat quality. Presumably marbled murrelets trade-off a number of factors when selecting nest sites, including microhabitat structure, patch and landscape scale predation risk, nest site access, and proximity to productive coastal feeding areas. For example, murrelets have

been shown to select for the presence of canopy openings that provide unobstructed flight access (Waterhouse et al. 2002), as well as foliage cover above the nest for protection against predators (Manley 1999). Although sufficient nest sites appear to be *available* at the anthropogenic edges we sampled, the number of *suitable* nest sites will be far fewer. Therefore, edge effects on moss growth and survival may have the potential to reduce the availability of suitable habitat below the required thresholds by murrelets. These effects may be strongest in highly fragmented landscapes, where a large proportion of habitat area is influenced by edge effects.

3.5 Management Implications

Our data suggest that edge effects on microclimate can significantly impact nest site availability at anthropogenic edges in south-western British Columbia. Therefore, in order to maximize murrelet habitat availability across the landscape, managers should minimize the ratio of anthropogenic edge to interior old-growth habitat. This can be accomplished by creating large, circular reserves of old-growth habitat, instead of small, linear patches of habitat. Management of the habitat matrix is also an important component in the mitigation of edge effects. However, more research needs to be conducted to determine at what point of forest regeneration microclimate and habitat variables are restored to interior forest conditions. This will help managers to determine the matrix age which is necessary to minimize edge effects over the long-term.

In comparison to patches with anthropogenic edges, patches containing natural edges provided the highest availability of potential nesting habitat for marbled murrelets. In addition, at Desolation Sound, other studies show that murrelets prefer to use these patches for nesting habitat (Zhankov et al. 2006). Therefore, old-growth forest patches containing suitable natural edges such as stream channels and avalanche chutes should

be preserved wherever possible. These patches need to be maintained at sufficient sizes so that anthropogenic edge effects caused by adjacent forest harvesting have minimal effects on murrelet habitat availability. This will maintain “cores” of habitat in the landscape that provide high densities of potential marbled murrelet nest sites.

3.6 Tables and Figures

Table 3.1. Significance of effects of microclimate variables in edge and interior plots in hard, soft, and natural-edged patches in the Nimpkish Valley, British Columbia.

Temperature	DF	F	P
Temperature			
Edge proximity	30	9.47	0.004
Edge-type	28	0.96	0.394
Date	30	57.16	<.0001
Date x Edge proximity	30	8.00	0.008
Maximum Temperature			
Edge proximity	31	0.98	0.330
Edge-type	28	0.9	0.420
Date	31	8.05	0.008
Minimum Temperature			
Edge proximity	30	5.74	0.023
Edge-type	28	0.59	0.561
Date	30	121.28	<.0001
Date x Edge proximity	30	5.29	0.029
Relative Humidity			
Edge proximity	24	0.03	0.858
Edge-type	21	2.49	0.107
Date	24	23.82	<.0001
Vapor Pressure Deficit			
Edge proximity	24	0.09	0.772
Edge-type	21	13.11	<0.001
Date	24	5.01	0.035

Table 3.2. Mean values (± 1 standard error) of microclimate variables between early (May 31 – June 10) and late (July 2 – July 11) sampling periods, and between edge and interior habitats in the Nimpkish Valley, B.C., 2007.

Variables	Mean Values			
	<i>Early</i>		<i>Late</i>	
	Edge	Interior	Edge	Interior
Temperature	9.6 \pm 0.25	9.09 \pm 0.25	11.78 \pm 0.29	11.77 \pm 0.27
Minimum Temperature	4.22 \pm 0.19	3.92 \pm 0.19	6.99 \pm 0.2	7.11 \pm 0.16
Maximum Temperature	19.21 \pm 0.58		22.73 \pm 0.97	
Relative Humidity	86.21 \pm 0.47		91.34 \pm 0.76	
Vapour Pressure Deficit	8.16 \pm 0.86		5.55 \pm 0.7	

Table 3.3. Significance of effects of habitat variables in edge and interior plots in hard, soft, and natural-edged patches in the Nimpkish Valley and around Desolation Sound, British Columbia.

Effect	Df	F	P
Platform Density			
Edge proximity	46	4.2	0.046
Edge-type	47	4.42	0.017
Region	47	0.94	0.337
Edge proximity x Edge-type	46	2.47	0.096
Platform Tree Density			
Edge proximity	48	6.63	0.013
Edge-type	47	4.87	0.012
Region	47	0.01	0.942
Epiphyte Cover			
Edge proximity	48	3.24	0.078
Edge-type	47	2.97	0.061
Region	47	2.41	0.128
Epiphyte Thickness			
Edge proximity	48	0.01	0.933
Edge-type	47	4.72	0.014
Region	47	4.79	0.034

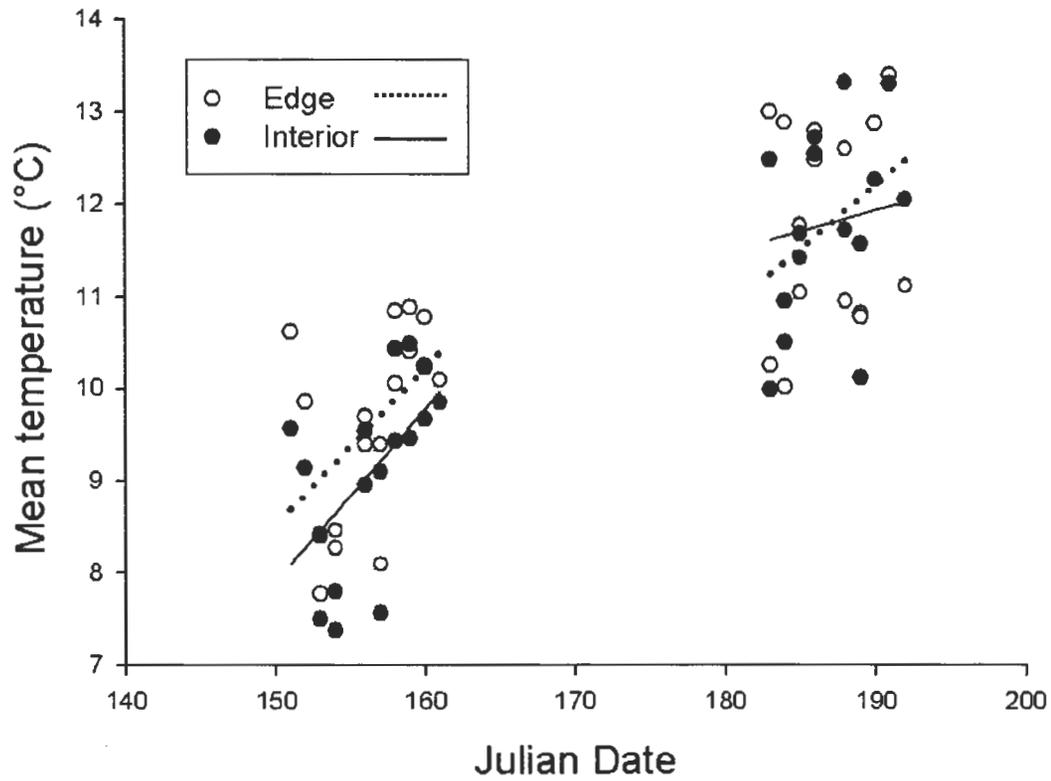


Figure 3.1. Change with time of mean temperature (°C), at nest sites in patch edges and interiors, in the Nimpkish Valley, British Columbia. Regression lines are plotted separately for edge and interiors both early and late in the season (151-161, and 183-192 julian dates, respectively).

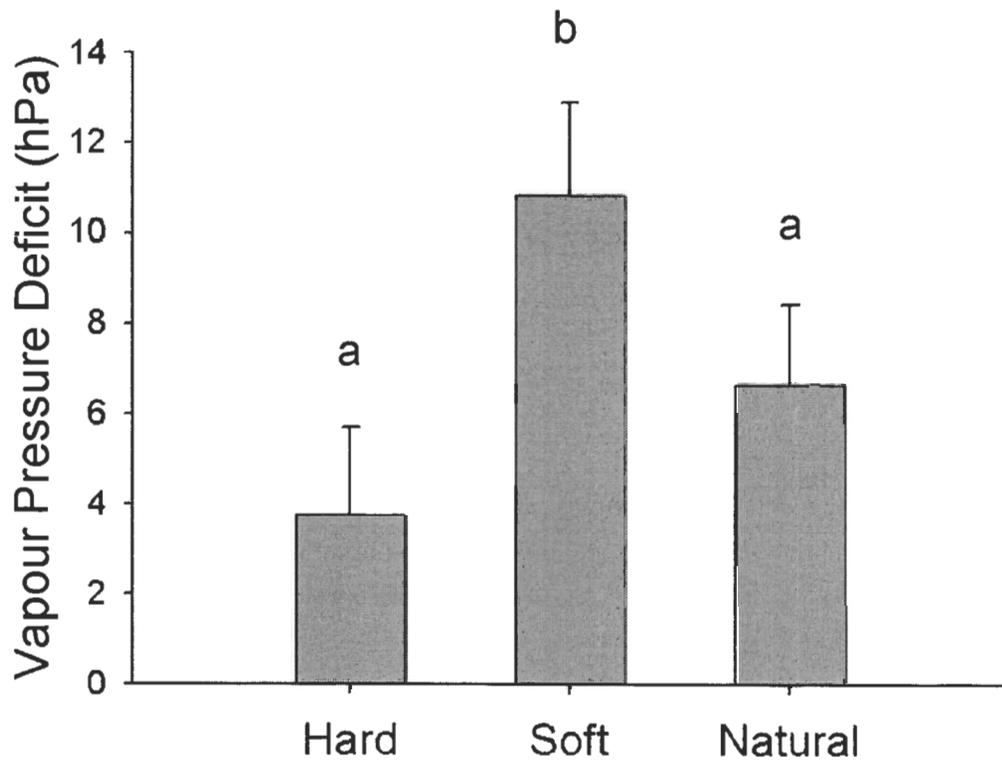


Figure 3.2. Vapour Pressure Deficit (least-squared means \pm 95% confidence limits) of artificial nest sites in hard, soft, and natural-edged patches in the Nimpkish Valley, British Columbia (values include both edges and interiors). Different letters represent significant post-hoc tests at $\alpha = 0.05$.

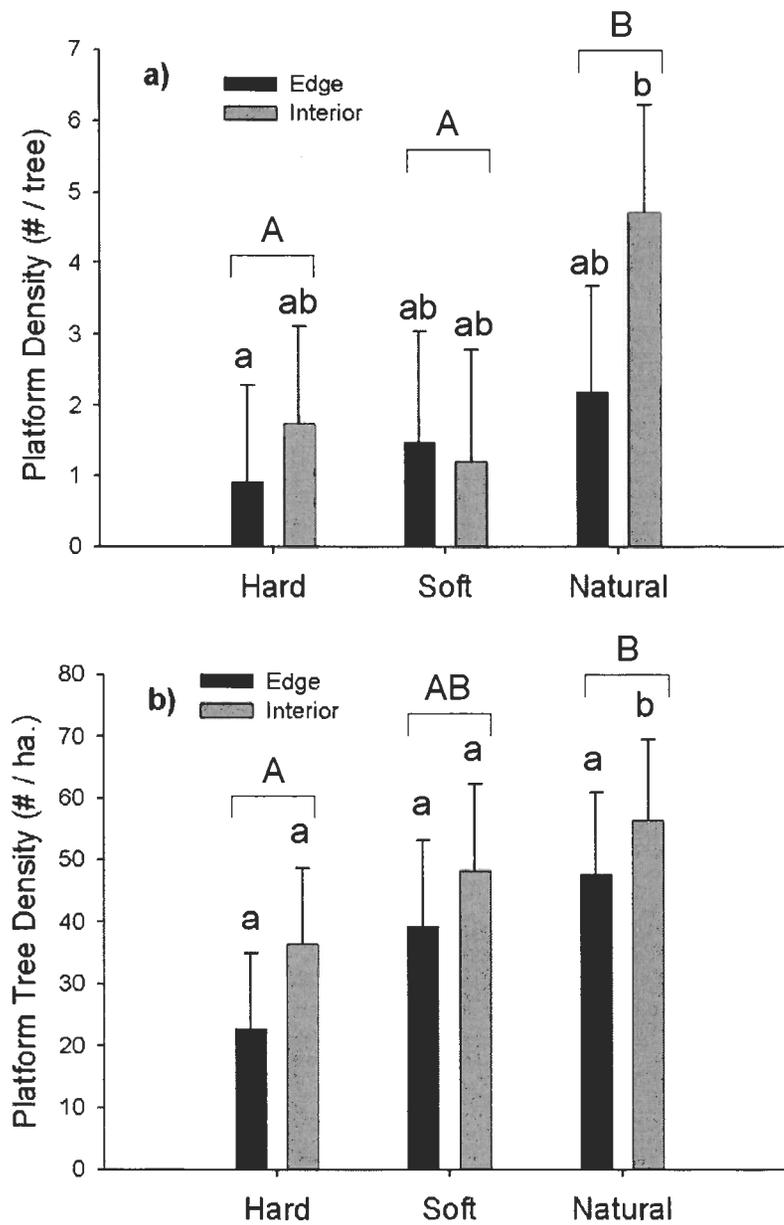


Figure 3.3. (a) Density of marbled murrelet nest platforms per tree, and (b) density of trees with at least one nest platform, in plots at edges and interiors of patches with hard, soft, and natural edge-types, in the Nimpkish Valley and Desolation Sound, British Columbia. Values are least-squared means \pm 95% confidence limits, and different letters represent significant post-hoc tests at $\alpha = 0.05$.

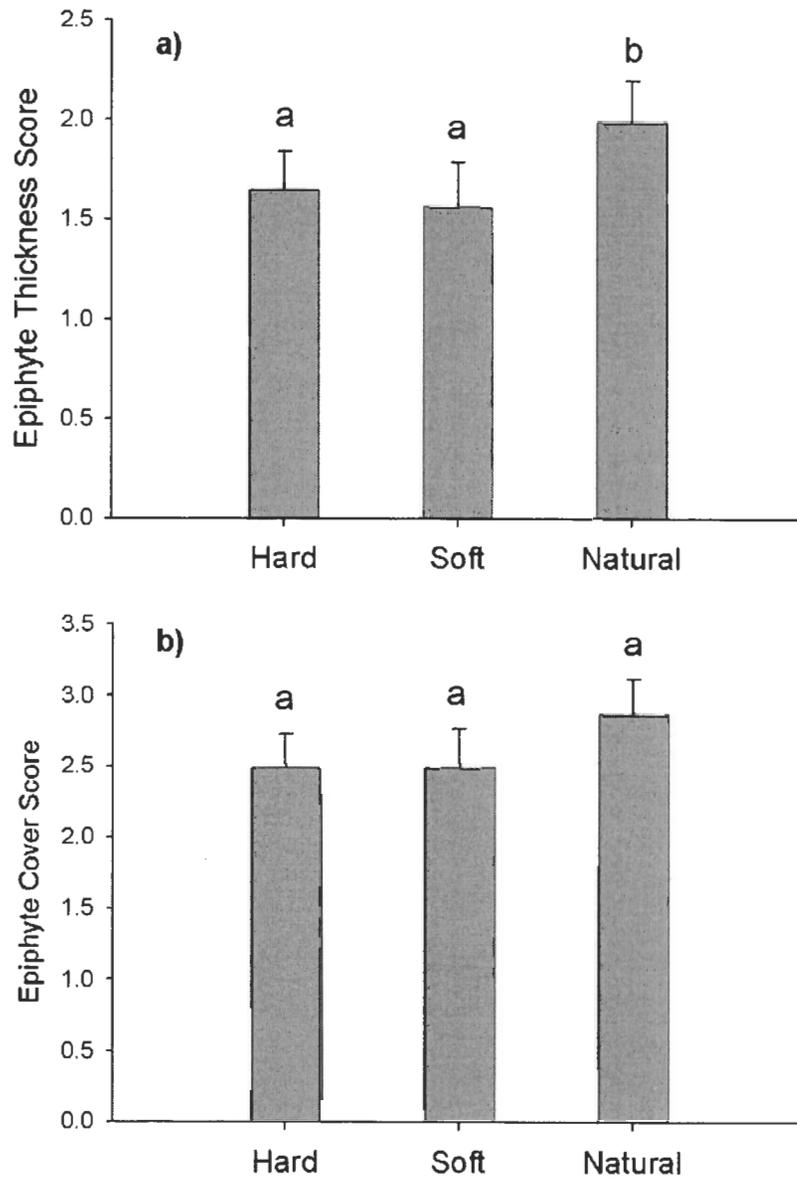


Figure 3.4. (a) Epiphyte thickness score and (b) epiphyte cover score of canopy trees in plots at patches with hard, soft, and natural edge-types, in the Nimpkish Valley and Desolation Sound, British Columbia (values include both edges and interiors). Values are least-squared means \pm 95% confidence limits, and different letters represent significant post-hoc tests at $\alpha = 0.05$.

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.
- Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225-255 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, UK.
- Batáry, P., and A. Báldi 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* **18**:389-400.
- Bates, J. W. 1992. Mineral nutrient acquisition and retention by bryophytes. *Journal of Bryology* **17**:223-240.
- Becker, B. H., M. Z. Peery, and S. R. Beissinger. 2007. Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Marine Ecology Progress Series* **329**:267-279.
- Bloxton, T. D., and M. G. Raphael. 2006. Breeding ecology of the marbled murrelet in Washington State. 2005 Season Summary. Pacific Northwest Research Station, Olympia, Washington.
- Bradley, J. E., and J. M. Marzluff. 2003. Rodents as nest predators: influences on predator behavior and consequences to nesting birds. *The Auk* **120**:1180-1187.
- Bradley, R. W. 2002. Breeding ecology of radio-marked marbled murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. M.Sc. Thesis. Simon Fraser University, Burnaby, B.C.
- Bradley, R. W., F. Cooke, L. W. Loughheed, and W. S. Boyd. 2004. Inferring breeding success through radiotelemetry in the marbled murrelet. *Journal of Wildlife Management* **68**:318-331.
- Bryant, A. A. 1994. Montane alternative silvicultural systems (MASS): pre-treatment breeding bird communities. Canada-British Columbia Partnership Agreement on Forest Resources Development: FRDA II. Canadian Forest Service and British Columbia Ministry of Forests, Victoria, B.C.
- Burger, A., T. A. Chatwin, S. A. Cullen, N. P. Holmes, I. A. Manley, M. H. Mather, B. K. Schroeder, J. D. Steventon, J. E. Duncan, P. Arcese, and E. Selak. 2004. Application of radar surveys in the management of nesting habitat of marbled murrelets *Brachyramphus Marmoratus*. *Marine Ornithology* **32**:1-11.
- 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 No. 387. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

- 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.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference*. Springer, New York, New York, USA.
- Busby, J. R., L. C. Bliss, and C. D. Hamilton. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecological Monographs* **48**:95-110.
- 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.
- Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas Fir forests. *Ecological Applications* **2**:387-396.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-Fir forests. *Ecological Applications* **5**:74-86.
- Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. *Bioscience* **49**:288-297.
- CMMRT. 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 No. 1.
- Conroy, C. J., V. Bahn, M. S. Rodway, L. Ainsworth, and D. Newsom. 2002. Estimating nest densities for marbled murrelets in three habitat suitability categories in the Ursus Valley, Clayoquot Sound. *in* A. E. Burger and T. A. Chatwin, editors. *Multi-scale studies of populations, distribution and the habitat associations of marbled murrelets in Clayoquot Sound, British Columbia*. Ministry of Water, Land, and Air Protection, Victoria, B.C.
- 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**.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.
- Driscoll, M. J. L., and T. M. Donovan. 2004. Landscape context moderates edge effects: nesting success of wood thrushes in central New York. *Conservation Biology* **18**:1330-1338.
- Esseen, P.-A. 2006. Edge influence on the old-growth forest indicator lichen *Alectoria sarmentosa* in natural ecotones. *Journal of Vegetation Science* **17**:185-194.

- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603-610.
- Fenton, N. J., and K. A. Frego. 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. *Biological Conservation* **122**:417-430.
- 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.
- Glime, J. M. 1978. Insect utilization of bryophytes. *Bryologist* **81**:186-187.
- Gray, L. J. 1993. Responses of insectivores birds to emerging aquatic insects in a riparian habitat of a tallgrass prairie stream. *American Midland Naturalist* **129**:288-300.
- Hamer, T., and D. J. Meekins. 1999. Marbled murrelet nest site selection in relation to habitat characteristics in western Washington, 1998 report. Hamer Environmental, Mount Vernon, WA.
- Hannon, S. J., and S. E. Cotterill. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. *Auk* **115**:16-25.
- 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.
- Harper, W. L., and B. K. Schroeder. 2004. Long-term radar monitoring of marbled murrelet populations in the Nimpkish Valley, Vancouver Island: 2003 progress report. Canadian Forest Products, unpublished report.
- 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. Unpublished report. Department of Wildlife, Humboldt State University, Arcata, California.
- Hylander, K. 2005. Aspect modifies the magnitude of edge effects bryophyte growth in boreal forests. *Journal of Applied Ecology* **42**.
- Hylander, K., M. Dynesius, B. G. Jonsson, and C. Nilsson. 2005. Substrate form determines the fate of bryophytes in riparian buffer strips. *Ecological Applications* **15**:674-688.
- Hylander, K., B. G. Jonsson, and C. Nilsson. 2002. Evaluating buffer strips along boreal streams using bryophytes as indicators. *Ecological Applications* **12**:797-806.
- Ibarzabal, J., and A. Desrochers. 2004. A nest predator's view of a managed forest: gray jay (*Perisoreus canadensis*) movement patterns in response to forest edges. *The Auk* **121**:162-169.
- Jonsson, B. G. 1997. Riparian bryophyte vegetation in the Cascade mountain range, Northwest USA: patterns at different spatial scales. *Canadian Journal of Botany* **75**:744-761.
- Klinka, K., J. Pojar, and D. V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. *Northwest Science* **65**:32-47.

- Lahiti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* **99**:365-374.
- Legendre, P., and L. Legendre. 1988. *Numerical Ecology*. Elsevier Science, Amsterdam, The Netherlands.
- 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.
- Longton, R. E. 1990. Bryophytes in terrestrial ecosystems. *Botanical Journal of Linnean Society* **104**:1.
- 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.
- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* **138**:298-307.
- Manley, I. A. 1999. Behaviour and habitat selection of marbled murrelets nesting on the Sunshine Coast. M.Sc. Thesis. Simon Fraser University, Burnaby, B.C.
- Manley, I. A., and K. Nelson. 1999. Habitat characteristics associated with nest success and predation at marbled murrelet tree nests (Abstract). *Pacific Seabirds* **26**:40.
- Marzluff, J. M., J. J. Millsbaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Stellar'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 155-170 in J. L. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. *Forest fragmentation: wildlife and management implications*. Brill Academic Publishers, Brill, Leiden.
- Masselink, N. M. 2001. Responses by Stellar's Jays to forest fragmentation on southwest Vancouver Island and potential impacts on marbled murrelets. M.Sc. Thesis. University of Victoria, Victoria, B.C.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* **66**:185-194.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. *Fragstats: spatial pattern analysis program for categorical maps*, University of Massachusetts, Amherst, USA.
- McShane, C., T. Hamer, H. Carter, G. Swartzman, D. Friesen, D. Ainley, R. Tressler, K. Nelson, A. Burger, L. Spear, T. Mohagen, R. Martin, L. Henkel, K. Prindle, C. Strong, and J. Keany. 2004. Evaluation report for the 5-year status review of the marbled murrelet in Washington, Oregon and California. Unpublished report.

- EDAW, Inc. Seattle, Washington. Prepared for the U.S. Fish and Wildlife Service, Region 1. Portland, Oregon.
- Meyer, C. B., and S. L. Miller. 2002. Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. *Conservation Biology* **16**:755-766.
- Meyer, C. B., S. L. Miller, and C. J. Ralph. 2002. Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas on the U.S. west coast. *Landscape Ecology* **17**:95-115.
- Muir, P. S., T. R. Rambo, R. W. Kimmerer, and D. B. Keon. 2006. Influence of overstory removal on growth of epiphytic mosses and lichens in Western Oregon. *Ecological Applications* **16**:1207-1221.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**:58-62.
- Nelson, K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). in A. Poole and F. Gill, editors. *Birds of North America*, No. 276. Academy of Natural Sciences, Philadelphia.
- 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, J. G.L. Hunt, M. G. Raphael, and J. F. Piatt, editors. *Ecology and conservation of the Marbled Murrelet*. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.
- Nelson, S. K., and A. K. Wilson. 1999. Marbled murrelet habitat characteristics on state lands in western Oregon. Oregon Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR.
- O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. *Ecology* **75**:1582-1592.
- 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., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications* **16**:1516-1528.
- Peery, M. Z., S. R. Beissinger, S. H. Newman, B. H. Becker, E. Burkett, and T. D. Williams. 2004a. Individual and temporal variation in inland flight behavior of marbled murrelets: implications for population monitoring. *Condor* **106**:344-353.
- Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams. 2004b. Applying the declining population paradigm: diagnosing causes of poor reproduction in the Marbled Murrelet. *Conservation Biology* **18**:1088-1098.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **135**:652-661.
- Ralph, C. J., R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-144, Pacific Southwest Research Station, Forest Service, U. S. Department of Agriculture., Albany, CA.

- Ralph, C. J., J. R. Sauer, and S. Droege. 1995. Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. Pacific Southwest Research Station, Forest Service, U.S. Dept. Agriculture, Albany, CA.
- Raphael, M. G. 2006. Conservation of the marbled murrelet under the Northwest Forest Plan. *Conservation Biology* **20**:297-305.
- 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., J. Fletcher, R.J., 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. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* **66**:634-640.
- 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.
- Rodway, M. S., and H. M. Regehr. 2002. Inland activity and forest structural characteristics as indicators of marbled murrelet nesting habitat in Clayoquot Sound. *in* A. E. Burger and T. A. Chatwin, editors. Multi-scale studies of populations, distribution and the habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. Ministry of Water, Land, and Air Protection, Victoria, B.C.
- SAS. 2003. SAS 9.1 for Windows. SAS Institute Inc., Cary, NC.
- Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology* **79**:2391-2402.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**:688.
- Singer, S. W., N. L. Naslund, S. A. Singer, and C. J. Ralph. 1991. Discovery and observations of two tree nests of the marbled murrelet. *Condor* **93**:330-339.
- Sisk, T. D., and J. Battin. 2002. Habitat edges in avian ecology: geographic patterns and insights for western landscapes. *Studies in Avian Biology* **22**:30-48.
- Stewart, K. J., and A. U. Mallik. 2006. Bryophyte responses to microclimate edge effects across riparian buffers. *Ecological Applications* **16**:1474-1486.
- Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conservation Biology* **11**:928-935.

- Sullivan, B. D. 1991. Additional vertebrate prey items of the red squirrel, *Tamiasciurus hudsonicus*. *Canadian Field-Naturalist* **105**:398-399.
- Tewksbury, J. J., L. Gamer, 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 III, F. R., 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.
- Tranquilla, L. M., T. D. Williams, and F. Cooke. 2003. Using vitellogenin to identify interannual variation in breeding chronology of marbled murrelets (*Brachyramphus marmoratus*). *Auk* **120**:512-521.
- 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.
- Vitz, A. C., and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* **127**:477-474 478 476.
- Waterhouse, F. L., R. Bradley, F. Markila, F. Cooke, and L. Lougheed. 2002. Use of airphotos to identify, describe, and manage forest structure of marbled murrelet nesting habitat at a coastal British Columbia site. Technical Report TR-016, Research Section, Vancouver Forest Region, BC Ministry of Forests, Nanaimo, BC.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**:1083-1100.
- 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. *in press*. 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*.
- 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.