Ecology and Conservation of Marbled Murrelets on the Western Olympic Peninsula: Temporal and Spatial Variation in Inland Activity and Implications for Forest Management

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Abstract

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Washington Department of Natural Resources (DNR) manages 110,000 ha of state forests on the western Olympic Peninsula for conservation and commercial objectives. These forests support widespread activity of the threatened, forest-nesting Marbled Murrelet (*Brachyramphus marmoratus*). I studied 4,748 surveys, conducted 1994-2001 in 16,000 ha of DNR-managed late-seral forests, to understand how murrelet activity varied temporally and with landscape characteristics. Activity varied at daily, seasonal, and annual scales. Weather had weak, inconsistent influences on daily activity. Seasonal activity correlated with survey date and peaked in mid-season. Annual activity declined over time and was correlated with ocean conditions, negatively with surface temperatures and positively with upwelling. I described temporal variability quantitatively to predict date-specific activity. Using observed deviations from those predictions, I calculated continuous probability density functions at 3 spatial scales representing competing hypotheses regarding the scale of murrelet responses. Multiple *a priori* models reflected hypotheses about murrelet responses to the characteristics and abundance of late-seral and interior forests, edge-contrast, and compositional diversity of landscapes. Cell-based modeling related murrelet activity to landscape characteristics indexed at multiple scales, models were judged by fit and parsimony. Addition of early-seral forest covariates to the best of those models evaluated hypotheses about murrelet responses to fragmentation. Murrelets responded to landscapes at the 50-ha scale.

Activity increased with the abundance of old-growth and other late-seral forests at the 200-m and 400-m scales respectively, without influence from their broader-scale abundance. Activity increased with edge-contrast and early-seral forests in the presence of locally abundant late-seral forests. This suggests marbled murrelets can tolerate substantial fragmentation and that habitat management at relatively fine scales may provide conservation benefits. I modeled marbled murrelet populations to provide an explicit, consistent framework to evaluate relationships between population processes and forest management under a prospective conservation strategy for DNR-managed lands in coastal Washington. The murrelet population on the western Olympic Peninsula appears more secure than that in southwestern Washington. The landscape context of potential murrelet nest sites strongly influenced their ability to contribute to stable populations and should be a focus of conservation-oriented management. Forest management can successfully integrate marbled murrelet conservation with other objectives.

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Chapter 1. Temporal Variability of Marbled Murrelet Activity in Old-growth Forests

Marbled murrelets are seabirds that forage in nearshore marine waters and fly tens of kilometers inland to nest on large trees characteristic of Pacific Northwest coastal forests. They are unique among alcids for their inland, tree-nesting habit (Nelson 1997, Gaston and Jones 1998). Range-wide, populations are believed to be declining in large part because logging has reduced the quantity and quality of their nesting habitat in coastal old-growth forests (Rodway et al. 1992, Piatt and Naslund 1995, U.S. Fish and Wildlife Service 1997). Declines led to the species listing as threatened in Washington, Oregon, and California under the U.S. Endangered Species Act (ESA) in 1992. Numerous studies of murrelet inland distribution and habitat use have been conducted since the late 1980s generally following an evolving point-count protocol that provided consistent methods to document presence or absence, and record and interpret behavior (Paton et al. 1990, Ralph et al. 1994, Evans Mack et al. 2003). These inland surveys are the basis for much of our current understanding of marbled murrelet forest habitat relationships.

The metric recorded during inland murrelet surveys is the "detection", defined as "the sighting or hearing of one or more birds acting in a similar manner and initially occurring at the same time" (Evans Mack et al. 2003). Acoustic detections (of calling birds) dominate the inland survey data because the small, dark, crepuscular, fast-flying murrelets are difficult to see in their dense, coastal-forest habitat. When possible, detections are classified based on interpretations of the bird's behavior - with “subcanopy behaviors”, defined as flights or landings at or below treetop level, being used to indicate that survey areas are “occupied”. Although numbers and breeding activity of murrelets can not be determined from inland surveys (Paton 1995), it is assumed that occupied areas are used by murrelets for nesting or other purposes essential to their life history (Evans Mack et al. 2003). Unoccupied survey areas are further classified as having “presence”, where murrelets were detected, or “probable absence” (Evans Mack et al. 2003). Inferences about murrelet habitat relationships have been based on comparisons of environmental characteristics between occupied and random or unoccupied sites (Grenier and Nelson 1995, Hamer 1995); occupied, presence, and absence sites (Miller and Ralph 1995, Raphael et al. 1995); and sites varying in murrelet activity (Kuletz et al. 1995, Rodway and Regehr 2002).

Inland surveys for marbled murrelets record substantial variation in activity levels at several temporal scales (O’Donnell et al. 1995, Jodice and Collopy 2000, Rodway and Regehr 2002). This variability appears to be influenced by phenomena other than murrelets’ responses to their inland habitat, including: interannual differences in breeding effort and other inland activity, within-season variability apparently related to breeding and other behavioral phenology, and day-to-day variability due to weather, at-sea foraging patterns, and a variety of observer effects including the inability of audio-visual observers to detect most of the murrelets recorded on radar as actually present at inland sites (Jodice and Collopy 2000, Burger 2001, Smith and Harke 2001, Cooper and Blaha 2002). However, specific patterns and mechanisms of this extrinsic variability are poorly understood, which reduces the utility of inland survey data for conservation purposes (Jodice et al. 2001, Smith and Harke 2001). Increasing our understanding of murrelet inland activity would improve the value of these data for planning, implementing, and monitoring conservation programs.

The Washington State Department of Natural Resources (DNR) manages 850,000 ha of forested State Trust Lands for the financial support of public beneficiaries, with approximately 500,000 ha in the inland range of the marbled murrelet (DNR, 1997, DNR 2006). Management of these state forests is authorized as compliant with the ESA if conducted according to terms of a multi-species Habitat Conservation Plan (HCP) agreed upon by DNR and U.S. Fish and Wildlife Service (DNR 1997). The marbled murrelet portion of the HCP is being implemented in a stepwise, interim approach that serves to focus knowledge and conservation measures while leading to a long-term strategy. Inland murrelet surveys in state forests have been a central component of this approach. Here I study some of those surveys retrospectively, with the broad objective of improving their value for informing land-management decisions important to murrelet conservation. I explored relationships among a variety of activity metrics to identify those that were most informative, investigated variability in those indices at 3 temporal scales (daily, seasonal, and annual), and investigated mechanistic explanations for the temporal patterns.

Methods

Study area -- I studied murrelet surveys from the Olympic Experimental State Forest (OESF), a DNR-managed forest on the western Olympic Peninsula, Washington, USA (Figure 1.1). The 110,000 ha OESF is west of the Olympic Mountains and spans coastal plain to mountain landforms and elevations of 35-1,020 m, with most land between 100 and 850 m. Climate is moist and maritime, with approximately 340 cm of annual precipitation. Forests at lower, middle, and higher elevations are in the *Picea sitchensis* (Sitka spruce), *Tsuga heterophylla* (western hemlock), and *Abies amabilis* (Pacific silver fir) Zones respectively (Franklin and Dyrness 1988). The OESF is managed as a sustainable commercial forest and is within a larger landscape (526,000 ha as defined by watersheds, Figure 1.1) of mostly (58%) commercial forests, with Olympic National Park, a wilderness area, and Olympic National Forest, which is currently managed to maintain or restore late-successional forests (U.S. Department of Agriculture and U.S. Department of the Interior 1994), comprising the remaining 29% and 12%, respectively.

Murrelet survey sites -- In 1994 as part of the HCP planning process, DNR initiated a prospective, 2-year study designed to provide an empirical definition of murrelet habitat, specific to the OESF, that used forest inventory and other geographic characteristics. This definition was to be based on characteristics of sites most likely to be occupied by murrelets (Washington State Department of Natural Resources 1997). Accordingly, DNR surveyed murrelets, following Ralph et al. (1994) at 54 sites that represented a gradient of forest structural complexity and age, and the available range of distances from marine waters (2-38 km). My preliminary analyses of that study (unpublished) suggested old, complex-structured forests were most likely to be occupied. DNR moved to initiate inland surveys in those areas of the OESF in advance of the empirical definition, anticipating the HCP agreement that was then being developed and the substantial work involved in comprehensive murrelet surveys in these forests.

I used DNR's GIS-based forest inventory, photo-interpretation, and field visits to identify murrelet survey sites. These were in older stands ≥8 ha, with fairly compact shapes (e.g., excluding riparian leave areas) that originated after natural disturbances and would be described as "old-growth" or mixed-age stands with a significant old-growth component, largely in the vertical or horizontal diversification stages of Franklin et al. (2002). I also included 31 sites with similar structure from the 1994 study. Much of the area to be surveyed was in large, irregularly-shaped patches (Figure 1.1). These were subdivided into survey sites following Ralph et al. (1994), that averaged 26 ha. Survey stations (mode = 5 per site) were planned using interpretation of stereo aerial photography and GIS, then established in the field using orienteering techniques (Evans Mack et al. 2003). Average area covered by survey stations was 7 ha.

Murrelet surveys -- Surveys were conducted from 1994 to 2001 according to the protocol described by Ralph et al. (1994) or its then-current update. DNR planned a minimum of 5 survey visits per year to each site, from 45 min before to 75 min after sunrise, between 1 May and 5 August, over 2 consecutive years to meet this protocol. In order to meet HCP objectives in a more economical manner, DNR employed a stopping rule for surveys conducted between 1996 and 2001. Surveys were discontinued at sites where subcanopy behavior was detected, thus fewer than the planned numbers of visits were conducted at many of those sites. I applied this stopping rule *post hoc* to data from 1994-1995 surveys, so they were truncated following visits where subcanopy behaviors were detected. Surveys were conducted by over 50 field biologists trained and certified according to Ralph et al. (1994). I implemented a process of field oversight and 3 levels of data review to further assure consistent results of high quality.

Exploratory analyses -- Much of this study consisted of exploratory analyses in which I searched for temporal patterns within the context of scientific models, i.e., “descriptions of how nature might work” (Hilborn and Mangel 1997). These models reflected general interpretations or hypotheses of marbled murrelet or alcid biology (Nelson 1997, Gaston and Jones 1998), and differed for analyses at each temporal scale. I explored weather as the process affecting daily variation in activity (Naslund and O’Donnell 1995) and considered other influences, including observational uncertainty, as background noise. I considered seasonal variation to be influenced by phenological patterns of behavior based on the calendar (O’Donnell et al. 1995), with possible influences of annual events on seasonal patterns. I considered marine influences on murrelet nutritional status (Ainley et al. 1995) and the passage of time (Beissinger and Nur 1997) as potential influences on annual activity.

Exploratory analyses risk finding effects that are spurious, particularly if objectives are ambiguous, sample size is small relative to numbers of parameters being estimated, data are complex relative to guiding biological theory, or “data dredging” is employed, i.e., data- rather than theory-based, hierarchical analyses (Anderson et al. 2001). But DNR was faced with the need to improve forest management for murrelet conservation with incomplete knowledge. Thus I sought patterns in these existing data, which I could propose as biologically reasonable hypotheses to aid management decisions, subject to further investigation in a program of adaptive management (Walters 1986). My principle approach was to search for patterns based on a limited set of simple, plausible biological models, using limited numbers of independent variables, and to inspect data plots rather than rely exclusively on statistical tests (Tukey 1980, Hilborn and Mangel 1997).

Activity indices -- I examined correlations among numbers of detections of different types per survey, based only on surveys with detections ($n = 1{,}614$): all detections, subcanopy detections, visual only, vocal only, both visual and vocal, with a visual component, and with a vocal component. I considered correlations significant if $p < 0.001$ because I wanted a conservative approach with such a large data set. I used logistic regression to examine the relationship of survey site status, a binary response, i.e., occupied or not, with murrelet activity indices. I examined the fit of logistic regression models with the deviance (D), which follows the chi-square distribution with degrees of freedom = n - (1 + number of parameters), and the Hosmer-Lemeshow goodness of fit statistic ($\hat{C}$) which also follows the chi-square distribution (Hosmer and Lemeshow 2000).

Temporal variation in activity.—Other authors have examined daily variation in activity relative to summarized weather conditions during each days' survey (Jodice and Collopy 2000, Rodway and Regehr 2002). I employed a different approach, based on results of preliminary analyses (Horton and Harrison 2001), in which I categorized observations of murrelet activity according to coincident, observer-defined weather conditions for ceiling height, percent cloud cover, and presence of fog or rain (Evans

Mack et al. 2001). Then I assessed observed versus expected activity under the null hypothesis of no influence of each of those elements of weather using chi-square tests. I computed predicted numbers of detections under the null hypotheses and compared them directly to observations in order to consider the biological, rather than statistical, significance of the departures from expectations.

I computed 3 indices for assessing seasonal influences on activity. For each date in the 97-day survey season over all surveys and years, I computed 1) the average numbers of detections per survey, detection rate or NDET, and 2) the proportion of surveys with detections, PWITH. I computed 3) average numbers of detections per survey, just for surveys with detections (WDET). I used survey date, represented as a series from 1 to 97, as the independent variable in polynomial regression analyses to fit curves to seasonal patterns in those activity indices. I applied the arcsine transformation to the proportion of surveys with murrelet activity for all regression analyses (Zar 1999, p. 278). I began with quadratic models and determined the maximum power of polynomial models using F tests to evaluate whether additional terms significantly improved their fit (Zar 1999, pp. 453-457). I chose a conservative $p < 0.01$ to allow additional terms in polynomial models because correlation among powers of the independent variable tends to improve fit merely due to multicollinearity (Zar 1999, p.457).

I used multiple linear regression to explore annual variability in murrelet activity. I computed the same 3 indices described above at an annual scale. For each of the 8 study-years I computed the average number of detections per survey, NDET; the proportion of surveys with detections, PWITH; and the numbers of detections just from surveys with detections, WDET. I hypothesized that sea surface temperatures (SST) and upwelling could influence marine processes important to murrelet foraging and nutritional status (Hunt 1995), and thus inland activity patterns. I obtained monthly average SST and SST anomalies for the coastal waters adjacent to the study area (http://coastwatch.pfel.noaa.gov/cgi-bin/elnino.cgi), and monthly upwelling index and anomaly values calculated for 48° N, 125° W (25 km offshore, http://www.pfeg.noaa.gov/products/PFEL). I averaged each parameter over consecutive 3-month periods that approximated the 4 seasons (e.g., winter: January, February, March) resulting in 16 variables that summarized characteristics of SST and upwelling during the 8-year study. I used calendar values for years (e.g., 1994, 1995) to represent the pasage of time. I reduced numbers of independent variables by examining a correlation matrix of oceanographic and murrelet activity indices, to exclude correlated independent variables or those not correlated with murrelet activity because I had potentially 17 independent variables with so few data ($n = 8$ years). I considered correlations with $p < 0.1$ to be significant at this step because that corresponded with a fairly strong linear relationship ($r > 0.6$). This data-based step in my process of model selection was consistent with my principle objective which was to find and describe patterns in the annual variability in murrelet activity indices that were based on plausible ecological mechanisms rather than to make inference about the ecological basis of that variability. I examined all subsets of the global model for each activity index, then selected and described the best models based on parsimony and fit, using Mallow's C_p

and the adjusted R^2 (R_{adj}^2, Zar 1999, pp. 429-433).

I conducted a nested analysis of variance, season nested within year, to assess the relative influence of the 3 temporal scales on variability in NDET. I represented seasonal effects by collapsing the 97-day survey season into 19 5-day periods with period 19 having 7 days. No surveys were conducted during 5 of the 152 period/year combinations, so I created 1 data point with the average seasonal value for each empty cell to enable this analysis.

Results

Murrelet surveys -- Field staff completed 4,748 protocol surveys at 2,463 survey stations comprising 631 sites (16,540 ha) from 1994 to 2001 (Table 1.1). Murrelets were detected during 1,614 (34%) of these surveys, which produced 7,555 total detections (6,592 of vocalizing birds, 1,440 murrelet sightings, and 689 of birds exhibiting subcanopy behavior). The median number of detections recorded during surveys with detections was 2, while 25% of those surveys recorded 5 or more detections up to a maximum of 72. Positive correlations existed among counts of each of the different detection types ($n = 1{,}614$, $0.32 < r < 0.98$, $p < 0.001$), including subcanopy with total detections ($r = 0.53$).

Activity indices -- Average number of total detections per survey, the detection rate or NDET, was a weak predictor of survey site status (occupied or not) at the 615 sites classified by protocol surveys ($D = 626.96$, $p[\chi^2_{613\text{ df}} > D] = 0.34$). This model predicted that the log of the odds of a site being occupied increased linearly with NDET, but model predictions did not fit the data well ($\hat{C} = 42.34$, d.f. = 8, $p < 0.001$). However, detection rate is the mathematical result of proportion of surveys with any detections (PWITH) and detections per survey just for surveys with detections (WDET), i.e., NDET = PWITH * WDET. These components of NDET index the consistency (PWITH) and intensity (WDET) of murrelet activity. Separately, PWITH and WDET contained more information than NDET about patterns of murrelet activity and were good predictors of site status, ($D = 550.98$, $P[\chi^2_{612\ \mathrm{df}} > D] = 0.96$), and model predictions fit the data better ($\hat{C} = 10.12$, d.f. = 8, $P = 0.256$). Thus, because detections per survey were the most abundant data and because they were correlated with the detection type (subcanopy behavior) generally agreed to be the most important indicator of murrelet habitat use, I used the detection rate, NDET, or its components, PWITH and WDET, to index murrelet activity in subsequent analyses.

Detection rates averaged 1.58 (CV = 306%) across the entire study ($n = 4{,}748$), while within-year CVs ranged from 219% to 403%. Coefficients of variation in NDET for 5-day periods across all years suggested increased variability early and late in the survey season (Figure 1.2). Annual ($P=0.03$) and season within year ($P<0.001$) effects contributed to variability in NDET (Table 1.2).

Day to day variability -- Murrelet activity deviated from expectations, based on the proportion of survey hours in different weather categories ($24 < \chi^2_{1\ \mathrm{df}} < 154$, $p < 0.001$). Murrelets were more active during periods where clouds created a low ceiling (at or below twice the height of the surrounding forest canopy), cloud cover was ∃90%, or fog was present. Reduced activity occurred during rainy periods. These analyses summarized approximately 9,500 survey hours and 7,500 detections, and found that observations deviated from expectations during: low-ceiling conditions when 140 (14%) more murrelet detections were recorded than expected; periods of ∃90% cloud cover, with 532 (12%) more detections than expected; foggy periods, with 296 (22%) more; and rainy periods with 217 (19%) fewer.

At least 10 surveys were conducted simultaneously from separate survey stations on 200 days (n surveys = 3,369) spread rather evenly across the survey season although mostly from the high effort years (Table 1.1, Figure 1.2), CVs of detection rates for those days averaged 200% and reflected the pattern from all surveys except in the last period, perhaps because only 2 days had 10 simultaneous surveys (Figure 1.2).

Seasonal variability -- Detection rates for each date of the 97-day survey season (average n surveys per date = 49.1, range 19 - 74) showed a pattern (Figure 1.3A) that was best described by a sixth-order polynomial relationship with survey date, $F_{6, 90} = 19.7$, $p < 0.001$, $R_{\mathrm{adj}}^2 = 0.54$. Both components of NDET contributed to this pattern: PWITH (Figure 1.3B) was described by a third-order polynomial, $F_{3, 93} = 31.5$, $p < 0.0001$, $R_{\mathrm{adj}}^2 = 0.49$; WDET by a fourth-order polynomial (Figure 1.3C), $F_{4, 92} = 21.1$, $p < 0.0001$, $R_{\mathrm{adj}}^2 = 0.46$. The consistency of murrelet activity varied less than its intensity across the survey season. Average PWITH over its 15-day peak (26 June - 11 July) was 50% greater than over its 15-day low (14 - 29 May, Figure 1.3B), while the peak in WDET (5 - 20 July) was 135% greater than its 18 May - 2 June low (Figure 1.3C).

Annual variability -- Correlations among oceanographic indices seemed to fall into 4 categories: 1) serial correlation between successive time periods such as fall and winter

SST; 2) related phenomena, such as the inverse correlation of summer upwelling and SST; 3) related indices, such as between SST and SST anomaly; and 4) inexplicably, likely due to chance. Upwelling and SST index and anomaly values were highly correlated so I did not include index and anomaly values as covariates in the same models. There were no linear temporal trends in any oceanographic variables ($n = 8$, $0.20 < p < 0.98$).

Seven correlations existed between annual averages of murrelet activity indices and oceanographic indices or year ($n = 8$, $0.62 < |r| < 0.80$, $0.02 < p < 0.10$). Detection rate was inversely related to the passage of time, while its components, PWITH and WDET, were correlated with the passage of time (negative), winter upwelling and upwelling anomaly (positive); and winter and summer SST and summer SST anomaly (negative) respectively. I developed additional independent variables from the interactions of summer and winter correlates of WDET, i.e., Summer SST*Winter SST and *Summer SST anomaly*Winter SST, because of their likely biological significance given marbled murrelet life history. I did not include interactions and their component terms in the same models because they were highly correlated. Thus, I constructed separate global models for PWITH that included either upwelling index or anomaly values, and time (Table 1.3). I formulated global models for WDET and NDET using oceanographic variables with univariate correlations, interactions, and time. I did not include index and anomaly covariates in the same models, nor did I include interactions with their component terms (Table 1.3).

Variability in the consistency of murrelet activity (arcsin-transformed PWITH) was best explained by a relationship with winter upwelling and time (Table 1.3, Figure 1.4). Intensity of murrelet activity was described by a relationship with summer SST anomaly and winter SST (Table 1.3, Figure 1.4). The best model describing variability in detection rates was a relationship with summer SST anomaly, winter upwelling anomaly, and time (Table 1.3, Figure 1.4), a hybrid of the models for its components.

Figure 1.4 illustrates that PWITH and WDET varied in parallel for the first 3 years of the study, then diverged so that for example, the second-highest WDET and the lowest PWITH combined in 1999 to result in a low NDET. Values of the 2 component indices were not correlated ($n = 8$, $r = 0.34$, $P = 0.41$). However there were 2 years, 1997 and 1999, in which these indices clearly diverged (Figure 1.4). Without 1997 and 1999, the indices tracked one another closely ($n = 6$, $r = 0.95$, $P = 0.004$).

Annual variability in seasonal patterns -- I investigated how seasonal patterns of PWITH and WDET varied between years to develop further insights about their relationships to murrelet life history. Inspection of average daily PWITH plotted across the survey season, with data from the 4 years of most consistent activity (1994, 96, 97, 2000, Figure 1.4) distinguished from the others, and best fit curves for those data, suggested that activity was more consistent throughout the season during high PWITH years (Figure 1.5A). A similar plot, with data classified by their occurrence in the 4 years of highest WDET (1994, 95, 96, 99, Figure 1.4) or not, suggested that a more pronounced late season activity peak distinguished the years of more intense activity (Figure 1.5B).

Discussion

Sources of Variability -- Estimates of murrelet activity from inland surveys contain variability due to biological processes that have both spatial and temporal components, as well as random variation and measurement error. I observed much greater relative variability in detection rates than has been reported in other studies, CV = 306% compared to, e.g., CV = 75% from 122 mid-July surveys at 25 stations over 6 years that recorded NDET = 23.34 in southeast Alaska (Smith and Harke 2001), CV = 61% (*n* = 572, NDET = 37.87) at 5 stations over 3 years in coastal Oregon (Jodice and Collopy 2000), and CV = 63% (*n* = 82, NDET = 46.44) at 2 stations during 1 year in the Queen Charlotte Islands (Rodway et al. 1993). Some of the greater variability I observed is due to the nature of the data, which likely follow a negative binomial distribution which has an intrinsic property of a higher CV with lower mean (Hilborn and Mangel 1997, p. 65). However, this study also encompassed greater spatial and temporal variability than those referenced above.

This study was based on surveys at 2,467 stations, 2 to 3 orders of magnitude greater than the others, and thus likely contained substantially greater variability in murrelet responses to varying forest characteristics. Additionally, the Oregon and Queen Charlotte studies were conducted at stations located in areas that were predetermined to have high, and presumably fairly consistent, levels of murrelet activity (Rodway et al. 1991, Jodice and Collopy 2000) unlike this and the Alaska study which were prospective inventory or sampling of broad landscapes and thus encompassed greater spatial variability. Season within year was predominant, followed by year to year variability as distinct temporal sources of variation in NDET in this study. All 3 other studies were of lesser duration, even the 6-year Alaska study was only 75% the length of this one and it surveyed only in mid-July, thereby avoiding much within-season variability. The stopping rule used in this study was an additional source of variability that could be classified as measurement, or sampling, error. It introduced a bias against repeating surveys in areas with more consistent and intense activity and thus contributed to a higher CV.

Biological Basis for Activity Indices -- It is evident that detection rate, NDET, is the mathematical result of the consistency, PWITH, and intensity, WDET, of murrelet activity and that patterns of variation in the component indices differ. I propose that PWITH, which indexes the spatial and temporal consistency in activity, i.e., the extent of broad-scale and regular visitation of inland sites, is influenced by the degree to which the surveyed population was establishing and attending nests. I offer WDET as an index to the interaction among numbers of murrelets and their vocal behavior, a phenomenon not necessarily linked with nest attendance.

Peery et al. (2004a) found that breeding, radio-tagged murrelets flew inland on over 80% of their sampling occasions, which spanned the inland survey season. Thus high PWITH years may occur when a greater proportion of the population is nesting as suggested by the season-long, more consistent activity during those years (Figure 1.5A). Murrelet vocal behavior is important to values of WDET because over 87% of all detections were of vocalizing birds. Intense vocal activity may result from courtship and nest prospecting by non-breeders (Nelson 1997) supplementing the activities of nesting murrelets, therefore high WDET years may result when high levels of social activity occur throughout the population. This is consistent with the much larger late season peak in intensity in those years (Figure 1.5B). Peery et al. (2004a) found 50% of their radio-tagged birds breeding in 2001 compared to 11% in 2000, thus I suggest that 2001 inland surveys in their study area would have recorded high PWITH. Approximately 2/3 of their behavioral samples of non-breeding murrelets that were physiologically in breeding condition showed inland flights in 2001 compared to about 1/4 in 2000, 2 of these 4 birds flew inland during the majority of their samples in 2001, presumably vocalizing while engaging in social activities, but only 1 of 8 did the same in 2000. These findings suggest that PWITH and WDET would have covaried during their 2-year study, and I found that PWITH and WDET covaried in 6 of 8 years in this study.

Daily variation -- The high levels of day-to-day and within-day variability in activity observed in this study were consistent with other findings (e.g., Naslund and O'Donnell 1995, Jodice and Collopy 2000). Relative variability increased at the end of the survey season (Figure 1.2) because less consistent activity increased variance in mean activity levels even relative to the overall lower activity in the late season (Figure 1.3).

Marbled murrelet activity has been reported to vary with daily weather (Naslund and O'Donnell 1995, Burger 2001, Cooper et al. 2001), and the PSG Protocol acknowledged this in its format for collecting weather data (Evans Mack et al. 2003). Rodway and Regehr (2002) found murrelet responses to be sufficiently consistent to support the use of a categorical weather variable, cloudy or clear, as a covariate in assessing relationships between murrelet activity, forest structure, and landform. In contrast, Jodice and Collopy (2000) concluded that variation in murrelet activity showed a weak and inconsistent relationship with weather. I propose that this study supports an intermediate position. Murrelet activity (or detectability) was greater during cloudy or foggy periods and diminished during rain. However, the relatively small deviations from expectations based on no response to weather (12 - 22%), compared with the high within-day variability I recorded from simultaneous surveys with similar weather (CV = 200%), suggests weather-related variability is best considered as background noise within these data.

Seasonal variation -- The seasonal pattern I observed was similar to those reported from inland surveys throughout the murrelet's range (e.g., O'Donnell et al. 1995, Rodway and Regehr 2002), with fairly constant early-season activity which increased from mid-June to a mid-July peak dropping rapidly to nearly no activity by early August. I propose that the higher-order variability suggested in Figure 1.3A is an artifact of the curve-fitting method, and that the general pattern is a better reflection of murrelet biology. This general pattern was also observed during radar monitoring on the Olympic Peninsula (Cooper et al. 2001) and so is due, at least in part, to an increase in actual numbers of murrelets visiting inland sites rather than to behavioral changes that lead to increased detectability. The activity peak has been attributed to an influx of subadults and other nonbreeders to inland sites (Nelson 1997), based on observations of similar behavior in other alcids (Gaston and Jones 1998). Bradley et al. (2002) found reduced overall levels of nest visitation by radio-tagged murrelets in July, which they offered as support for this hypothesis. However, Peery et al. (2004a) found no clear seasonal pattern to the frequent inland flights made by radio-tagged, non-breeding murrelets that were physiologically in breeding condition, and that murrelets not in breeding condition rarely flew inland.

I found that both consistency and intensity of activity contributed to the late season peak, but that the greatest contribution was from the over 2-fold increase in intensity. If intensity indexes the interaction among numbers of murrelets flying inland and their vocal behavior, then my observations are further support for the hypothesis that the activity peak results from social behavior of non-breeders because behavioral observations of murrelets attending nests (Manley 1999) and estimates of their energetic demands (Hull et al. 2001) suggest that breeders are unlikely to exhibit intense vocal behavior at this point in the nesting cycle.

Annual variation -- Annual average detection rates and consistency of activity varied with SST and upwelling, and declined over time during this study. Predicted NDET and PWITH, normalized to average SST and upwelling values, corresponded to 14% and 7% annual declines over the 8-year study. These were somewhat greater than the 4-7% population decline suggested by Beissinger and Nur (1997), and were observed during a period when no old-growth forests were harvested in the study area. Although relationships between numbers of murrelets and activity metrics are unknown, annual averages of PWITH and NDET are influenced by the spatial consistency of activity, which must relate to the abundance of murrelets in the forest. No temporal pattern was evident in WDET, consistent with the notion that murrelet behavior influences values of this index.

More direct estimates of murrelet populations on and around the Olympic Peninsula did not suggest a general decline in abundance during the latter parts of this study. Radar studies conducted 1998-2000 in 3 western Olympic Peninsula watersheds did not indicate declines (Raphael et al. 2002a), nor were they evident in breeding season population estimates from adjacent marine waters during 2000-2004 (Miller et al. 2006). Murrelets visiting old-growth forests in the OESF are likely a small fraction of those using Olympic Peninsula uplands. Murrelet numbers are correlated with the abundance of potential habitat at the watershed scale (Burger 2001, Raphael et al. 2002a) and the fragmented old-growth stands in the OESF comprise a small fraction of potential murrelet habitat on the Olympic Peninsula, most of which is in Olympic National Park or Olympic National Forest. Consistent, high levels of murrelet activity were found in the 370,000 ha Olympic National Park (Hall 2000), which contains much potential nesting habitat in an unfragmented, wilderness setting. It is plausible that the declining activity I observed is the consequence of breeding dispersal from lower to higher quality habitat (Greenwood and Harvey 1982), a notion that is consistent with the observation of an inverse relationship between murrelet activity in old-growth patches and the time since timber harvests in their neighborhoods (Meyer et al. 2002).

Alcid behavior and population biology have been widely observed to vary with ocean conditions, and mechanisms accounting for a variety of these relationships have been proposed and evaluated (e.g., Wilson and Manuwal 1986, Ainley et al. 1995, Bertram et al. 2001). Similar patterns and mechanisms have been proposed for marbled murrelets (Hunt 1995, Nelson 1997), but quantitative studies, particularly of oceanographic influences on inland behavior, are lacking. I observed strong covariation of murrelet activity with ocean conditions over the 8-year course of this study, activity was more consistent when winter upwelling indices were higher, and was more intense when winter and summer SSTs were lower. Coastal upwelling is a wind-driven phenomenon and wintertime prevailing winds along the Washington coast are southerly, producing onshore transport of surface waters with coastal downwelling which results in negative upwelling index values (Tomczak and Godfrey 2003). Thus consistent murrelet activity was associated with weaker winter downwelling, average winter upwelling for the 4 years of highest PWITH was -46 m^3 per second per 161 kilometers of coastline compared to -82 across the 8-year study. Marbled murrelets occur year-round off Washington's open coast, but it is likely that many individuals shift their winter range to protected inner waters (Nelson 1997), thus wintertime marine conditions on the Washington coast may not directly influence these birds. However, weaker winter downwelling appears to increase springtime biological productivity by reducing upper ocean stratification which allows optimal levels of light and nutrients to stimulate phytoplankton production (Polinova et al. 1995, Gargett 1997, Logerwell et al. 2003). This process was termed "winter preconditioning" by Logerwell et al. (2003), who found improved survival of tagged coho salmon (*Oncorhynchus kisutch*) smolts released following winters with weaker downwelling. Winter preconditioning could operate to improve the nutritional status of murrelets entering the breeding season, and thus the consistency of their inland activity, by increasing phytoplankton forage for planktonic copepods preyed upon by sand lance (*Ammodytes hexapterus*) that are primary prey for murrelets (Bertram et al. 2001, Mackas et al. 2001, Logerwell et al. 2003).

The intensity of murrelet activity varied inversely with winter and summer SSTs. I hypothesize that the interaction effect of winter and summer SST is due in part to a winter preconditioning effect of SST. Inverse relationships of many components of biological productivity with year-round SSTs in the northeast Pacific are widely recognized, e.g. McGowan et al. (1998). Lower spring and summer SSTs off the Washington and Oregon coasts have been associated with increased coho salmon survival by Cole (2000) and Ryding and Skalski (1999) who proposed mechanisms related to increased biological productivity promoted by seasonal upwelling that also has an inverse relationship with SST. This should also support a more abundant prey base for marbled murrelets, which I propose would, in concert with the effects of winter preconditioning, enable physiological conditions in a broad segment of the local population favorable for high-intensity inland activity, both breeding and social activity among non-breeders.

Examination of the 2 years (1997, 1999, Figure 1.4) in which PWITH and WDET diverged offers additional support for my hypotheses regarding mechanisms linking murrelet activity with ocean conditions, and regarding the biology of the indices. Observations of the lowest PWITH and second-highest WDET in 1999 were consistent with model predictions, as that year had very high winter downwelling (-144 m^3 per s per 161 km of coastline) which predicted the inconsistent activity and below normal winter and summer SSTs which predicted the high-intensity activity (Figure 1.4). The observed high value for PWITH in 1997 was 14% less than predicted by the low winter downwelling that year (-40 m^3 per s per 161 km of coastline) but the observed low-intensity activity was predicted by median winter and warm summer SSTs (Figure 1.4). I suggest that in 1999, lack of a winter preconditioning effect may have limited murrelet breeding thus consistent inland activity while the later development of favorable ocean conditions allowed high-intensity social activity which appeared during the large late season peak as was common to high WDET years (Figure 1.5B). The opposite pattern occurred in 1997, when I suggest that winter preconditioning promoted consistent inland activity which was later diminished by subsequently unfavorable ocean conditions so that the observed annual PWITH was less than predicted, while poor ocean conditions during the survey season limited the birds' nutritional status and participation in intense social activity. I propose that years when ocean conditions associated with high PWITH and WDET co-occur would be those in which murrelet fecundity was greatest because a greater proportion of the population would initiate breeding and ocean conditions would be favorable for maintaining the energy balance of adults and provisioning nestlings throughout the breeding season. During my 8-year study, there were only 2 such years.

Scope and Limitations -- Several qualities of these data support their use in this exploratory, retrospective study and lend credibility to the hypotheses I developed. The design controlled for many extrinsic sources of variability. Data were collected under a common protocol, and within forest stands of similar structural complexity. The study area was geographically discrete, and was subject to a common set of land uses and oceanographic processes. And the study was relatively long-term, and collected abundant data that were capable of showing broad patterns that might have been swamped by temporal and/or random variation in a smaller or less extensive data set. My findings provide a valuable adjunct to the information in the abundant inland survey data from the Olympic Peninsula, and can improve the effectiveness of forest management in a region important to murrelet conservation. The general consistency of these findings with range-wide murrelet activity patterns and biological responses to ocean conditions in the eastern Pacific suggests they have some generality. The concepts and methods of this study can, and should be applied more broadly and likely can provide similar increments to knowledge in other parts of the murrelets' range.

However, it is not appropriate to draw firm conclusions about marbled murrelet activity from this study, where data were not collected in a design intended to address questions about temporal variability (Jodice and Collopy 2000). Analyses were retrospective and primarily correlational, thus can not be used to determine cause and effect. Uneven distribution of effort among years could have caused chance events to unduly influence annual averages from years with relatively low effort. Non-random assignment of surveys across the study area could have influenced annual averages in unpredictable ways if spatial patterns in murrelet activity occurred at that scale. The stopping rule introduced a bias against data from sites with more consistent and intense activity. The murrelet activity I recorded was >85% vocal, so results are biased towards particular types of behavior. Finally, the generally limited understanding of the biological basis of activity observed during inland surveys did not allow specific inferences about murrelet life history.

Management Implications

Effective forest management that integrates commercial and conservation objectives requires better information on responses of marbled murrelet populations to stand and landscape conditions (Marzluff et al. 2000). Forest management can be better informed as to the influence of forest conditions, while monitoring and research programs need to distinguish responses to forests from those to other factors. Separating temporal variability due to marine processes and inherent life-cycle patterns from spatial variability due to murrelet responses to forests is essential to these efforts and to the information value of existing and future data. I propose a method to do that for inland survey data, based on the existence of clear temporal patterns, plausible biological mechanisms that explain the patterns, and the assumption that spatial variation in murrelet activity is independent of temporal variation. I illustrate this with the data and models presented here, and suggest that similar models be developed and applied to appropriate data sets from elsewhere in the murrelet's range. This approach will allow a clearer picture of the types of forest conditions that attract varying levels of murrelet activity, and thus suggest management pathways for effective, efficient conservation and restoration of murrelet habitat.

Two levels of temporal variation can be addressed, seasonal and annual. I propose that detection rates be adjusted for seasonal variability using the best fit polynomial illustrated in Figure 1.3A, as $NDET_{adj\_s} = NDET_{obs} * (NDET_p/NDET_d)$, where $NDET_p$ is the predicted seasonal peak detection rate and $NDET_d$ is the predicted value for the day observations were made. This would have the effect of increasing the "weight" of observations made away from the seasonal peak according to average seasonal patterns, similar in concept to the method of Miller and Ralph (1995, Meyer et al. 2002) that is based on 10-day average detection rates. Adjustments for annual variation in activity can be achieved similarly and in concert with adjustments for seasonal variation using the multiple regression model described in Figure 1.4. The mid-study year (1997) and average summer SST and winter upwelling anomalies predict an annual average detection rate, $NDET_{avg}$, which can be used as a reference value for the final adjustment as $NDET_{adj\_f} = NDET_{adj\_s} * (NDET_{avg}/NDET_{y})$ where $NDET_{y}$ is the observed annual average detection rate for the year in which data were collected.

Analysis of spatial variability in activity at the finest scale requires using detection rates as the response variable because its component indices, which are based on averages, do not apply well to results from individual survey stations as most stations received 1 or 2 visits. But inference about murrelet habitat associations from inland surveys are probably best made at broader spatial scales (Rodway and Regehr 2002), where consistency and intensity of activity could provide additional information about murrelet responses to forest characteristics. If spatial analyses were at the scale of, for example, 100 ha neighborhoods (*sensu* Raphael et al. 2002b) where often 10-30 surveys were conducted over 2 years, WDET indices could be calculated and adjusted following the format proposed above. Adjusting neighborhood PWITH values requires a different approach as consistency is indexed as the proportion of surveys recording murrelet activity or the average of a string of 0s and 1s denoting negative or positive survey findings. In adjusting this index, I propose that surveys count more or less towards the denominator in the average based on whether they were conducted on dates where detections were more or less likely. Seasonal adjustments would follow the model described above, using the polynomial illustrated in 1.3B, except that the n for each survey would be adjusted as: $n_{\text{adj\_s}} = 1 * (\text{PWITH}_{\text{d}})/\text{PWITH}_{\text{p}})$, where PWITH_{d} is the predicted value for the survey date and PWITH_{p} is the predicted seasonal peak proportion of surveys with detections. Annual adjustments based on the multiple regression from Figure 1.4 would be up or down relative to the prediction for mid-study and average winter upwelling, $\text{PWITH}_{\text{avg}}$.

These adjustments should compensate for much of the annual and seasonal variability I observed, thus permitting a clearer view of the spatial variability which is presumably in response to forest characteristics. This can potentially result in meaningful improvements in forest management for murrelet conservation. However, no clear standard exists against which to compare inferences drawn from spatial patterns of activity. Any such inferences, and consequent management actions, must be viewed as hypotheses and implemented and evaluated in an adaptive management program (Marzluff et al. 2000). Although this analysis and its proposed applications are unique to these data, I suggest this approach be applied to other large sets of marbled murrelet inland survey data to potentially improve their information value.

Inland surveys are becoming less important as a tool for murrelet research and monitoring, better methods have been developed that provide a clearer picture of murrelet biology - mark-recapture (Cam et al. 2003), physiological indices (McFarlane Tranquilla et al. 2003), radar (Burger 2001, Raphael et al. 2002a), and radio-telemetry

(Bradley et al. 2004, Peery et al. 2004a). But understanding temporal variability in murrelet life history traits will remain important in predicting and monitoring results of conservation programs, regardless of how data are collected. The mechanistic hypotheses I proposed offer testable predictions that can be challenged with a variety of methods, with retrospective analysis of other data sets, prospective studies of murrelet inland activity, or possibly even studies directed at the processes themselves.

Table 1.1. Marbled murrelet survey effort, Olympic Experimental State Forest, Washington, USA, 1994-2001. Multiple surveys were conducted according to a 2-year protocol at discrete survey sites.

	Survey Sites Initiated		
Year	**Number**	**Hectares**	**Number of Surveys**
1994	31	634	107
1995	0	0	111
1996	235	5,598	1,001
1997	193	5,386	1,668
1998	62	1,677	947
1999	31	871	391
2000	79	2,374	375
2001	0	0	148
Total	631	16,540	4,748

Table 1.2. Nested analysis of variance to assess the influence of year to year and season within year effects on variablility in detection rates from marbled murrelet surveys, Olympic Experimental State Forest, Washington, USA, 1994-2001.

Source	**DF**	**SS**	**MS**	**F**	**P**
Year	7	1,366	195.1	2.25	0.0332
Season within Year	144	12,466	86.6	4.05	0.0007
Error	4,601	98,409	21.4		
Total	4,752				

Table 1.3. The global and most parsimonious models (lowest Mallow's C_p) describing annual variability in 3 indices of marbled murrelet inland activity, Olympic Experimental State Forest, Washington, USA, 1994-2001. Model fit described with the adjusted R^2 (R_{adj}^2), all models included an additional parameter for a non-zero intercept.

Model parameters	**C_p**	**R_{adj}^2**
Proportion of surveys with detections, PWITH		
Winter upwelling index, year	3.0	0.86
Winter upwelling anomaly (anom), year	3.0	0.86
Average detections per survey with detections, WDET		
Summer sea-surface temperature (SST), winter SST, year	6.9	0.63
Summer SST anom, winter SST, year	5.9	0.72
Summer SST*winter SST, year	6.0	0.65
Summer SST anom*winter SST, year	11.6	0.50
Summer SST anom, winter SST	4.7	0.75
Average detections per all surveys, NDET		
Summer SST, winter SST, winter upwelling index, year	12.2	0.53
Summer SST anom, winter SST, winter upwelling anom, year	4.7	0.75
Summer SST*winter SST, winter upwelling index, year	13.7	0.53
Summer SST anom*winter SST, winter upwelling anom, year	3.2	0.78
Summer SST anom, winter upwelling anom, year	3.0	0.79

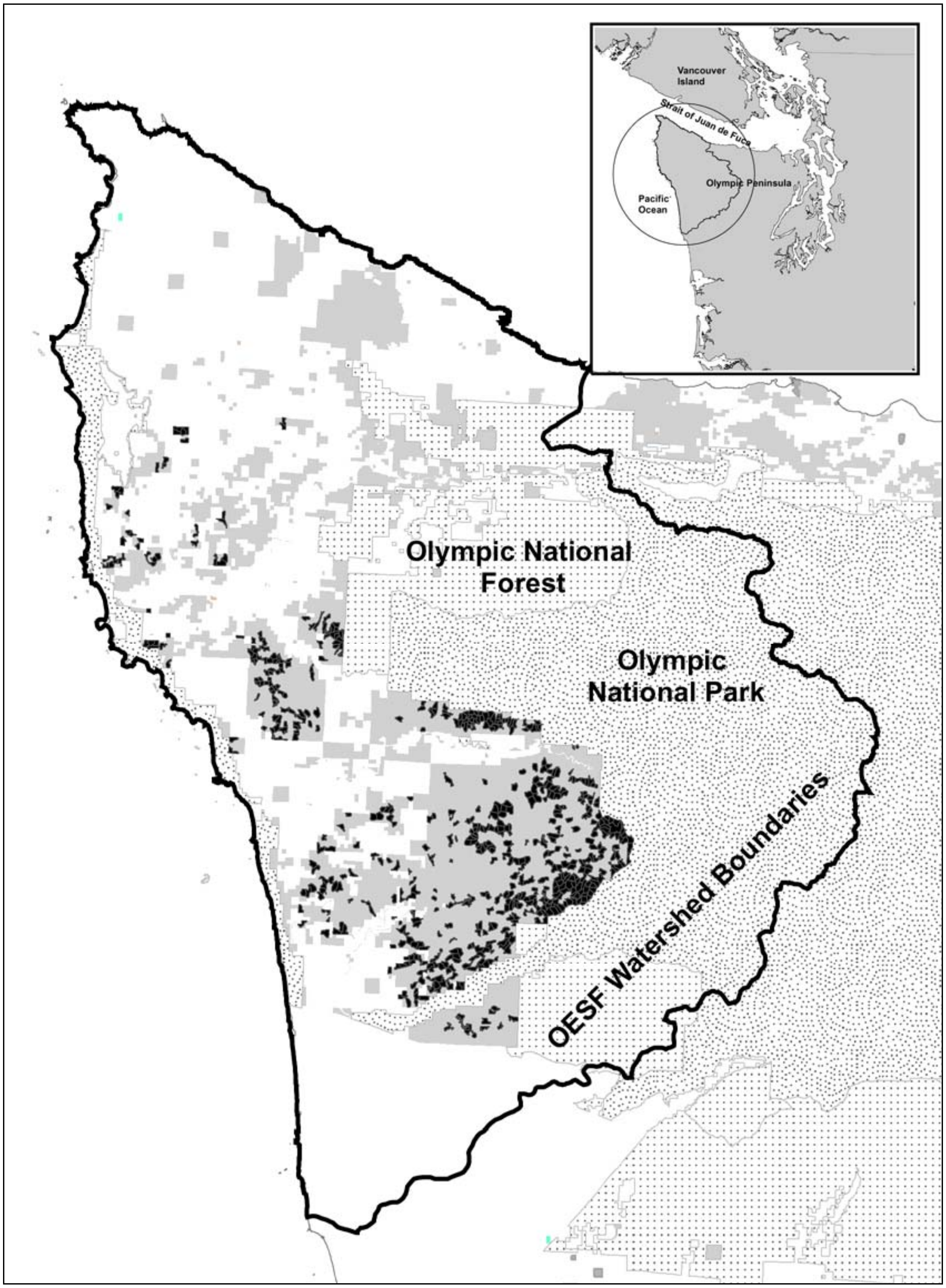


Figure 1.1. Study area map showing the Olympic Experimental State Forest (OESF) in grey shading and locations of 4,748 marbled murrelet surveys in black, Washington, USA, 1994-2001. Inset map shows regional geography with the study area circled.

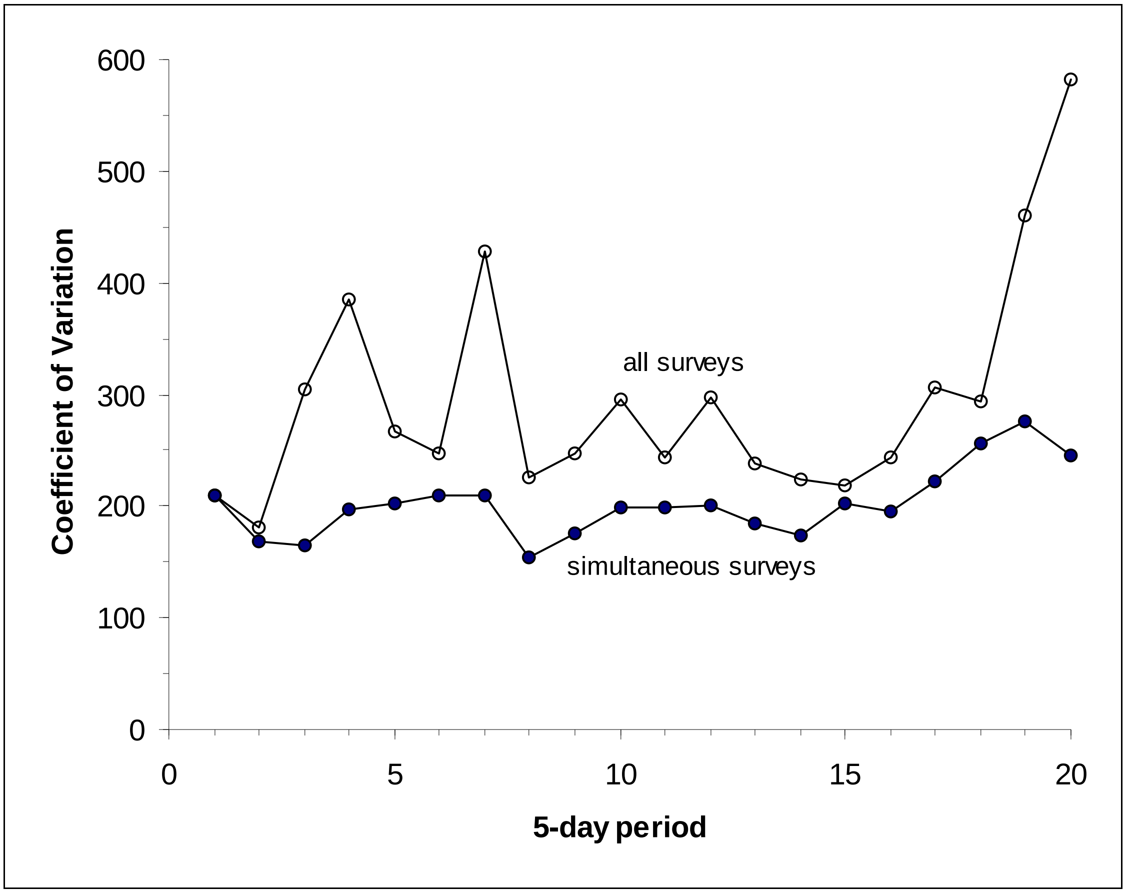
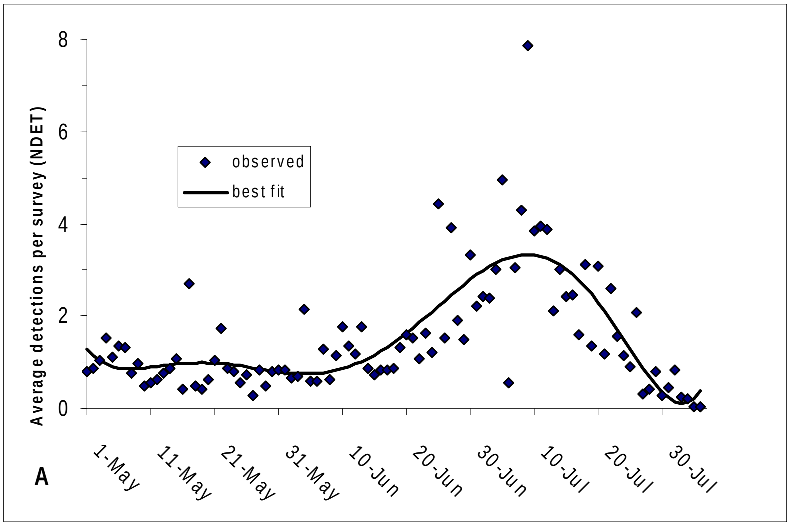
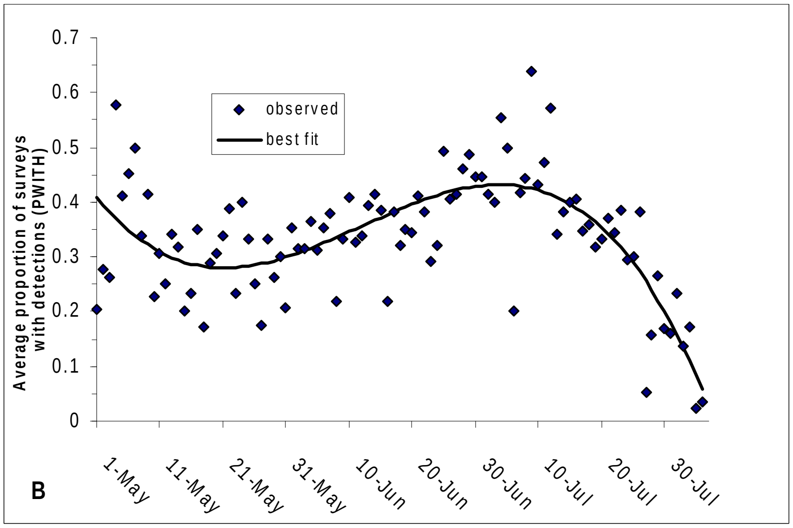


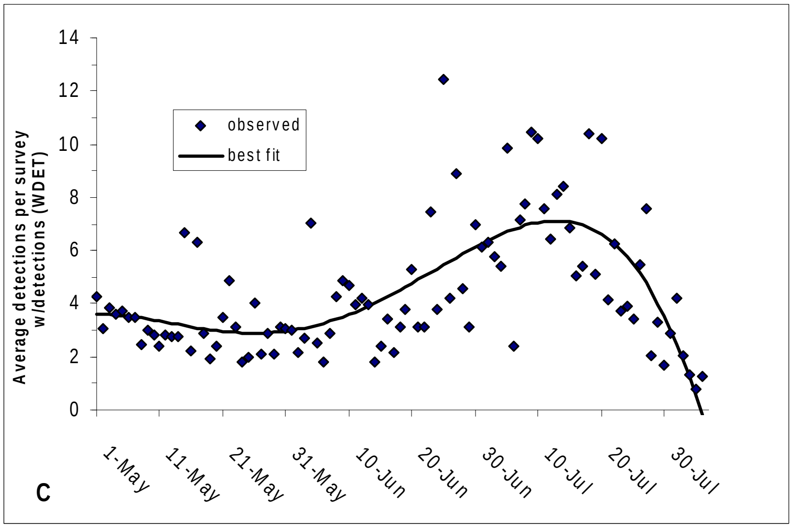
Figure 1.2. Variability in numbers of marbled murrelet detections per survey, for 20 5-day periods across the 97-day survey season. Open circles are from all surveys (*n* = 4,748), closed circles are averages of daily CVs from simultaneous surveys on 200 dates with ∃10 surveys (*n* dates for periods 1-19 averaged 10.4, range 8 - 13; period 20 had 2 dates; *n* surveys = 3,369), in the Olympic Experimental State Forest, Washington, USA, 1996-2000.

[figure on following page]

Figure 1.3. Variation in marbled murrelet activity across the 97-day survey season, based on 4,748 murrelet surveys in the Olympic Experimental State Forest, Washington, USA, 1994-2001. Observations are: (A) average numbers of detections per survey (NDET) for each date, (B) average proportion of surveys with any detections (PWITH, back-transformed for plotting) for each date, (C) average numbers of detections per survey with detections (WDET) for each date.


8
6
4
2
0
Average detections per survey (NDET)
observed
best fit
1-May
11-May
21-May
31-May
10-Jun
20-Jun
30-Jun
10-Jul
20-Jul
30-Jul
A


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Average proportion of surveys with detections (PWITH)
observed
best fit
1-May
11-May
21-May
31-May
10-Jun
20-Jun
30-Jun
10-Jul
20-Jul
30-Jul
B


14
12
10
8
6
4
2
0
Average detections per survey w/detections (WDET)
observed
best fit
1-May
11-May
21-May
31-May
10-Jun
20-Jun
30-Jun
10-Jul
20-Jul
30-Jul
C

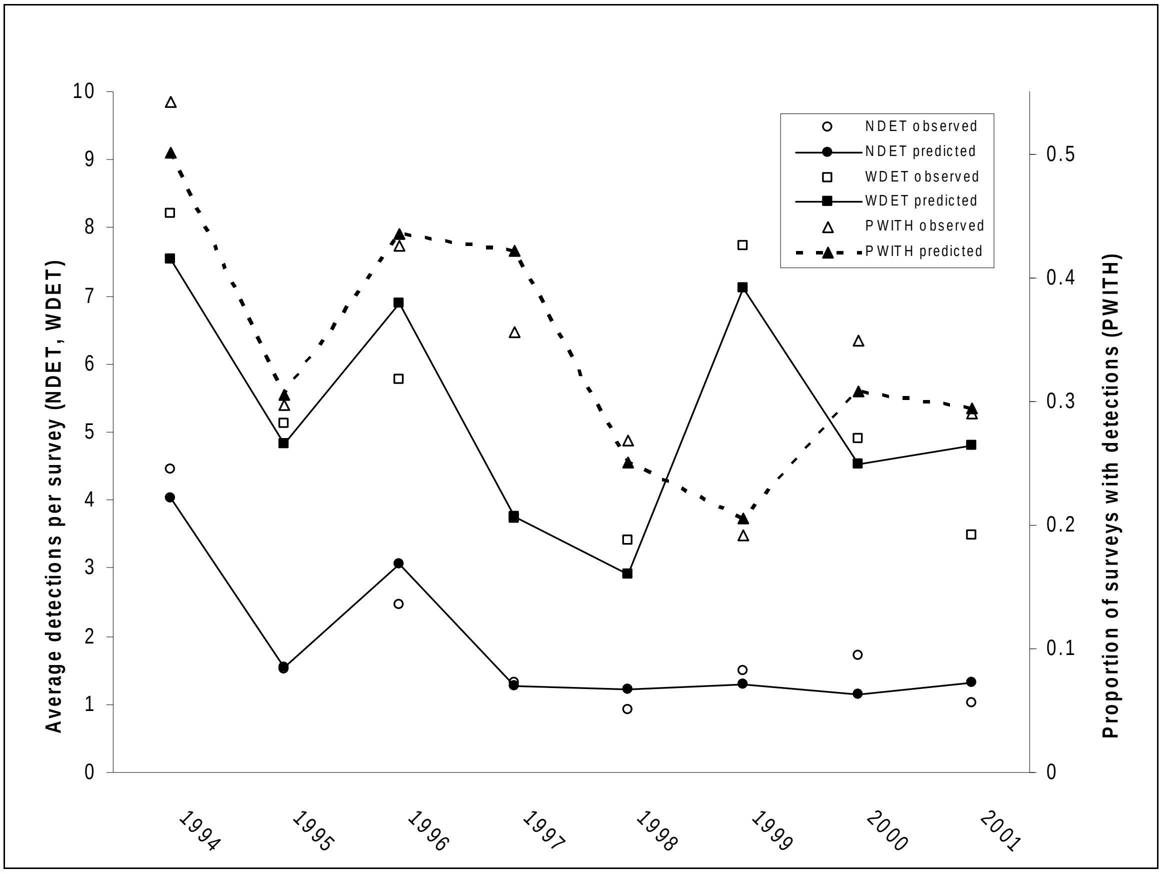


Figure 1.4. Annual variability in marbled murrelet activity, based on 4,748 murrelet surveys in the Olympic Experimental State Forest, Washington, USA, 1994-2001. Observations are annual averages of: numbers of detections per survey (NDET), numbers of detections per survey with detections (WDET), and proportion of surveys with any detections (PWITH). Predictions are from the multiple regression models, and are connected by lines for ease of interpretation: NDET = 508.8 - 0.74*Summer SST Anomaly + 0.01*Winter Upwelling Anomaly - 0.25*Year ($R_{adj}^2 = 0.79$, $F_{3,4} = 10.0$, $P = 0.02$), WDET = 14.5 - 1.28*Summer SST Anomaly - 1.09*Winter SST ($R_{adj}^2 = 0.75$, $F_{2,5} = 11.7$, $P = 0.01$), arcsin-transformed PWITH = 46.8 + 0.002*Winter Upwelling - 0.023*Year (back-transformed for plotting, $R_{adj}^2 = 0.86$, $F_{2,5} = 22.5$, $P = 0.003$).

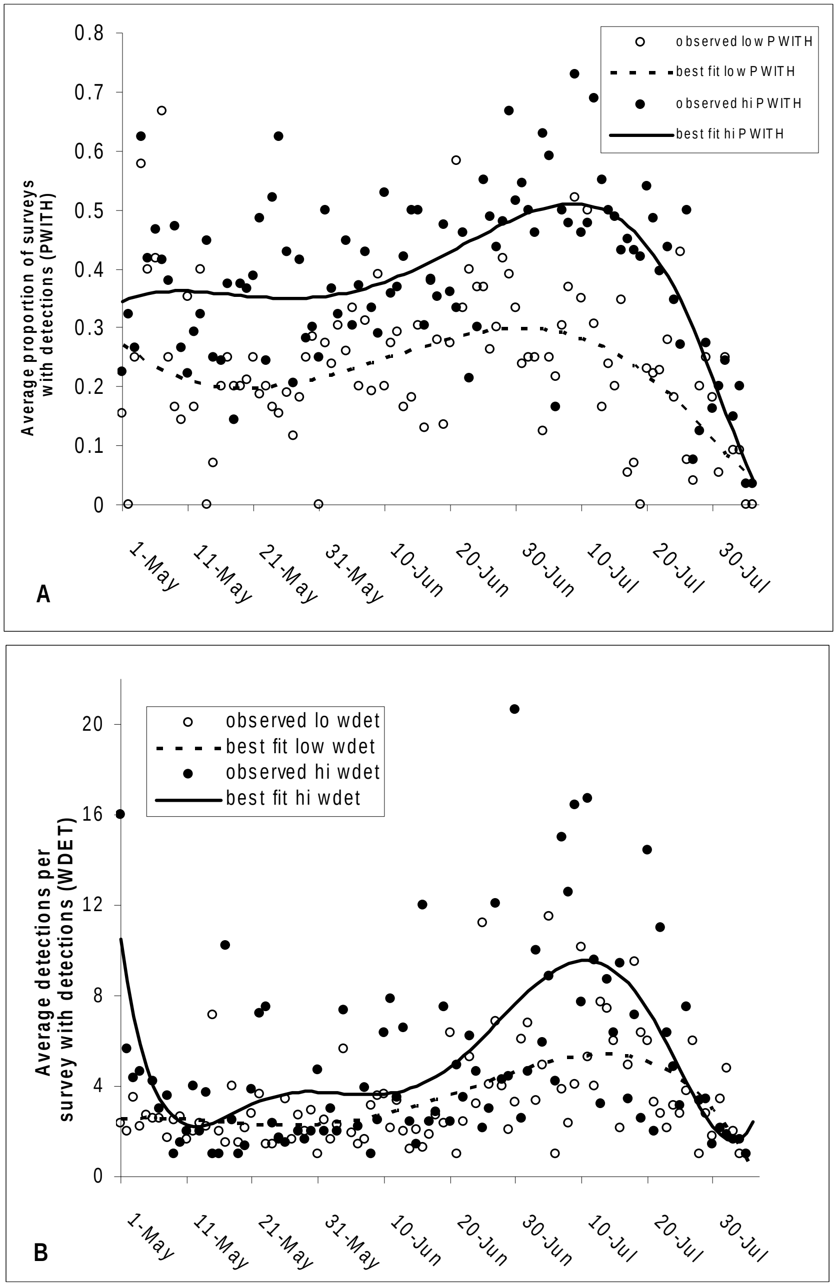


Figure 1.5. A comparison of seasonal patterns in: (A) the average daily proportion of marbled murrelet surveys with detections (PWITH) from the 4 years (1994, 96, 97, 2000) of highest PWITH compared with the other years; and (B) the average daily numbers of detections from surveys with detections (WDET) from the 4 years (1994, 95, 96, 99) with the highest average WDET compared with the other years. Best fit curves were 3rd to 6th-order polynomials using survey date, $0.14 < R_{adj}^2 < 0.46$, $p < 0.001$. Curves were fit to arcsin-transformed PWITH and back-transformed for plotting. Based on 4,748 murrelet surveys in the Olympic Experimental State Forest, Washington, USA, 1994-2001.

Chapter 2. Spatial Variation in Marbled Murrelet Inland Activity: Landscape-level Influences on the Western Olympic Peninsula, Washington

The majority of North American temperate forests are utilized by society for the production of natural resources. It will require significant effort to discover and implement management approaches that conserve the biodiversity these forests support within a broader framework that provides sustainable social, economic, and ecosystem services. While ecological reserves are important in this effort, a comprehensive and multiscaled approach to forest management applied broadly across commodity-producing as well as reserved lands is necessary for successful conservation outcomes (Lindenmayer and Franklin 2002). Effective conservation of individual endangered species can be challenging within such an approach because of scaling differences among species (Wiens 1989) and the complex task of reconciling those differences in comprehensive plans (Bunnell and Huggard 1999, Schwartz 1999).

The Washington State Department of Natural Resources (DNR) recognized the need for a comprehensive and multiscaled approach in proposing an unique management strategy that seeks to better integrate commercial and conservation objectives at multiple scales for 110,000 ha of state forests on the western Olympic Peninsula, the Olympic Experimental State Forest (OESF, DNR 1997). Conservation of the threatened marbled murrelet (*Brachyramphus marmoratus*) is a management focus in the OESF, thus there is a need for information on its relationships with forests at multiple spatial scales. The marbled murrelet was listed as a Threatened Species in Washington, Oregon, and

California under the U.S Endangered Species Act in 1992. The survival and recovery of this secretive, forest-nesting seabird appear to depend substantially on effective conservation and management of its inland habitat (U.S. Fish and Wildlife Service 1997). Stand-level characteristics of its nesting habitat have been described (Nelson 1997, Raphael et al. 2002b). However, there is uncertainty regarding the broader-scale context of nest sites, with findings suggesting that murrelets are more prone to nest in concentrations of large contiguous patches of old forest (e.g., Raphael et al. 1995, Meyer et al. 2002) contrasting with those that have observed nesting in smaller than average patches and in association with high-contrast edges (Meyer and Miller 2002, Zharikov et al. 2006). Thus, further information on the influence of landscape pattern and composition on murrelet forest use can advance management directed at improving the conservation value of existing and restored older forest patches. This is particularly important for conserving murrelets in forests with commercial objectives because it appears that, at best, only minimal levels of timber harvest are consistent with maintaining structural characteristics of forests that provide suitable nesting opportunities. It is possible that improved knowledge can enable more effective management of forest composition and pattern around patches of potential murrelet nest sites and help meet multiple objectives.

The most valuable information for managing wildlife populations addresses the interaction of the primary population processes, reproduction, mortality, and immigration/emigration, with limiting factors such as habitat availability (Williams et al. 2002). However, this type of information is particularly difficult to gather on the secretive marbled murrelet, thus most of our current understanding of their relationships with forests derives from less direct audio-visual (Hamer 1995, Raphael et al. 1995, Meyer et al. 2002, Rodway and Regehr 2002) and radar (Burger 2001, Raphael et al. 2002a, Cooper et al. 2006) studies that associated murrelet activity patterns with forest characteristics. DNR conducted extensive audio-visual studies of murrelet inland activity in the OESF as part of a stepwise, interim approach to murrelet conservation that served to focus knowledge and conservation measures while leading to a long-term conservation strategy (DNR 1997). Here I examine those studies retrospectively to discover the relationship of murrelet inland activity with landscape composition and pattern, and to clarify the influence of scale on those relationships with the broad objective of informing a comprehensive approach to forest management that integrates conservation and commercial objectives for state forests.

Inferences about murrelet resource use from inland surveys are best made at broad spatial scales (Rodway and Regehr 2002), as audio-visual observers likely detect birds associating with general areas rather than discrete survey points. I used kernel techniques (Silverman 1986) to map murrelet activity as continuous probability density functions and cell-based modeling to relate them to landscape pattern and composition (Marzluff et al. 2004). These methods differ from the site or plot-based analyses used in previous studies (e.g., Raphael et al. 1995, Meyer et al. 2002) and provide several advantages including: 1) better consideration of the continuous phenomenon of resource use (Marzluff et al. 2001), and more appropriate estimation of a probabilistic and continuous measure of murrelet activity across the study area rather than classification of forest patches as used or unused; 2) increased analytical sensitivity provided by the continuous activity metric; 3) reduced concern that measurement error during inland surveys results in mis-classifications, due to the continuous nature of the activity metric; and 4) consideration of the entire distribution of murrelet activity, rather than a few difficult to observe behaviors at discrete sample points.

I investigated several broadly-formed, non-exclusive and potentially interacting hypotheses. These are based on the assumption that nesting rates, thus habitat value, are proportional to levels of inland activity (Table 2.1). The scope of my investigation was influenced by my specific objective that findings be readily accessible to managers, thus I avoided composite landscape indices such as those derived from principal components analysis (Raphael et al. 1995) and sought metrics that measured attributes that could be predictably influenced by forest management. My scope was also constrained by the landscape mosaic in my study area which resulted from its unique land ownership patterns and history of natural and anthropogenic (logging) disturbances. While this mosaic presented substantial contrasts in landscape conditions, there were no wilderness areas nor any distinctly isolated old forest patches.

Study Area and Methods

Study area -- The 110,000 ha OESF, Washington, USA (Figure 1.1) is west of the Olympic Mountains and spans coastal plain to mountain landforms from 35-1,020 m elevation. Climate is moist and maritime, with approximately 340 cm of annual precipitation. Forests at lower, middle, and higher elevations are in the *Picea sitchensis* (Sitka spruce), *Tsuga heterophylla* (western hemlock), and *Abies amabilis* (Pacific silver fir) Zones respectively (Franklin and Dyrness 1988). The OESF is managed as a sustainable commercial forest and is within a larger landscape (526,000 ha as defined by watersheds, Figure 1.1) of private and tribal commercial forests (241,000 ha), Olympic National Park (121,000 ha), and Olympic National Forest (50,000 ha). Stand (i.e., contiguous, relatively homogenous groups of trees) ages on DNR-managed lands (2006) reflect the intensive harvest of native forests that occurred about 1960-1990, with 36% older than 50 years, 40% between 25 and 49 years old, 21% aged 13-24 years old, and 3% 12 years old or younger. Other commercial forests are managed for sustainable timber production with a rotation age of about 50 years. Stand ages there are approximately evenly distributed across that range except for about 15% of the land base that is reserved for riparian and upland endangered species conservation. Olympic National Park is a wilderness area and most of Olympic National Forest is currently managed to maintain or restore late-successional forests (U.S. Department of Agriculture and U.S. Department of the Interior 1994).

Forest cover -- I mapped forest cover using classified satellite imagery acquired in 1991 (25 x 25 m pixels), which achieved overall 93% accuracy and distinguished among late-seral types (large sawtimber and old-growth) with 85% accuracy (WDFW 1994). This classification focused on the 4 most mature of 9 mapped cover types: old-growth, dominant dbh ≥ 76 cm, 3 or more canopy layers with less than complete canopy cover; large sawtimber, dominant dbh 51-76 cm, 2 or 3 canopy layers with greater canopy closure than old-growth; small sawtimber, dominant dbh 36-51 cm, 1 or 2 canopy layers; and pole timber, dominant dbh 25-35 cm, 1 canopy layer (WDFW 1994). Other land cover was assigned to: sapling, closed canopy stands <25 cm dbh; open-canopy/mixed conifer, sparsely-stocked stands of smaller stature often in forested wetlands; open areas, which were largely regenerating clearcuts in the study area; water; and cloud/cloud shadow (WDFW 1994). I used DNR data to update the base map for subsequent timber harvest on DNR-managed lands and used orthophotography acquired in summer 1994 and 2001 to map land cover in areas of cloud/cloud shadow and timber harvests on other ownerships, and created maps that depicted 2 additional groupings of mature forest: old-growth and large sawtimber grouped as "late seral"; and old-growth, large and small sawtimber grouped as "mature", thus my final map products depicted 10 cover types: old-growth (OG), large sawtimber, late seral (LT), small sawtimber, mature (MT), open-canopy/mixed-conifer, pole, sapling, open, and water. I estimated dates of timber harvest from DNR records or aerial photography and used my estimate of mid-study (1997) conditions for analyses.

Murrelet activity -- Murrelet inland activity was recorded during 4,748 surveys at 2,463 stations comprising 631 sites (16,540 ha) from 1994 to 2001 according to the protocol described by Ralph et al. (1994) or its then-current update and to meet specific DNR objectives (see Chapter 1). Surveys were conducted in DNR-managed older forests above a minimum patch size of 8 ha, that originated after natural disturbances and would be described as "old-growth" or mixed-age stands with a significant old-growth component, largely in the vertical or horizontal diversification stages of Franklin et al. (2002). The satellite classification depicted these patches as a heterogeneous mix of all cover types, dominated by old-growth (40%) and large sawtimber (28%). The average nearest-neighbor distance between survey stations was 229 m (S.E. = 90 m). I found that detection rate, i.e., murrelet detections per survey visit, was an effective index of habitat use and that it showed consistent patterns of temporal variation (Chapter 1). Within-season variation in detection rates, probably due to phenological changes in behavior patterns conformed to a polynomial relationship with survey date, while inter-annual variability was correlated with local oceanography and the passage of time. I used those relationships to predict date-specific expectations for murrelet activity, then used a transformation of the residual, $\ln\left(\frac{1}{n}\sum_{i=1}^{n}\frac{\text{observed}+0.5}{\text{expected}}\right)+2.5$, to provide a normally-distributed, non-negative index to activity at each station averaged over n survey visits (Chapter 1).

I produced probability density functions that quantified spatial patterns of murrelet activity as utilization distributions (UD, *sensu* Marzluff et al. 2004) by applying the quadratic kernel function (Silverman 1986) in ArcMap 9.1 (ESRI, Inc.) to activity indices across the 2,463 survey stations. The shape of these utilization distributions depend on the smoothing parameter or bandwidth such that insufficient smoothing (bandwidth too small) results in distributions that are unduly influenced by sampling artifacts, while excessive smoothing (bandwidth too large) obscures important features of the distribution (Jones et al. 1996). Because this aspect of marbled murrelet inland activity is not well understood, I produced utilization distributions at 3 spatial scales to represent competing hypotheses regarding the scale at which marbled murrelets perceive and react to landscape pattern in my study area: 13 ha, or “patch” scale; 50 ha, “stand” scale; and 95 ha, “neighborhood” scale, using 200, 400, and 550 m bandwidths respectively. I chose the patch scale because 200 m is the maximum effective distance for audio-visual detection of murrelets (Evans et al. 2000) and because that is the approximate scale of fine-grained topographic variation in my study area that often defines what human observers interpret as an identifiable patch within a larger stand. I chose the stand scale because that is near the modal size of older forest stands in the study area, as a result of the medium-grained topographic variation that DNR’s forest inventory often uses to delineate stands within larger contiguous blocks of forest and because of the size distribution of remnant patches resulting from timber harvest. I chose the neighborhood scale as an upper limit because it approximates the area I have frequently observed traversed by circling murrelets at inland locations, a behavior that is believed to reflect their association with at least a portion of that area (Evans et al. 2000), and because greater smoothing would often encompass large areas devoid of older forests given the degree of fragmentation in my study area. I then separately examined correlations between UD_{patch}, UD_{stand}, and $UD_{neighborhood}$ and spatially defined indices of landscape composition and pattern.

Developing multiple working hypotheses -- I expressed the broadly-formed, non-exclusive and potentially interacting hypotheses (Table 2.1) as explicit, quantitative statements . I first selected a limited set of indices of the landscape characteristics thought to influence murrelet responses and determining an informative range of spatial scales over which to calculate these indices. Then, I refined the descriptions as discrete, explicit hypotheses using those landscape indices to express quantitative models that predicted murrelet activity patterns and arbitrated among those descriptions by testing how well they fit my observations.

Among the large variety of landscape metrics, many can be strongly correlated with one another and contain redundant information (Turner et al. 2001). I explored the data (Eberhardt 2003) to help focus on the most informative landscape indices, at spatial scales where contrasts in murrelet activity were most evident, and to search for non-linear relationships. At this stage, I examined univariate correlations among landscape indices and between landscape and murrelet activity indices, and how scale influenced those correlations. These were calculated for a geographically-stratified (by watershed, n = 8), random, 10% sample of the 2,463 murrelet survey stations, and used average murrelet activity index values from each station. I used FRAGSTATS (McGarigal et al. 2002) to calculate a variety of metrics categorized by FRAGSTATS as class (i.e., specific to a cover-type within a plot) and landscape (i.e., encompassing all cover-types within a plot), and ArcMap 9.1 (ESRI, Inc.) to calculate geographic (e.g., elevation, slope) indices for 200, 400, 800, 1600, 2400, and 3200 m radius circular plots around the sampled stations (n = 251). These plots covered 13, 50, 201, 804, 1809, and 3217 ha respectively. I examined correlations and scatter plots within scales, among class, landscape, and geographic indices, and between those and murrelet activity indices. Appendix A provides details of these analyses and their results, however in summary: 1) Many indices (Table A.1) were correlated ($p < 0.05$) between and within cover-type classes (Tables A.2, A.3, A.4). Strong inverse relationships between early (open and sapling) and late (old-growth and large saw) seral class metrics were predominant among between-class correlations (Tables A.2, A.3), these were obviously due to the historic pattern of timber harvest. 2) Many correlations existed among landscape (Table A.5) and geographic (Table A.6) indices. 3) Over half of all correlations with murrelet activity were of class metrics for characteristics of early and late seral cover types at 400 and 800 m scales (Table A.7). Inverse relationships with several indices of landscape edge contrast were predominant among the relatively fewer correlations of murrelet activity with whole-landscape indices (Table A.7). 4) Fewer than 10% of all correlations with murrelet activity were with class or landscape metrics at scales greater than 1600 m (Table A.7, Figure A.1) and nearly 90% of the strongest 25% of those correlations were at the 400 and 800 m scales (Figure A.1). 5) Murrelet activity was not correlated with geographic or topographic characteristics. 6) I did not observe non-linear relationships of murrelet activity with class or landscape characteristics (Table A.7). Thus I depicted my hypotheses using a restricted set of simple indices of the extent, context, and configuration of potential nesting habitat (forests of old-growth and/or large sawtimber), a limited set of whole-landscape indices including an index of edge contrast, and to limit the scales at which these indices were calculated to 200, 400, 800, and 1600 m radii. I used linear regression to confront the hypotheses with murrelet activity data.

Incorporating results of the exploratory analyses summarized above and in Appendix A with the broad hypotheses summarized in Table 2.1, I developed 5 “families” of increasingly complex models as quantitative expressions of those hypotheses: “just habitat” models predicted that murrelets responded only to the density of cover types that were potential nesting habitat, old-growth alone and in combination with large sawtimber; “core habitat” models introduced core area, i.e., interior forest, as a potential covariate of murrelet activity; “edge and habitat” models combined high-contrast edge and potential nesting habitat while “edge and core habitat” models combined edge and core area of habitat; finally, “habitat, core, edge, and evenness” models introduced compositional diversity as a potential covariate of murrelet activity. Within each model family, I proposed specific models that encompassed spatial scales and combinations of covariates that were potentially meaningful to murrelets and tractable to forest managers (Table 2.2). For example, I hypothesized that murrelets responded to the most structurally-complex forest, OG, at finer scales while the abundance of late seral forest in general, LT, was important at broader scales. Thus specific models incorporated OG abundance calculated at 200, 400, or 800m scales but LT abundance at 400, 800, or 1600 m scales. I did not incorporate the hypothesis of a time-delayed response to fragmentation at this stage of the analysis.

Landscape composition and pattern -- I calculated indices of landscape composition and pattern using ArcMap 9.1 (ESRI, Inc.) and FRAGSTATS (McGarigal et al. 2002) based on the 10-category landscape maps. I resampled the cover type grid to 50 x 50 m, using nearest-neighbor interpolation for categorical data (ArcMap 9.1, ESRI, Inc.) to accommodate computational limitations with my large data set. All indices were developed with circular moving-window analyses (McGarigal et al. 2002) to produce continuous surfaces in which the value at each cell is the index of interest calculated over the appropriate radius. I indexed the abundance of potential marbled murrelet nesting habitat, OG and LT, at 200, 400, and 800 m radii for OG and 400, 800, and 1600 m for LT. I derived similar indices separately, at 200, 400, 800, and 1600 m radii, for interior LT and MT forest as the core area (CORE), which was defined relative to edge contrast as being over 100 m from an edge with open areas, 80 m from sapling, and 50 m from pole or open-canopy/mixed-conifer.

I indexed the amount of edge and edge contrast using the FRAGSTATS contrast-weighted edge density routine (CWED, McGarigal et al. 2002), weighting edges relative to their contrast as 1 minus the ratio of the average heights of juxtaposed cover types: OG and large sawtimber 55 m, small sawtimber 40 m, pole timber 21 m, open canopy/mixed conifer 18 m, sapling 8 m, open (regenerating clearcut) 3 m. Thus, edge between OG and small sawtimber was weighted 1 – (40/55) = 0.27 while the weight of edge between OG and open was 1 – (3/55) = 0.95. The CWED routine expresses edge as weighted linear distance per unit area (m per ha), calculated for each cell in the moving-window analyses for radii of 200, 400, 800, and 1600 m. I indexed the diversity of cover types using Shannon's evenness index (SHEI), which provides a dimensionless index that approaches 1 as land cover within the analysis window becomes equally apportioned among all possible cover types and approaches 0 as the window becomes dominated by a single cover type. I calculated SHEI in moving window analyses with radii of 200, 400, and 1600 m.

Analyses -- The kernel technique produces a continuous response surface in which murrelet activity index values at any pixel are correlated with those of their neighbors merely because of proximity. I accounted for this spatial autocorrelation by using regression models that assume spatial correlation in error decreases with distance between pixels (Marzluff et al. 2004). In this approach, two additional parameters for the range (distance) of spatial dependence and the smoothness (number of derivatives) of the response surface are jointly estimated with coefficients of resource indices in regression models. Solutions to these models are obtained with a maximum likelihood procedure (Marzluff et al. 2004, Handcock 2006) which was computationally-demanding with my large data set.

I addressed the computational demands by an approach of stratified-random sampling without replacement from the UDs. I stratified each UD by quartile, so that each sample contained equal numbers from the highest, lowest, and two intermediate quartiles of murrelet activity. Then I randomly selected pixels within each quartile so that each of the UD were parsed into samples of approximately 1,000 pixels. The patch-level UD was fully encompassed within 100 samples, while UD_{stand} and $UD_{neighborhood}$ required 160 and 210 samples respectively. I calculated maximum likelihood solutions for each sample, for each of the 55 models (Table 2.2), for the patch, stand, and neighborhood UDs using software developed by Handcock (2006). I used Akaike's Information Criteria (AIC, Burnham and Anderson 2002) to rank candidate models within each sample according to fit and parsimony, and to derive additional evidence to meet my objectives. The simplest models among my 55 candidates (Table 2.2) had 5 parameters while the most complex had 8 because, in addition to the landscape covariates, there were 2 parameters for spatial autocorrelation plus an intercept and error term.

For each sample, I selected the model with the lowest AIC, then calculated the proportion of samples for each UD scale that model *i* was ranked as best (π_i) to provide a measure of uncertainty in model selection. I calculated the difference between the AIC of the best model in each sample and the remaining *i* models as Δ_i and determined the set of top models within each sample as those with $\Delta_i \leq 8$ (Burnham and Anderson 2002). For those *R* top models, within each sample, I calculated Akaike weights (w_i, Burnham and Anderson 2002). I averaged those w_i across all samples for each scale ($N_{patch} = 100$, $N_{stand} = 160$, $N_{neighborhood} = 210$) to calculate $\overline{w_i}$, then calculated the evidence ratio, w_1/w_i (Burnham and Anderson 2002). I assessed the relative importance of covariates by comparing the sums of $\overline{w_i}$ across all top models in which each covariate occurred (Burnham and Anderson 2002). For the top models, I calculated average standardized coefficients and their 95% confidence intervals for the landscape covariates as a measure of the direction and relative strength of their influences on murrelet activity (Marzluff et al. 2004, Handcock 2006).

Response to fragmentation -- To reduce the overall number of dimensions in the model selection exercise, I evaluated the hypothesis of a time-delayed response to fragmentation following the initial selection of best models for describing the association of murrelet activity with current landscape conditions. Early seral areas that resulted from the 30 years of intense logging were classified either as open (OP) or sapling (SAP), with sapling stands approximately 15 years older than open. If murrelet activity declined as a delayed reaction to nearby fragmentation, I hypothesized that otherwise comparable areas would have less activity if sapling was predominant among early seral land cover. I added additional covariates that indexed the abundance of the early seral cover types at 200, 400, and 800 m radii to the best models (model$_B$) describing covariation of murrelet activity with current landscapes, in 3 configurations: 1) model$_B$ + OP + SAP, 2) model$_B$ + OP, 3) model$_B$ + SAP. Thus, for each of the best models selected for current conditions, I evaluated 9 additional models, 3 configurations of covariates and 3 scales (200, 400, 800 m) at which early seral abundance was indexed.

With all 3 configurations, the strong inverse relationship between early and late seral cover types would likely improve model fit but unless the addition of early seral covariates added appreciably to their fit, the penalty for overfitting would result in higher AIC values and none would be selected over model$_B$. If configuration 1 models were selected, I suggest that would indicate a general effect of early seral cover that persisted at least 30 years. Selection of configuration 2 models would suggest that effects of early seral cover diminished after about 15 years, while selection of configuration 3 models would suggest a delayed reaction.

Results

Patch Scale -- There was a high degree of uncertainty that any of the 55 candidate models was the best description for variation in murrelet activity at the patch (13 ha) scale. Nearly half of the candidates (27 of 55) were among the top models in at least one sample, and 16 were the best model at least once (Table 2.3). Less than 80% of the cumulative weight of evidence was contained within the 7 top models as ranked by their

$\overline{w}_i$, and no model was selected as best in more than 35% of the samples (Table 2.3). Examination of the top 6 models, as ranked by $\overline{w}_i$ (Table 2.3), illustrates they would be ranked differently based on their π_i. This lack of coherence is additional evidence as to the uncertainty in selecting a best model for describing murrelet activity at the patch scale.

Stand Scale – At the stand (50 ha) scale, 3 models were clearly superior (only ones with $\Delta_i \leq 8$ in any of the 160 samples; Table 2.4). Two of these top models had 96% of the weight of evidence supporting them. Those top 2 models used covariates for the abundance of old-growth at the 13 ha scale, late seral at the 50 ha scale, and contrast-weighted edge density at the 50 ha scale; and late seral at the 50 and 201 ha scales (models 34 and 10 respectively; Table 2.4). Model 34, with $\overline{w}_i = 0.81$, was selected as best in 130 of 160 samples. Evidence ratios (Table 2.4) confirm this ranking of relative evidence among the top models. Coherence among rankings based on $\overline{w}_i$ or π_i is additional evidence the rankings are appropriate(Table 2.4).

All 3 top models shared the abundance of late seral forest at the 50 ha scale as a parameter while 2 used the abundance of old-growth at the 13 ha scale; $\overline{w}_i$ summed to 1 and 0.85 for models that included those covariates. Standardized coefficients for those most important parameters were similar both in sign and relative importance in all models (Table 2.4). The most influential of these parameters was always late seral forest at the 50 ha scale, with substantial but somewhat less influence from old-growth at the 13 ha scale (Table 2.4). Murrelet activity increased with the abundance of old-growth and late seral forest at these scales, but in the presence of abundant late-seral forest at the 50 ha scale it decreased with broader-scale (800 m radius, 201 ha) abundance of late-seral forest (model 10, Table 2.4). In the best model, murrelet activity increased with the abundance of high-contrast edge at the 50 ha scale (model 34, Table 2.4), however the standardized coefficients for the parameters of this model demonstrate that the influence of edge contrast was considerably less than the combined influence of late seral and old-growth forest. Edge contrast at the 50 ha scale was relatively more important than late seral forest at the 2 km^2 scale as the $\overline{w_i}$ of the 2 top models using those as covariates were 0.81 and 0.15 respectively; Table 2.4.

Neighborhood Scale -- The evidence for models describing murrelet use at the scale of 95 ha neighborhoods was somewhat less clear than for those describing use at the stand scale, with 7 candidates occurring among the top models in at least one sample. While 76% of the weight of evidence supported the same 2 models (34 and 10) that garnered nearly all the support in stand-scale analyses, 20% of the evidence supported model 11, which was based on the abundance of late seral forest at the 50 and 804 (1600 m radius) ha scales (Table 2.5). Evidence ratios (Table 2.5) demonstrated that the strength of evidence was with the top 4 models, one of which was selected as the best model in 209 of 210 samples.

The abundance of late seral forest at the 50 ha scale was the most important and influential covariate in all 4 top models and it always covaried with murrelet activity (Table 2.6). Three covariates were approximately equal in importance, the abundance of old-growth at the 13 ha scale, late seral forest at the 2 km^2 scale, and edge contrast at the

50 ha scale, as $\overline{w}_i$ summed over models containing those covariates was 0.40, 0.39, and 0.37 respectively. The abundance of late seral forest at the 8 km^2 scale was a covariate only in model 11 with $\overline{w}_i$ = 0.20 (Tables 2.5, 2.6). Covariates indexing the broader-scale abundance of late seral forest (once each at 2 and 8 km^2) and fine-scale (13 ha) abundance of old-growth each occurred in 2 of the top 4 models, although never together (Table 2.6). As in the stand-scale analyses, in the presence of abundant late seral forest at the 50 ha scale murrelet activity was inversely related to abundance of late seral forest at broader spatial scales (models 10 and 11, Table 2.6) and activity increased with the 50 ha scale abundance of edge contrast (model 34, Table 2.6). However, the abundance of late seral forest at the 50 ha scale, alone or in concert with old-growth at the 13 ha scale was the predominant influence in those models.

Response to fragmentation – I used the 3 top models for murrelet activity at the stand scale (Table 2.4) as the basis for evaluating additional influences of fragmentation. With 9 models that incorporated early seral covariates based on each of the top 3 (i.e., 9 * 3 = 27) plus those 3 models, I brought 30 models to this analysis. Models incorporating fragmentation effects were better at describing murrelet activity patterns than those without. The top models for murrelet activity were consistently improved by the addition of covariates indexing the abundance of early seral forests, as the best models without those covariates were never included among the top models (Table 2.7). Although 17 of the 30 models received some support, as indicated by their inclusion in the set of top models in at least 1 of the 160 samples, nearly 99% of the weight of evidence was with the top 7 among them, with 91% of the evidence supporting the top 4 models (Table 2.7). Only those top 7 were ever selected as the best model in the 160 samples (Table 2.7). Six of the 7 top models were variations of model 34 (old-growth at 13 ha scale, late seral and edge contrast at 50 ha) that was the best description of murrelet activity without early seral covariates.

Late seral covariates were most important in the top 7 models, as $\bar{w}_i$ summed to 0.99 and 0.97 across models that used the abundance of late seral forest at the 50 ha scale and old-growth at the 13 ha scale, respectively. Several early seral covariates were important as well, with $\bar{w}_i$ summing to 0.62, 0.45, and 0.29 for models with open and sapling at the 2 km^2 scale, and open at the 50 ha scale, respectively. Among the 7 top models, the 4 that included abundance of early seral cover at relatively broader scales (50 or 201 ha) received substantially more support than those that included the fine-scale (13 ha) abundance of open and sapling cover (Table 2.7). Standardized coefficients for all but 1 of the early seral covariates were positive in those 4 models (Table 2.8), indicating that murrelet activity generally increased in the presence of early seral cover. Early seral covariates that were inversely related with murrelet activity, sapling cover at the 50 and 13 ha scales, and open at 13 ha, were relatively less important as their w_i summed to 0.10, 0.08, and 0.05, respectively.

Visual examination of the data and model predictions provide another context for evaluating these results (Figures 2.1, 2.2). I predicted activity levels based on model averaged coefficients for all covariates from the best models listed in Table 2.8 (Burnham and Anderson 2002). Figure 2.1 depicts approximately 25 km^2 of my study area where patches of late seral forest occurred in a highly fragmented setting in which the extreme lower right corner is federal land where I conducted no murrelet surveys. Figure 2.1A shows areas of highest murrelet use (upper quartile of activity mapped at the stand scale) on a map of land cover and illustrates the relationship of activity to concentrations of late seral forests and fragmentation. Observed high use areas are superimposed on model predictions in Figure 2.1B and show a general concordance among observed and expected murrelet activity, while a comparison of Figures 2.1A and 2.1B gives a sense of how late seral forests and fragmentation combine to predict activity. Figure 2.2 shows an equivalent area from a less fragmented portion of my study area in which the lower right corner again is federal land where I conducted no murrelet surveys. Further inspection of Figures 2.1 and 2.2 demonstrate that substantial amounts of the high-activity areas overlap edges between late and early seral forest, particularly in fragmented settings such as exemplified in Figure 2.1.

Discussion

Scale of marbled murrelet response to landscape characteristics – Marbled murrelets reacted to the landscape pattern in my study area at approximately the scale of “stands”, i.e., 400 m radius or 50 ha. I make this inference because of the large weight of evidence that their activity patterns mapped at the stand scale were correlated with a discrete set of landscape pattern and composition metrics, compared with very little support that patch-scale mapping of their activity covaried with landscape characteristics and the more diffuse evidence spread among the larger set of top models describing these relationships with neighborhood-scale activity maps. It appears that mapping activity patterns more broadly at the neighborhood scale obscured some of the consistent spatial patterning in the murrelet inland behavior I observed, while the more fine-grained mapping at the patch scale was dominated by sampling artifact (Jones et al. 1996). The spatial pattern of survey stations probably did not constrain these analyses because with their average 220 m nearest-neighbor distance, they were sufficiently dense to allow resolution of fine-grained variation if it did occur.

Marbled murrelets visit forests to establish and attend nests, however, much inland activity is also likely due to social behavior of non-breeders (Nelson 1997). It was not possible to distinguish breeders from non-breeders with the survey methods used in this study, but I recorded most activity during the late-season peak which appears to be driven by non-breeders (Nelson 1997, Gaston and Jones 1998, Chapter 1). These non-breeders apparently visit the forest to gain and maintain familiarity with nesting habitat, establish and maintain pair bonds, and prospect for future nests (Naslund 1993, Gaston and Jones 1998). This type of behavior is likely less spatially-focused than that of birds attending nests, and may have contributed to the spatial pattern I observed. Nearly all the activity recorded in this study is of murrelets in flight, often vocalizing (Chapter 1). It may be that the high-speed and limited maneuverability characteristic of marbled murrelet flight (Nelson 1997) requires this scale of spatial patterning even when birds are focused on spatially discrete resources such as individual nest trees. Conversely, the scale of murrelet activity may largely result from the unique landscape pattern of my study area, however that landscape provided a broad range of contrasts with 3-88% late seral forest surrounding (800 m radius) my survey stations. Or it may be that murrelets perceive, then respond to potential nesting habitat at this scale because of interactions among their physical capabilities, behavior patterns, and the physical, biological, and anthropogenic patterning of the landscape. I suggest that at least part of the pattern in their response is a somewhat general phenomenon because it occurred across the range of landscape conditions within my study area. Regardless of its causation, detecting the scale at which marbled murrelet activity covaried with landscape pattern enables better discrimination of resources that influence their behavior and can inform better decisions for their conservation (Weins 1989).

Marbled murrelet responses to landscape composition and pattern -- High levels of murrelet activity were consistently associated with concentrations of old-growth and late seral forest at the scale of patches and stands, old-growth within a 200 m radius (13 ha) and late-seral forest within 400 m (50 ha). In the satellite classification, old-growth and large sawtimber pixels intermingled in the same late seral forest patches, but those classified as old-growth contained trees of greater stature and had more complex canopy structure (WDFW 1994). Not surprisingly, murrelets appeared to be attracted to nesting habitat in late seral forest, with additional evidence that the local abundance of very large trees and extremely complex structure added to its general attractiveness. However none of the best models indicated that murrelet activity increased with the broader-scale abundance of old-growth or late seral forest, rather there was some indication of an inverse relationship in the presence of the fine-scale abundance of those features. This differed from findings of several other studies which found that nest sites (Ripple et al. 2003) or inland activity (Raphael et al. 1995, Meyer and Miller 2002) were associated with the broad-scale abundance of late seral forests. Possible, non-exclusive explanations for these disparate findings include, my findings reflected a local phenomenon related to 1) the unique landscape pattern of my study area and/or 2) to unique behavior of murrelets nesting there, or 3) the phenomenon I observed actually occurred in those other studies but their analyses were not structured to detect it.

The western Washington (Raphael et al. 1995) and Oregon Coast Range (Ripple et al. 2003) study areas are mosaics of private, state, and federal forest lands with ecological conditions and timber harvest histories rather similar to my study area, thus there is little support for the first explanation. Marbled murrelet inland behavior and habitat use seem broadly similar across Washington and Oregon (e.g., Nelson 1997), however the second possible explanation can not be ruled out with current information. I suggest that at least part of the disparity can be accounted for with the third explanation. Similar to those other studies, I found consistently positive univariate correlations of murrelet activity with the broad-scale abundance of late seral forest, however those models did not provide the best fit to my murrelet data. My analytical approach differed in that I used cell-based modeling with landscape covariates derived at multiple spatial scales to fit a continuous, probabilistic measure of murrelet activity, while those others used plot-based analyses with landscape covariates only at the scale of their often large plot sizes to model binary murrelet responses. Thus, they would not have been able to detect how responses covaried simultaneously with landscape characteristics at multiple scales. Additionally, it may have been difficult to resolve finer-grained relationships using binary responses. For example, Meyer and Miller (2002) found positive relationships with the amount of old-growth forest at the scale of their smallest plots (400 m) but models fit their data best with their largest plot sizes (3200 m, 32 km^2). They argued that since murrelet responses were integrated across broad areas in their large plots, unoccupied large plots were truly unused by murrelets, unlike their unoccupied smaller plots which were often close to occupied areas thus there was less certainty that their binary murrelet responses were correctly classified at finer scales.

Contrary to my *a priori* expectations, in the presence of locally abundant old-growth (13 ha scale) and late seral (50 ha scale) forest, murrelet activity increased with the abundance of high-contrast edges. And in my subsequent analyses that added early seral covariates to those models, the weight of evidence indicated that murrelet activity also increased with the abundance of early seral stages at the 400 and 800 m scales, particularly the open class which resulted from clearcut harvests of late seral forest within the previous 15 years. The unanticipated high levels of murrelet activity associated with high-contrast edge and early seral forest, i.e., fragmentation, were consistent and well-supported by the evidence, although taken together, covariates that indexed fragmentation were less than half as influential as those that indexed potential nesting habitat. While these findings are somewhat counter to the notion that marbled murrelets require interior old-growth forests (Meyer and Miller 2002), similar relationships have been discovered in other studies. Zharikov et al. (2006) found that murrelets nested closer than expected to recent clearcuts in southwestern British Columbia, Meyer and Miller (2002) found that murrelets were more likely to occupy large plots with abundant high-contrast edges in southern Oregon. However both of those studies described relationships with fragmentation at much broader scales than I observed. These findings implied that timber companies as well as murrelets were attracted to the same areas of old-growth forest (Zharikov et al. 2006). This is unlikely in my study where the correlation of murrelet activity with fragmented late seral and old-growth forests occurred at much finer scales. The most influential covariates of murrelet activity in my study area, the abundance of late seral forests at the 50 ha scale and old-growth at 13 ha, had strong inverse relationships with all the influential covariates that indexed fragmentation. Thus murrelets demonstrated high activity at places in this landscape that retained a high abundance of potential nesting habitat at the patch and stand scales despite substantial fragmentation. Likewise, even though there were strong positive correlations of the abundance of late seral forest across scales, I found high activity where those forests were abundant within 400 m but relatively scarce within 800 m. These findings raise questions important to marbled murrelet ecology and conservation: 1) Are murrelets truly attracted to fragmented nesting habitat, or are there alternative explanations for my findings? 2) If murrelets select nest sites in fragmented settings, what are the implications for the Olympic Peninsula portion of their population?

My findings do not appear to be due to greater detectability of birds in more fragmented portions of the landscape, as detections were more frequent from survey stations within late seral patches than from those on their edges (Horton and Harrison 2000). Nearby timber harvests may have displaced murrelets to remaining habitat, but watershed-scale studies that used radar to relate murrelet numbers to habitat area (Burger 2001, Raphael et al. 2002a) suggested that birds did not pack into habitat that remained after timber harvest. Within-watershed packing would not have been detected in those studies, so it remains a possible explanation for my findings although it seems unlikely that birds which apparently disperse freely among watersheds (Burger 2001, Raphael et al. 2002a) would preferentially exhibit such fine-grained dispersal within watersheds. Due to the juxtaposition of DNR-managed land with other ownerships, portions of the periphery of the utilization distribution (i.e., mapped low activity areas) occurred over contiguous late seral forest in National Park or National Forest lands merely because I had no survey stations there. It is possible this introduced an artifactual relationship of low activity with unfragmented late seral forest, however less than 7% of the lowest quartile of the UD was over those federal lands so the influence of this artifact was rather small.

The positive relationship among marbled murrelet activity and fragmentation appears to be due in part to the scale at which I mapped their activity, however the primary source of this relationships is due to the high levels of murrelet activity that occurred in and around late seral fragments (Figures 2.1, 2.2). I propose that my findings reflect an actual phenomenon that occurred during my study, marbled murrelets tolerated substantial fragmentation so long as potential nesting habitat was sufficiently abundant. The high use of fragmented habitat may be due to the tendency of murrelets to conduct display flights and access their actual or potential nesting areas over and through canopy gaps (Nelson 1997), in this case clearings that resulted from timber harvest. The phenomenon appeared to be persistent, in that I failed to detect much evidence that activity declined at late seral patches where 15-30 year-old saplings were abundant in the fragmented matrix. This is somewhat puzzling in light of the overall decline in activity levels across the study area over the course of the 8-year study, even though no late seral forests were harvested during that time (Chapter 1) and more direct estimates of abundance did not detect declines (Cooper et al. 2006, Miller et al. 2006). To reconcile these apparently inconsistent observations, I posit that murrelets left the OESF broadly as a delayed response to the overall decline in the abundance of nesting habitat but because of their affinity for canopy gaps, those that remained continued to be attracted to local concentrations of potential nesting habitat in these uniquely fragmented settings. However, widespread very high levels of marbled murrelet activity in nearby, abundant, unfragmented nesting habitat in the wilderness of Olympic National Park (Hall 2000), as well as in less fragmented portions of my study area, demonstrate that contiguous old forests provide high-quality habitat and are consistent with other observations that at the watershed scale, the abundance of murrelets and their inland habitat are correlated (Burger 2001, Raphael et al. 2002a).

The extent to which marbled murrelets actually nest in fragmented habitat in the OESF is not known. Murrelets nesting in fragmented settings may experience reduced nest success as higher levels of predation have been observed at actual (Manley and Nelson 1999) and simulated (Raphael et al. 2002b, Malt and Lank 2007) nests near edges with early seral stands. However this is not an unequivocal phenomenon, Raphael et al. (2002a) found the lowest predation rates at simulated murrelet nests in fragmented landscapes >5 km from human settlements and recreation areas and did not detect significant edge effects on predation in those settings that reflect the large majority of the OESF. If predation risk is higher near edges with early seral stands, it should be a transient phenomenon as succession in early seral stands leads to "soft edges" where Malt and Lank (2007) found low predation on simulated nests at edges with 20-40 year-old stands, possibly because nest predators such as Steller's jays (*Cyanocitta stelleri*) avoid those dense, closed-canopy stands (Raphael et al. 2002b, Marzluff et al. 2004). In the Oregon Coast Ranges where no extensive wilderness areas exist, Ripple et al. (2003) found that murrelets nested more frequently in habitat patches with abundant neighboring stands of dense, 30-50 year old timber, suggesting that habitat patches may become more attractive as successional processes in their surroundings provide an increasingly secure context. These situations were not available during my study due to the historic timing and pattern of timber harvests, however they will develop abundantly over the upcoming decades.

On the Olympic Peninsula, the substantial majority of nesting habitat for marbled murrelets occurs in unfragmented settings on the Olympic National Forest and National Park (Raphael et al. 2006). Since the inland abundance of murrelets correlates with that of their nesting habitat (Burger 2002, Raphael et al. 2002a), the predominant influences on population processes will occur in those areas. While the potentially more risky, fragmented habitat patches appear to be attractive to murrelets in the OESF, it does not appear they constitute an ecological trap (Battin 2004) as the temporal trends in abundance summarized above (Chapter 1, Cooper et al. 2006) suggest that birds are not abandoning the likely superior wilderness habitat for these areas. Although murrelets nesting in these fragmented settings may be in local sinks (Pulliam 1988), over the next several decades growth in the surrounding early seral stands will provide what may be an increasingly secure environment around many of these potential nesting areas and possibly increase the proportion of these habitat patches that can serve as local sources. Over the still longer-term, as late seral nesting habitat is restored in the OESF and other sustainably managed forests throughout the range of the marbled murrelet, increased nesting opportunities that span a range of conditions can increase the carrying capacity for this species.

Implications for Forest Management -- My findings are relevant to managers of commercial forests with objectives for pro-active conservation and restoration of marbled murrelet habitat. Marbled murrelets can be attracted to nesting habitat in fragmented settings in managed forests, thus management to maintain and/or restore local concentrations of high-quality habitat may serve conservation objectives. Further fragmentation of existing late-seral forests is not justified, because it would diminish the overall abundance of potential nesting habitat which is likely the principal factor limiting marbled murrelet distribution and abundance. Streamside areas and unstable hill slopes, which are abundant in many forest properties (e.g. nearly 40% of the OESF) can be managed to provide habitat that attracts nesting marbled murrelets and support other conservation and commercial objectives. Managers should seek to establish a high density of potential nesting habitat within discrete areas of approximately 400 m radius (50 ha). The principal management focus should be to provide local concentrations of habitat because habitat abundance had twice the influence on activity as did fragmentation. Management for commercial and other objectives can provide a variety of contexts around these habitat patches, which may be appropriate until further research elucidates these influences on population processes.

It appears that a multiscaled approach to integrate conservation and commercial objectives can enable some commercial forest properties to serve marbled murrelet conservation. In such an approach, forest managers might implement extensive, commercially-oriented silvicultural treatments in portions of their properties where murrelet conservation was not consistent with other objectives and more fine-grained application of a variety of management actions, including no harvest and silviculture designed to restore murrelet habitat (e.g., DeBell et al. 1997, Tappeiner et al. 1997) in other areas where murrelet conservation was a focal objective. However, indirect measures of habitat use such as I used in this study can not inform wildlife and forest managers of the key population processes that occur in inland habitat, nesting and fledging rates. Direct studies of marbled murrelet nesting ecology in managed-forest settings can help refine forest management and enable more effective integration of conservation and commercial objectives.

Table 2.1. List of broadly-formed hypotheses used to structure investigations of the covariation of marbled murrelet inland activity with landscape pattern and composition (1994-2001) in the Olympic Experimental State Forest, Washington, USA.

Hypotheses	**Covariates**	**Direction of relationship(s)**	**References**
Murrelets respond to habitat pattern at multiple spatial scales, from the scale of stands (50 ha) to small watersheds (3200 ha)	Abundance, configuration, and context of habitat	various	Meyer et al. (2002), Raphael et al. (1995)
Murrelets are attracted to abundant and/or contiguous habitat	Habitat abundance and contiguity	+	Burger (2001), Raphael et al. (2002a)
Murrelets are attracted to interior forest habitat	Abundance of interior forest habitat	+	Meyer and Miller (2002)
High-contrast edges can influence murrelet responses	Edge contrast	+ or -	Ripple et al. (2003), Meyer et al. (2002)
Murrelets are attracted to particular geographic and topographic qualities	Streams, elevation, slope, topographic complexity	+	Hamer (1995)
Compositional diversity of landscapes can diminish their attractiveness	Landscape diversity metrics	-	Marzluff and Restani (1999), Marzluff et al. (2003)
Murrelets demonstrate a time-lag in their negative responses to fragmentation	Time since fragmentation	-	Meyer et al. (2002), Chapter 1

Table 2.2. Candidate models for evaluating covariation of marbled murrelet inland activity with landscape pattern and composition (1994-2001) in the Olympic Experimental State Forest, Washington, USA. Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG; late seral, LT; mature, MT; or the density of interior forest, classified by type, [Type] CORE. Landscape metrics index contrast-weighted edge density, CWED; and Shannon's evenness index, SHEI.

Just Habitat				
Model #	**v1**	**v2**	**v3**	**v4**
1	OG_200			
2	OG_400			
3	OG_800			
4	OG_200	LT_400		
5	OG_200	LT_800		
6	OG_400	LT_800		
7	LT_400			
8	LT_800			
9	LT_1600			
10	LT_400	LT_800		
11	LT_400	LT_1600		

Table 2.2. continued

Core Habitat				
Model #	**v1**	**v2**	**v3**	**v4**
12	LT CORE_200			
13	LT CORE_400			
14	LT CORE_800			
15	LT CORE_1600			
16	OG_200	LT CORE_200		
17	OG_200	LT CORE_400		
18	OG_200	LT CORE_800		
19	OG_200	LT CORE_1600		
20	OG_200	MT CORE_200		
21	OG_200	MT CORE_400		
22	OG_200	MT CORE_800		
23	OG_200	MT CORE_1600		
24	OG_400	LT CORE_400		
25	OG_400	LT CORE_800		
26	OG_400	LT CORE_1600		
27	OG_400	MT CORE_400		
28	OG_400	MT CORE_800		
29	OG_400	MT CORE_1600		
Edge and Habitat				
Model #	**v1**	**v2**	**v3**	**v4**
30	OG_200	CWED_200		
31	OG_400	CWED_400		
32	LT_400	CWED_400		
33	LT_800	CWED_800		
34	OG_200	LT_400	CWED_400	
35	OG_400	LT_800	CWED_400	
36	OG_400	LT_800	CWED_800	

Table 2.2. continued

Edge and Core Habitat				
Model #	**v1**	**v2**	**v3**	**v4**
37	LT CORE_200	CWED_200		
38	LT CORE_400	CWED_400		
39	LT CORE_800	CWED_800		
40	OG_200	LT CORE_200	CWED_200	
41	OG_200	LT CORE_400	CWED_400	
42	OG_400	LT CORE_400	CWED_400	
43	OG_400	LT CORE_800	CWED_800	
44	OG_200	MT CORE_200	CWED_200	
45	OG_200	MT CORE_400	CWED_400	
46	OG_400	MT CORE_400	CWED_400	
47	OG_400	MT CORE_800	CWED_800	
Habitat, Core, Edge and Evenness				
Model #	**v1**	**v2**	**v3**	**v4**
48	OG_200	LT CORE_200	CWED_200	SHEI_200
49	OG_400	LT CORE_400	CWED_400	SHEI_400
50	OG_400	LT CORE_800	CWED_800	SHEI_1600
51	OG_400	LT CORE_800	CWED_1600	SHEI_1600
52	OG_200	MT CORE_200	CWED_200	SHEI_200
53	OG_400	MT CORE_400	CWED_400	SHEI_400
54	OG_400	MT CORE_800	CWED_800	SHEI_800
55	OG_400	MT CORE_800	CWED_1600	SHEI_1600

Table 2.3. The average weights of evidence ($\bar{w}_i$) for models with $\Delta_i \leq 8$ in at least one sample, frequencies that models were selected as best (π_i), and ratios of evidence relative to the top model in correlation analyses of marbled murrelet activity, mapped at the patch (200 m) scale, with landscape pattern and composition (N = 100). Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG; late seral, LT; mature, MT; or the density of interior forest, classified by type, [Type] CORE. Landscape metrics index contrast-weighted edge density, CWED; and Shannon's evenness index, SHEI.

Model	**Covariates**	$\bar{w}_i$	π_i	**Evidence Ratio**
52	OG_200, MT CORE_200, CWED_200, SHEI_200	0.226	0.35	
48	OG_200, LT CORE_200, CWED_200, SHEI_200	0.199	0.15	1.1
34	OG_200, LT_400, CWED_400	0.103	0.18	2.2
44	OG_200, MT CORE_200, CWED_200	0.099	0.08	2.3
40	OG_200, LT CORE_200, CWED_200	0.074	0.02	3.1
4	OG_200, LT_400	0.060	0.08	3.8
30	OG_200, CWED_200	0.036	0.03	6.2
1	OG_200	0.025	0.03	8.9
23	OG_200, MT CORE_1600	0.018	0.01	12.4
19	OG_200, LT CORE_1600	0.018	0.01	12.7
20	OG_200, MT CORE_200	0.017	-	13.2
5	OG_200, LT_800	0.017	-	13.6
16	OG_200, LT CORE_200	0.017	0.01	13.7
18	OG_200, LT CORE_800	0.014	0.01	16.3
17	OG_200, LT CORE_400	0.014	0.01	16.4
22	OG_200, MT CORE_800	0.014	0.01	16.6
21	OG_200, MT CORE_400	0.013	-	17.5
45	OG_200, MT CORE_400, CWED_400	0.009	-	25.0
41	OG_200, LT CORE_400, CWED_400	0.009	0.01	25.4
10	LT_400, LT_800	0.007	0.01	31.4
32	LT_400, CWED_400	0.004	-	56.5
7	LT_400	0.004	-	57.7
11	LT_400, LT_1600	0.003	-	86.4
12	LT CORE_200	0.000	-	696.4
37	LT CORE_200, CWED_200	0.000	-	841.1
49	OG_400, LT CORE_400, CWED_400, SHEI_400	0.000	-	2932.0
53	OG_400, MT CORE_400, CWED_400, SHEI_400	0.000	-	3176.1

Table 2.4. The average standardized regression coefficients and their 95% confidence intervals, weights of evidence ($\bar{w}_i$) for models with $\Delta_i \leq 8$, frequencies that models were selected as best (π_i), and ratios of evidence relative to the top model in correlation analyses of marbled murrelet activity, mapped at the stand (400 m) scale, with landscape pattern and composition (N = 160). Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG and late seral, LT. Landscape metrics index contrast-weighted edge density, CWED.

Model	**Covariates, their Average Standardized Coefficients and 95% Confidence Intervals (N = 160)**			$\bar{w}_i$	π_i	**Evidence Ratio**
34	OG_200	LT_400	CWED_400	0.814	0.844	
	422.5 ± 9.5	580.4 ± 9.6	144.4 ± 5.2			
10	LT_400	LT_800		0.146	0.150	5.6
	1,198.2 ± 7.6	-446.7 ± 9.2				
4	OG_200	LT_400		0.040	0.006	20.4
	415.5 ± 9.4	515.5 ± 9.4				

Table 2.5. The average weights of evidence ($\bar{w}_i$) for all models with $\Delta_i \leq 8$, frequencies that models were selected as best (π_i), and ratios of evidence relative to the top model in correlation analyses of marbled murrelet activity, mapped at the neighborhood (550 m) scale, with landscape pattern and composition (N = 210). Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG; late seral, LT; mature, MT; or the density of interior forest, classified by type, [Type] CORE. Landscape metrics index contrast-weighted edge density, CWED; and Shannon's evenness index, SHEI.

Model	**Covariates**	$\bar{w}_i$	π_i	**Evidence Ratio**
10	LT_400, LT_800	0.390	0.410	
34	OG_200, LT_400, CWED_400	0.370	0.395	1.1
11	LT_400, LT_1600	0.201	0.176	1.9
4	OG_200, LT_400	0.034	0.014	11.4
49	OG_400, LT CORE_400, CWED_400, SHEI_400	0.005	0.005	83.0
53	OG_400, MT CORE_400, CWED_400, SHEI_400	0.001	-	372.5
32	LT_400, CWED_400	0.000	-	1010.8

Table 2.6. Average standardized coefficients for landscape pattern and composition covariates of the best 4 models describing marbled murrelet activity mapped at the neighborhood (550 m) scale (N = 210). Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG and late seral, LT. Landscape metrics index contrast-weighted edge density, CWED.

Model	**Covariates, their Average Standardized Coefficients and 95% Confidence Intervals (N = 210)**		
10	LT_400	LT_800	
	962.0 ± 5.7	-273.7 ± 7.2	
34	OG_200	LT_400	CWED_400
	158.6 ± 5.2	689.1 ± 6.2	97.0 ± 3.2
11	LT_400	LT_1600	
	892.0 ± 4.1	-224.0 ± 5.8	
4	OG_200	LT_400	
	155.6 ± 5.2	651.5 ± 6.1	

Table 2.7. Model structure, average weights of evidence ($\bar{w}_i$), frequencies that models were selected as best (π_i), and ratios of evidence relative to the top model for all models with $\Delta_i \leq 8$ that included fragmentation covariates for describing the relationship of marbled murrelet activity mapped at the stand (400 m) scale to landscape composition and pattern (N = 160). Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG; late seral, LT; open, OP; sapling, SAP. Landscape metrics index contrast-weighted edge density, CWED.

Base Model	**Base Model Covariates**	**Early Seral Covariates**		$\bar{w}_i$	π_i	**Evidence Ratio**
34	OG_200, LT_400, CWED_400	OP_800	SAP_800	0.453	0.556	1.0
34	OG_200, LT_400, CWED_400	OP_400	-	0.193	0.225	2.4
34	OG_200, LT_400, CWED_400	OP_800	-	0.166	0.106	2.7
34	OG_200, LT_400, CWED_400	OP_400	SAP_400	0.101	0.038	4.5
34	OG_200, LT_400, CWED_400	OP_200	SAP_200	0.030	0.019	15.1
34	OG_200, LT_400, CWED_400	-	SAP_200	0.029	0.031	15.9
10	LT_400, LT_800	OP_200	SAP_200	0.017	0.025	26.9
10	LT_400, LT_800	-	SAP_200	0.003	-	162.1
34	OG_200, LT_400, CWED_400	-	SAP_400	0.002	-	182.3
4	OG_200, LT_400	OP_800	SAP_800	0.002	-	226.8
4	OG_200, LT_400	OP_200	SAP_200	0.002	-	227.6
10	OG_200, LT_400	OP_400	-	0.001	-	307.3
10	LT_400, LT_800	OP_400	SAP_400	0.001	-	719.5
10	LT_400, LT_800	-	SAP_400	0.000	-	1794.7
10	LT_400, LT_800	OP_800	-	0.000	-	4326.9
4	OG_200, LT_400	-	SAP_200	0.000	-	5241.6
4	OG_200, LT_400	OP_800	-	0.000	-	5638.5

Table 2.8. Average standardized coefficients for landscape pattern and composition for the best models that included early seral land cover covariates for describing marbled murrelet activity mapped at the stand (400 m) scale (N = 160). Covariates are abbreviated following the format, [Class or Landscape Metric]_Scale (in meters). Class metrics index the density of forest types, old-growth, OG; late seral, LT; open, OP; sapling, SAP. Landscape metrics index contrast-weighted edge density, CWED.

Average Standardized Coefficients and 95% Confidence Intervals (N = 160)				
Base Model Covariates			**Early Seral Covariates**	
OG_200	LT_400	CWED_400	OP_800	SAP_800
347.3 ± 9.7	853.6 ± 12.6	200.3 ± 5.8	273.3 ± 6.5	95.4 ± 5.7
OG_200	LT_400	CWED_400	OP_400	
391.7 ± 9.4	928.3 ± 12.4	343.2 ± 7.6	335.7 ± 7.3	
OG_200	LT_400	CWED_400	OP_800	
363.6 ± 9.6	791.8 ± 11.3	220.2 ± 5.8	248.6 ± 6.2	
OG_200	LT_400	CWED_400	OP_400	SAP_400
394.1 ± 9.5	897.1 ± 15.6	340.7 ± 7.6	314.7 ± 9.3	-24.6 ± 6.2
OG_200	LT_400	CWED_400	OP_200	SAP_200
384.3 ± 9.5	520.6 ± 9.3	187.2 ± 5.6	-42.0 ± 7.1	-154.4 ± 5.1
OG_200	LT_400	CWED_400		SAP_200
396.1 ± 9.2	552.1 ± 9.3	187.2 ± 5.6		-142.7 ± 4.4
LT_400	LT_800		OP_200	SAP_200
981.4 ± 12.3	-384.3 ± 9.3		-139.3 ± 7.0	-169.8 ± 5.7

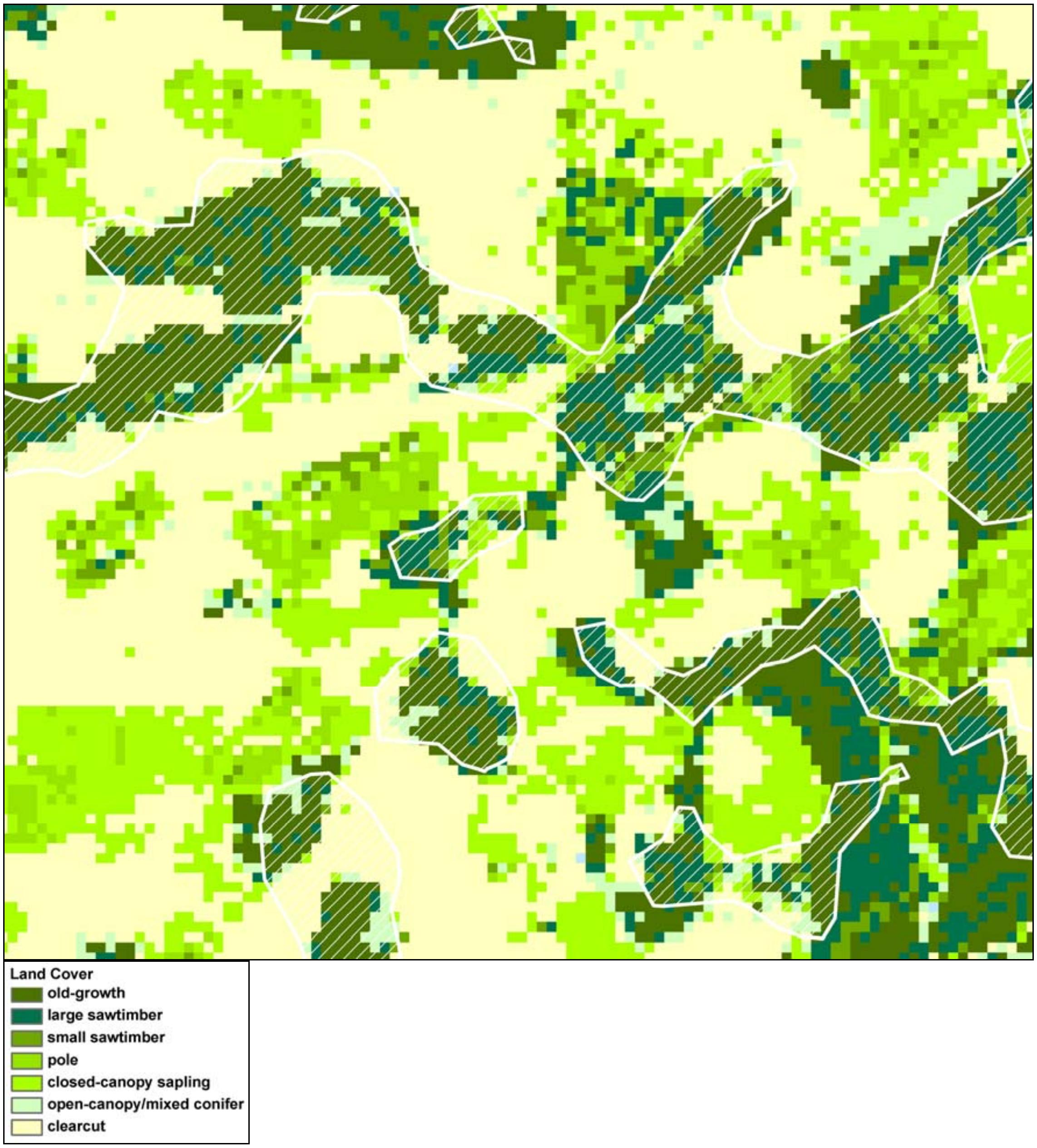


Figure 2.1A. Land cover and observed high levels of marbled murrelet activity (upper quartile of activity mapped at the 50 ha scale, represented by hatched polygons outlined in white) in a 25 km^2 portion of the Olympic Experimental State Forest (1:26,000 scale) with relatively high levels of fragmentation of late seral forests.

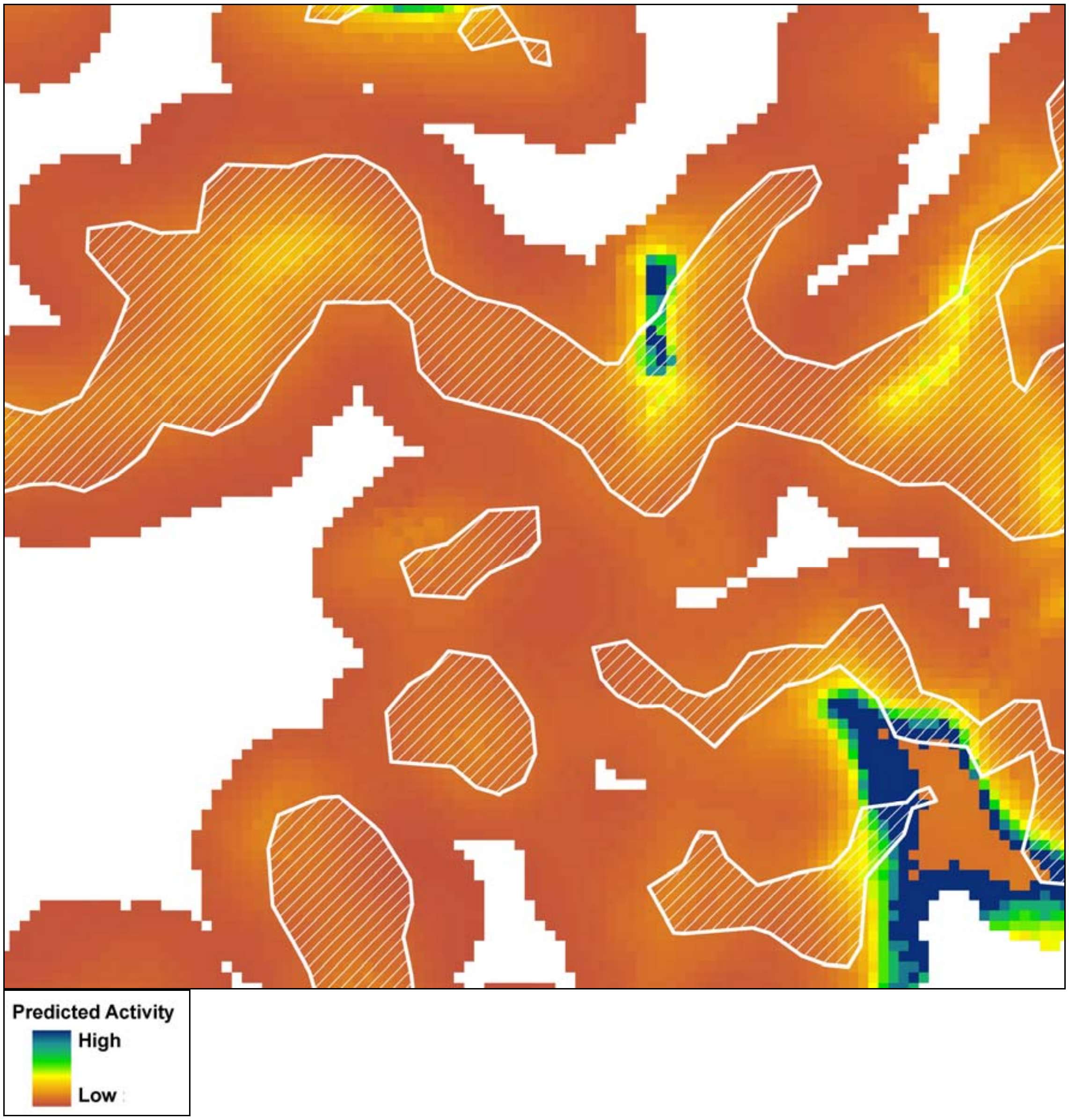


Figure 2.1B. Predicted levels of marbled murrelet activity and observed high levels of marbled murrelet activity (upper quartile of activity mapped at the 50 ha scale, represented by hatched polygons outlined in white) in a 25 km^2 portion of the Olympic Experimental State Forest (1:26,000 scale) with relatively high levels of fragmentation of late seral forests.

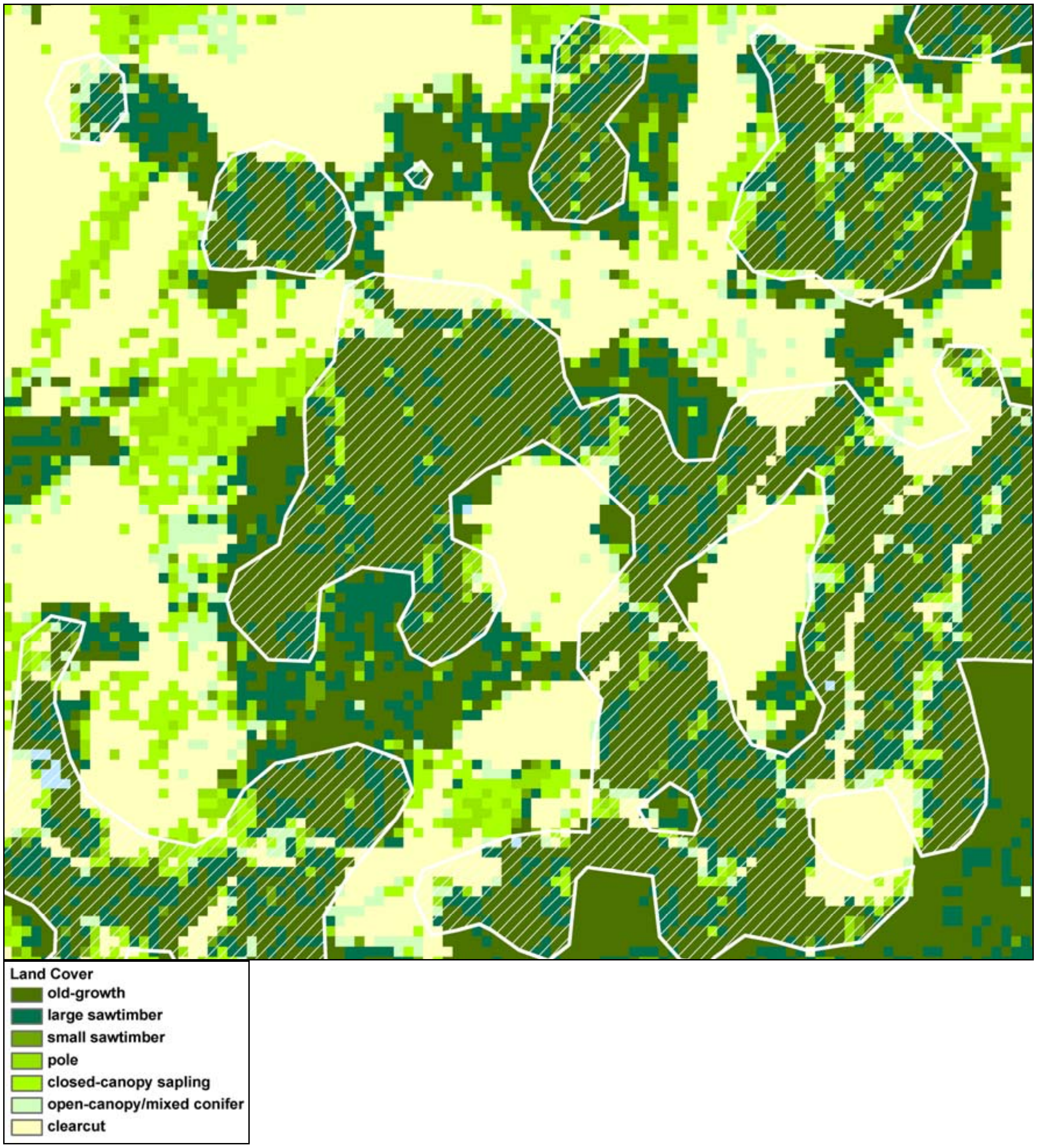


Figure 2.2A. Land cover and observed high levels of marbled murrelet activity (upper quartile of activity mapped at the 50 ha scale, represented by hatched polygons outlined in white) in a 25 km^2 portion of the Olympic Experimental State Forest (1:26,000 scale) with relatively low levels of fragmentation of late seral forests.

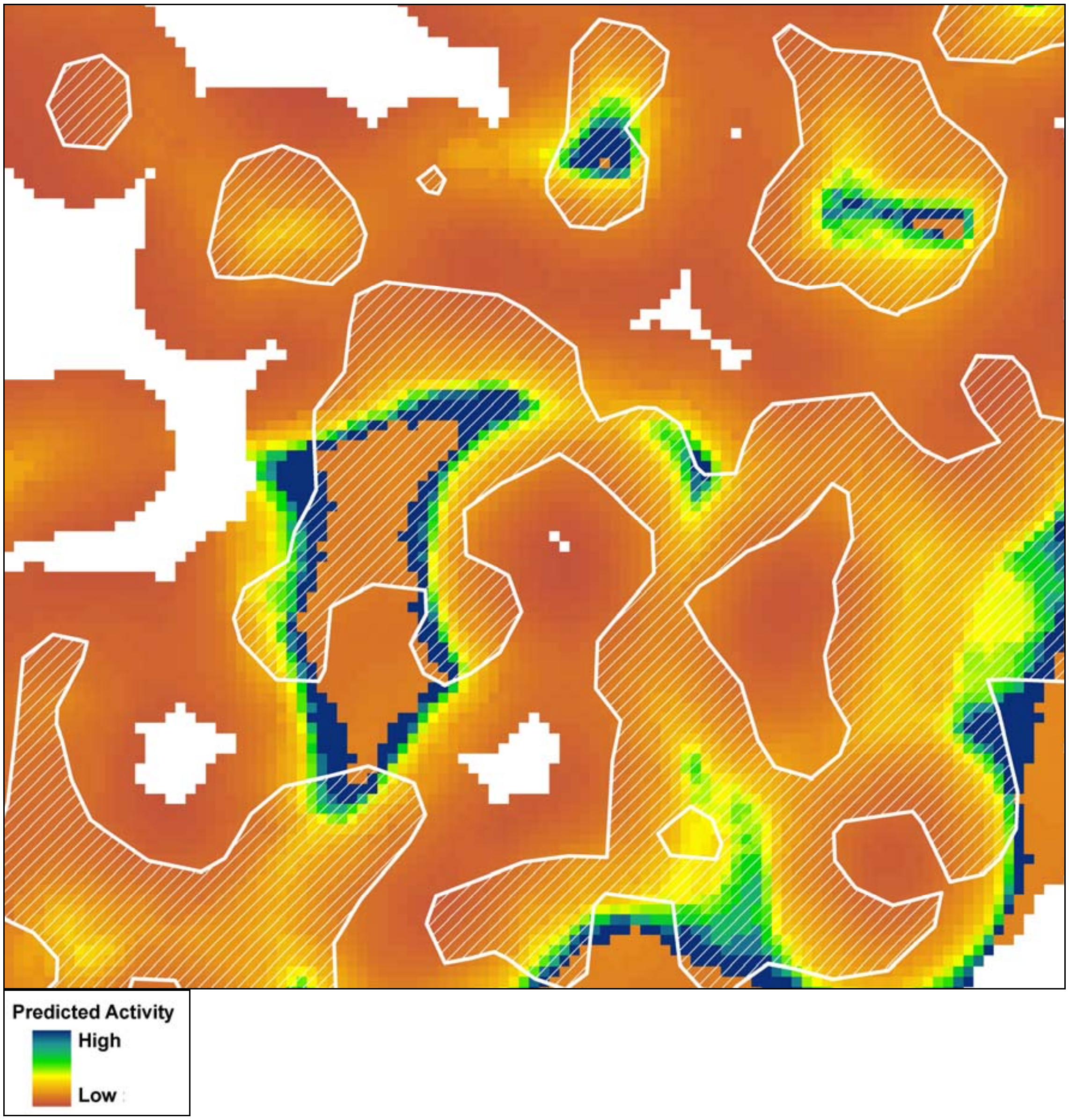


Figure 2.2B. Predicted levels of marbled murrelet activity and observed high levels of marbled murrelet activity (upper quartile of activity mapped at the 50 ha scale, represented by hatched polygons outlined in white) in a 25 km^2 portion of the Olympic Experimental State Forest (1:26,000 scale) with relatively low levels of fragmentation of late seral forests.

Chapter 3. Predicting Marbled Murrelet Population Responses to a Realistic Approach to Managing Multiple-use Forests for Marbled Murrelet Conservation: the DRAFT Washington Department of Natural Resources Marbled Murrelet Conservation Strategy

Effective conservation of rare or declining species requires an integrated understanding of population processes, their cause-and-effect relationships with environmental influences, and ultimately how management affects key population processes (Williams et al. 2001, Sinclair et al. 2006). Achieving that level of knowledge requires long-term, large-scale experimental or observational studies, however land and wildlife managers frequently must plan and implement management actions before achieving reliable, integrated knowledge (Marzluff et al. 2000). In most cases it is not feasible to employ a strictly precautionary approach to minimize conservation risk in the face of uncertainty, because natural resources management decisions must be made in consideration of their broad ecological, economic, and social context (Johnson 1997). Trade-offs between species conservation and other objectives can be explored with simulation models to reveal potential solutions that better integrate among competing objectives (Carey et al. 1999). Likewise, population modeling can highlight key uncertainties about the relationship of management with population processes, thus informing the design of research and monitoring efforts to resolve them (Burgman et al. 1993).

The marbled murrelet (*Brachyramphus marmoratus*) was listed, in 1992, as a Threatened Species in Washington, Oregon, and California under the U.S Endangered Species Act because those populations were believed to be declining, principally because fecundity was insufficient to maintain a stable population (U.S. Fish and Wildlife Service 1997). It was proposed that timber harvests reduced the amount of nesting habitat in older forests, thus decreasing the proportion of the population that could find nest sites; and that nests in forests fragmented by logging were subject to deleterious edge effects, especially predation, that reduced their success rate (U.S. Fish and Wildlife Service 1997). Subsequent research suggested that potential nesting habitat and murrelet abundance covary at the scale of watersheds (Burger 2002, Raphael et al. 2002a), that nest failure can contribute to declining populations (Peery et al. 2004b), and that fragmentation can influence nest success (Raphael et al. 2002b) although there is uncertainty as to the nature and extent of those effects (Raphael et al. 2002b, Zharikov et al. 2006). Thus the survival and recovery of this secretive, forest-nesting seabird may depend on effective conservation and management of its inland habitat that leads to the increased abundance and security of nest sites resulting in increased rates of nesting and fledging.

Forest management can be more or less effective at achieving murrelet conservation while also attending to other ecological, social, and economic objectives, depending in part on how well management actions actually address key population processes. Uncertainty about the mechanistic relationships of those processes with the composition, structure, configuration, and context of forests limits the ability of forest and wildlife managers to effectively integrate murrelet conservation with other objectives. However, the Washington State Department of Natural Resources (DNR) is required to conserve marbled murrelets as well as achieve a broad suite of ecological, social, and economic objectives. Thus, DNR drafted a plan for marbled murrelet conservation on state forests along the Pacific Coast of Washington that focused on increasing the amount and quality of nesting habitat to support greater rates of nesting and nest success (DNR 2007). That draft implements DNR's Habitat Conservation Plan (DNR 1997) and predicted the current and future capability of state forests to provide murrelet nest sites and the edge environment of those nest sites under the proposed approach to habitat management. It did not predict how that management might influence murrelet population processes nor did it examine how the quantity, quality, configuration, and context of murrelet habitat might influence conservation outcomes. Nevertheless, it provides a robust set of baseline data that reflect a realistic forest management scenario to achieve marbled murrelet conservation while considering the broad objectives for ecological, economic, and social outcomes from Washington's State Forests (DNR 2006).

I use population modeling to provide an explicit, consistent framework to represent current knowledge and assumptions about marbled murrelet ecology and responses to habitat conditions (Beissinger et al. 2006). My objectives are to: 1) estimate current and predicted future habitat conditions for marbled murrelets, 2) project marbled murrelet population responses to current and predicted future habitat conditions, 3) explore potential conservation consequences of the uncertainty about mechanistic relationships between murrelet demographic rates and habitat conditions, 4) evaluate the potential role of marbled murrelet dispersal behavior in the relationship of population processes with habitat conditions, 5) evaluate the potential for realistic forest management scenarios based on the DNR draft murrelet conservation strategy (DNR 2007) to achieve marbled murrelet conservation, and 6) explore the conservation consequences of alternative forest management scenarios. I do not intend this modeling to provide an assessment of extinction risk, nor do I propose that modeling results be viewed as explicit predictions of future murrelet abundance or vital rates. I intend that results from these exercises be viewed in a relative sense to inform the development, evaluation, and possible implementation of alternative management approaches to murrelet conservation (Beissinger and Westphal 1998), and to help focus research and monitoring efforts to resolve key uncertainties about the relationship of murrelet populations to forest management.

Background

Marbled murrelet population ecology -- Marbled murrelet populations appear to be influenced by forest habitat in two dimensions that can be estimated and predicted with forest inventory and modeling techniques. The quality and quantity of habitat influences the numbers of nest sites available, while the context of that habitat influences nest success. The interaction of those dimensions of habitat influence the numbers of juvenile murrelets that enter the population and thus the rate of population growth or decline. Forest stands with large trees that support large limbs, and with complex canopy structure provide opportunities for murrelets to locate and access their platform nest sites (Nelson 1997). Murrelet use becomes increasingly likely as large trees and canopy complexity increase within forest stands (Burger 2002). Those attributes increase as forest succession proceeds, and their development can be influenced by silviculture (Franklin et al. 2002). Forest inventory data can be used to estimate the occurrence and abundance of large trees and complex canopy structure while forest growth models can predict their development under a variety of silvicultural regimes (DNR 2007).

Forest landscapes, such as discrete areas defined by watersheds, are visited by murrelets in numbers proportional to the abundance of potential nesting habitat within them. Radar studies of marbled murrelet inland behavior on the Olympic Peninsula (Raphael et al. 2002a) and estimates of habitat abundance (Raphael et al. 2006) indicated a consistent relationship of 1 murrelet per approximately 396 acres of habitat. Radio-telemetry studies of murrelet inland behavior (Peery et al. 2004a) suggest that approximately 43% of the population is likely to be detected with radar thus a carrying capacity (*K*) of 170 acres per murrelet (i.e., 396 * 0.43) may be proposed. Applying this relationship to habitat estimates for coastal areas of Washington (Raphael et al. 2006) predicts a population within 10% of estimates derived from at-sea surveys (Miller et al. 2006).

Nelson and Hamer (1995) hypothesized that edges between early and late seral forest support abundant marbled murrelet nest predators and/or lead to decreased concealment of murrelet nests. Subsequent observations at a collection of murrelet nests in British Columbia, Washington, Oregon, and California found diminished nest success within 50 m of the forest edge (Manley and Nelson 1999). However there is considerable uncertainty around the hypothesis of a simple relationship between a nest's proximity to stand edges and its success. Elements of this uncertainty include what types of edges are risky (Malt and Lank 2007) and the lack of a negative edge effect at a large sample (N = 137) of murrelet nests located with radio-telemetry in southwestern British Columbia (Zharikov et al. 2006). Additional uncertainty derives from the apparently complicated relationship among the interaction of human residential, agricultural, and recreational developments with edge effects (Raphael et al. 2002b). An experiment on the Olympic Peninsula used simulated murrelet nests to test the effects of stand structure, fragmentation, and human influence on predation risk (Marzluff et al. 2000, Raphael et al. 2002b). This research, which did not find a simple relationship of increased predation risk in proximity to stand edges (Raphael et al. 2002b), led to a spatially-explicit prediction of predation risk that explained variability in nest predation as a multivariate linear function of the composition and pattern of the surrounding landscape at a fairly broad scale (Marzluff et al. 2003). This model was tested in 2001-2002 by replicating the simulated nest experiment and by studying the fates of natural songbird nests in areas predicted to have either low or high predation. Results from those tests were in accordance with model predictions (Marzluff et al. 2003). Regardless of the uncertainty and competing views, nest-site security is likely a key influence of forest habitat on murrelet populations.

Marbled murrelet dispersal behavior -- Avian dispersal occurs when established breeders change nest sites and when young birds leave their natal sites to breed elsewhere, categorized as breeding and natal dispersal respectively (Greenwood and Harvey 1982). Dispersal behavior in colony-nesting alcids has been well-studied with observations of banded birds but the secretive, non-colonial nesting habits of marbled murrelets preclude these methods, thus generalizations from their colonial relatives and assumptions about their nesting ecology are the basis for inference about their dispersal behavior (Divoky and Horton 1995). Most alcids demonstrate considerable fidelity to their nest sites, with breeding dispersal related to dynamics of their nesting habitat, mortality of pair-members, the availability of nest sites, and nesting success (Divoky and Horton 1995). Breeding dispersal in marbled murrelets is predicted to be similarly low, although high rates of nest failure (Divoky and Horton 1995) and the dynamic nature of their forest habitat (Lertzman et al. 1996, Franklin et al. 2002) could be expected to increase the rate and possibly the distance of breeding dispersal (Divoky and Horton 1995). Most dispersal in alcids is probably due to natal dispersal, and marbled murrelets are likely to exhibit high rates of natal dispersal relative to other alcids because of their large breeding range, extensive areas of inland nesting habitat, and high vagility (Divoky and Horton 1995). Natal dispersal is generally favored over philopatry as nesting resources, including potential mates and nest sites, become less predictable (Clobert et al. 2001). Departure and settlement decisions by a wide range of species in both breeding and natal dispersal can be informed by a variety of environmental cues to habitat suitability, including the behavior of conspecifics (Danchin et al. 2001). These cues likely direct marbled murrelet natal and breeding dispersal as well. Divoky and Horton (1995) noted that marbled murrelet dispersal could confound interpretations of the role particular habitat areas play in their conservation, with immigration potentially maintaining population levels in sink areas (Pulliam 1988). This phenomenon has been documented in the central California marbled murrelet population (Peery et al. 2006a).

DNR draft conservation strategy -- The abundance and distribution of murrelets and their inland habitat varies regionally within Washington, as does the distribution and abundance of DNR-managed lands and murrelet habitat on them. On the western Olympic Peninsula, where DNR manages the Olympic Experimental State Forest (OESF, DNR 1997), 46% of the 1.8 million-acre land base as defined by watershed boundaries is within the federally-managed Olympic National Forest and National Park, 15% is managed by DNR, while lands managed by corporations or tribal governments for commercial timber production comprise most of the remainder (Figure 3.1). Marbled murrelets and their habitat are rather abundant (Miller et al. 2006, Raphael et al. 2006). Murrelet habitat is estimated to comprise 32% of the land base and is of relatively high quality in the old-growth forests that are particularly abundant on the federal lands which contain 74% of the murrelet habitat. DNR-managed land contains 12.5% of the murrelet habitat in OESF where existing conservation agreements for DNR-managed lands (DNR 1997) direct substantial habitat conservation that is consistent with murrelet conservation objectives. This contrasts sharply with southwest Washington (SWWA), where there is essentially no federal land or federally-managed habitat (Figure 3.1). Marbled murrelets and their inland habitat are relatively scarce in SWWA (Miller et al. 2006, Raphael et al. 2006), with 11% of the 2.5 million-acre land base estimated to be murrelet habitat. Although DNR-managed lands comprise 13% of the land base, they contain 28% of the murrelet habitat in an area dominated by forest industry lands (Figure 3.1). Existing conservation agreements for DNR-managed lands in SWWA are much less consistent with murrelet conservation objectives than are those in OESF (DNR 1997).

DNR's approach to murrelet conservation explicitly relies on forest management to achieve its goal of increasing the size and stability of the murrelet population in Washington (DNR 2007). The regional differences outlined above led to region-specific approaches to achieve these objectives. In SWWA, the draft DNR strategy designated approximately 61,000 acres of state forests near the Pacific coast as 25 separate Marbled Murrelet Management Areas that ranged in size from 30 to approximately 12,000 acres, based on the interaction of conservation objectives and patterns of murrelet activity, land ownership, forest type and cover. The draft strategy recommends these areas be managed to produce as much high-quality marbled murrelet habitat as possible, as rapidly as possible. Other state forests in SWWA will also provide murrelet habitat as a byproduct of existing conservation agreements and other policies, however no explicit role or intentional management for murrelet conservation was described for lands outside the Management Areas.

In OESF, the draft strategy designated 8 Marbled Murrelet Emphasis Areas comprising 38,600 acres, based on their position in the lower elevation Sitka Spruce zone (Franklin and Dyrness 1988) which is poorly represented in the federal land base, and their location in larger blocks of DNR-managed lands or adjacent to the coastal strip of Olympic National Park (Figure 3.1). The draft strategy recommends these emphasis areas be managed to maintain or restore high-quality marbled murrelet habitat over 50% of their individual areas, with silvicultural regimes and/or harvest schedules that reduce edge effects in the remainder. Existing conservation agreements and other policies are explicitly acknowledged as providing substantial additional murrelet habitat and conservation benefit outside these emphasis areas. In OESF, the strategy called for intentional management to reduce edge effects in selected locations outside the emphasis areas.

The DNR draft strategy used the relationships summarized in the section on murrelet population ecology to estimate the abundance and stand-level quality of potential murrelet habitat across the analysis areas. Current habitat abundance and stand-level quality was estimated by compositing classified satellite imagery (http://www.fs.fed.us/r5/rsl/projects/mapping/) with DNR forest inventory data in a grid-based GIS environment (ArcMap 9.1, ESRI, Inc.). Future habitat abundance and quality was projected for 2067, which is the contractual term of the Habitat Conservation Plan (DNR 1997). Projections for DNR-managed forests outside Marbled Murrelet Management or Emphasis Areas were based on the statewide 10-year harvest and management schedule (DNR 2004) and were combined with those developed explicitly to meet murrelet conservation objectives within the management and emphasis areas as well as additional portions of the OESF (DNR 2007). A set of simple assumptions were applied to other lands in the analysis areas (DNR 2007). Spatial analyses determined the locations of edges between potential habitat and early seral forests in the current and projected future land cover mosaics. These processes resulted in spatially explicit estimates of current and projected future stand-level quality and amounts of potential marbled murrelet habitat, as well as its context and provided the basis for the population modeling I report and discuss below.

Methods

Estimating carrying capacity -- The following descriptions summarize methods presented in greater detail in DNR (2007). The estimate of *K* for marbled murrelets in Washington presented above, 1 murrelet per 170 acres of potential nesting habitat, was based on a classification that implied murrelet habitat is a binary phenomenon (Raphael et al. 2006), which was appropriate given the objectives of their analysis. However that classification summarized an analysis which indexed habitat suitability over a range of 0-100, applied to each pixel in their satellite land cover data (http://www.fs.fed.us/r5/rsl/projects/mapping/). That index reflected their estimate of a gradient in habitat quality that was due in large part to variability in stand structure and composition. Their methods were not directly applicable to predicting habitat suitability from DNR's high-resolution forest inventory or to projections of that inventory into the future. Thus I estimated *K* to reflect a gradient in stand-level habitat quality, appropriate to DNR's forest inventory and models that projected its growth.

Two attributes that are directly related to the abundance and availability of potential nest sites, platforms and canopy complexity, appear to be good predictors of stand-level habitat quality for marbled murrelets (reviewed by Burger 2002). Both were inferred from DNR's forest inventory. The number of canopy layers was estimated following Crookston and Stage (1999) while platform abundance was estimated with the model developed by Duke (1997). Habitat quality was inferred from the relationship between murrelet use and the structure of DNR-managed stands in SWWA. Murrelet use was estimated with inland surveys (Evans Mack et al. 2003) at 355 sites. All possible subsets of logistic regression models using covariates for platform abundance, numbers of canopy layers, and their interaction were fit to observations from the 355 sites to predict the probability those sites were used. Model selection and averaging techniques (Burnham and Anderson 2002) were then used to predict a quantitative relationship in which habitat quality increased with platform abundance and canopy complexity.

Model-averaged predictions were generalized to stages of stand development that broadly reflect the ability of managed forests to support biodiversity (Carey and Curtis 1996), according to average platforms and layering in each stage. This generalization enabled the use of forest growth models DNR developed and employed in estimating environmental impacts of potential alternatives for sustainable forest management (DNR 2004). Further generalizations were applied to classified forest cover on federal and private lands and to their projected future forest cover. Estimated values for this habitat quality index, or P_{stand}, ranged from 0.13 to 0.89 over the range of cover types with some potential as murrelet habitat (Table 3-14 in DNR 2007). Those P_{stand} values were used to modify the basic relationship of K = 1 murrelet per 170 acres such that $K_{stand} = P_{stand} * K$, reflecting the assumption that habitat quality is a function of nest-site abundance and availability. In the SWWA plan area, substantial areas of DNR-managed and other lands are distant from marine waters that support high densities of marbled murrelets during the breeding season (Raphael et al. 2006). I used 40 miles as the threshold distance to define those areas (Hull et al. 2001) and modified their carrying capacity estimates as K_{stand} * 0.25.

I projected the development of marbled murrelet habitat on federal and private forests. By 2067, early and mid-seral stands resulting from previous timber harvests in what are now designated as Late Successional Reserves on the Olympic National Forest (USDA and USDI 1994), were projected to become potential murrelet habitat (P_{stand} = 0.20, Table 3-14 in DNR 2007). Early and mid-seral streamside forests resulting from previous timber harvests on private timberlands were projected to become potential murrelet habitat (P_{stand} = 0.13, Table 3-14 in DNR 2007) because of current forest practices rules in Washington.

Estimating nest-site security -- I developed 2 independent estimates of nest-site security based on the models of predation risk described above. I used those models to classify murrelet habitat based on its relative security, with 3 classes reflecting high-, medium-, and low-security sites in which nest success was assumed to diminish from class to class. I identified edges between areas of potential murrelet habitat, i.e., with $P_{stand} > 0$ and early seral cover types, then classified the security of that habitat based on its distance from the nearest edge. High security areas were ≥ 150 m from an edge, based on observations that no murrelet nests beyond that distance from an edge failed due to predation (Manley and Nelson 1999). Low security habitat was within 50 m of an edge, while habitat at intermediate distances was classified as medium security.

The risk of nest predation as a function of landscape composition and pattern was indexed with the following equation that predicted days until predation, *D*, observed in the artificial nest experiment summarized above (Marzluff et al. 2003),

$$D = 8.04 - 8.16 * \text{patch density (at 5 km)} + 1.10 * \text{contrast-weighted edge density (at 2 km)} - 10.31 \text{ Shannon-Weaver evenness index (at 2km).}$$

This index is best viewed as a measure of relative predation risk (Marzluff et al. 2003). Following Marzluff et al. (2003), I classified the composite grids for current and projected future land cover according to Green et al. (1993), resampled those grids to 500 m pixels, calculated landscape indices with the program Fragstats (McGarigal et al. 2002), then used ArcMap 9.1 (ESRI, Inc.) to express that function across the analysis areas and to classify the security of potential marbled murrelet habitat. I ranked the potential murrelet habitat by predicted risk, separately within OESF and SWWA and for current and projected future land cover estimates, then divided it into quartiles. I classified the least risky quartile as high security habitat, the most risky quartile as low security, and the intermediate 2 quartiles as medium security. I rescaled these predation risk indices from 0-100 (high to low risk) in order to compare indices between current and future conditions and among analysis areas.

The quality-security matrix -- I summarized current and projected future marbled murrelet habitat in 3 by 3 matrices in which one dimension reflected stand-level habitat quality and the other dimension reflected landscape-level nest-site security. Following the models and assumptions detailed above, the 9 bins encompass low, medium, and high levels of stand-level habitat quality, defined as $0.36 \geq P_{stand} \geq 0.13$, $P_{stand} = 0.47$, and $P_{stand} \geq 0.62$ respectively (Table 3-14 in DNR 2007), cross-classified by their levels of nest-site security. Summaries of the composite grids that represented current and projected future conditions in OESF and SWWA were used to populate the matrices with the *K* estimated for each of the 9 combinations of habitat quality and security.

Population modeling -- I used a stochastic, stage-structured, female only, metapopulation model to project murrelet population responses under varying assumptions about habitat, demographic responses to habitat, and dispersal. I used RAMAS Metapop v 5.0 (Akçakaya and Root 2005) to conduct this modeling. Subpopulations were represented by individual cells in the quality-security matrices with *K* estimates halved to accommodate the female-based model, using vital rates that differed among high, medium, and low security cells such that subpopulations in high security habitat had growth rates greater than 1 and subpopulations in medium and low security habitat had projected growth rates less than 1, 1.0222, 0.9898, and 0.9623 respectively. I included 5 life stages in all models, juveniles, subadults in their 2nd, 3rd, and 4th years, and adults, with vital rates taken from the literature. I did not vary survival rates among models. I assumed that adult and subadult survival averaged 0.882 (Table 3.1), the average of male and female survival reported for marbled murrelets in central California (Peery et al. 2006b) that inhabit a marine environment similar to that off the Washington coast (Hunt 1995). I assumed juvenile survival averaged 0.618 (Table 3.1), 70.1% of adult survival (Beissinger and Nur 1997). I assumed a phased-in maturity such that the proportion of subadults attempting breeding increased each year from 0.05 to 0.4 to 0.6, and that 95% of adults attempted breeding (Steventon et al. 2003). I assumed high, medium, and low rates of realized fecundity, i.e., female juveniles recruited to the population, of 0.32, 0.225, and 0.155 (Steventon et al. 2003) from high, medium, and low security habitat respectively. When modified by the proportions of each stage attempting breeding, average recruitment varied from 0.008 to 0.304 (Table 3.1) with standard deviations based on an 18% coefficient of variation, which was the midpoint between the lower and higher environmental variability scenarios modeled by Steventon et al. (2003).

I simulated varying patterns of dispersal, both random and directed, among the 9 source and sink subpopulations. I assumed that natal dispersal was most frequent, and that dispersal probability halved with each stage such that adults dispersed at 6.25% the rate of juveniles to reflect the greater propensity for alcids to engage in natal rather than breeding dispersal (Divoky and Horton 1995). Dispersal scenarios were no dispersal, random dispersal, and directed dispersal towards subpopulations in higher stand-level habitat quality, towards subpopulations in habitat providing higher nest-site security, and towards both stand-level habitat quality and nest-site security. Base dispersal rates (before applying the stage-related dispersal probabilities) ranged from 0.01 to 0.06, with rates increasing according to quality/security gradients in the directed dispersal scenarios. I assumed a coefficient of variation of 0.20 in dispersal rates in all scenarios.

For the base model runs, I specified carrying capacities for each subpopulation according the values in the appropriate quality-security matrix. I specified starting populations rounded to the nearest 10 above K and began simulations with the stable age distribution resulting from the vital rates in each projection matrix (Burgman et al. 1993). Each metapopulation was projected over 100 years, with 500 simulations that incorporated demographic responses to environmental variability as the standard deviations in vital rates (Table 3.1). I assumed that subpopulations would experience similar environmental fluctuations since they represented a metapopulation inhabiting a discrete geographic area, thus their vital rates were correlated among populations (r = 0.6).

Comparison and evaluation of conservation outcomes -- I compared estimates of K, classified in quality-security matrices, between current and future habitat conditions predicted to result from DNR's draft conservation strategy and other existing land-use policies. I also compared predictions of the relative security of potential marbled murrelet habitat between the edge-effects and landscape index to predation risk models. These comparisons provided estimates of the capability of current and future land cover to provide nest sites for marbled murrelets, the relative security of this potential habitat, and an indication of the uncertainty in predicting habitat suitability as a function of its capacity to provide secure nest sites.

I conducted the 100-year population projections under static habitat conditions that reflected either the current (2004) or future (2067) habitat conditions predicted to result from DNR's draft conservation strategy and other existing land-use policies. Comparisons of metapopulations projected under present and future conditions, different dispersal scenarios, and the 2 independent models for nest-site security provided estimates of their trajectories and ending population sizes as evaluation criteria. Additional criteria for evaluating conservation outcomes were ending population sizes and the duration of local extirpations for the 9 individual subpopulations simulated to occupy the 9 bins in the quality-security matrices.

I conducted a *post hoc* evaluation of several alternative approaches to marbled murrelet conservation, 2 each in OESF and SWWA. Those alternative conservation scenarios were largely based on the DNR draft conservation strategy, with modifications to explore possibilities for increasing the strategies' efficiency, i.e., achieving equivalent conservation while retaining more of the land base to serve multiple objectives. I evaluated the conservation effectiveness of those scenarios with the same criteria noted above, and assessed their relative efficiencies based on the land base devoted to providing marbled murrelet nesting habitat.

Results

Quality-security matrices -- Carrying capacity estimates across all lands, cross-classified by nest-site security, suggest that by 2067 under DNR's draft conservation strategy and other existing land-use policies the OESF may be able to support 25% more marbled murrelets than estimated for current habitat conditions (Table 3.2), while in SWWA, K was predicted to double (Table 3.3). Current estimates for the OESF suggest that 88% of K occurs in high-quality habitat (Table 3.2), which is consistent with the extensive areas of old-growth forests there. Little original forest cover remains in SWWA and this is reflected in the estimate that only 1% of the current K is provided by high-quality habitat (Table 3.3). While K was predicted to increase in all classes of stand-level habitat quality in both areas, trends were predicted to differ between OESF and SWWA. Most of the predicted increase in OESF occurred in low-quality habitat (Table 3.2), while in SWWA large increases were predicted in both low- and high-quality habitat (Table 3.3). Carrying capacity on DNR-managed lands in OESF was predicted to double by 2067 under the draft conservation strategy (Table 3.4), with substantial predicted increases in *K* from both low- and high-quality habitat. Similar results were predicted for DNR-managed lands in SWWA, with overall *K* more than doubling and a nearly 50-fold increase in *K* provided by high-quality habitat (Table 3.5).

Estimates of nest-site security based on edge effects differed between OESF and SWWA (Tables 3.2, 3.3). In OESF, 70% of *K* occurs greater than 50 m from edges. Edge-influenced habitat is relatively more abundant in SWWA, where 42% of *K* is currently within 50 m of an edge. The greatest increase in *K* predicted for 2067, following implementation of DNR's draft conservation strategy and other existing land-use policies, occurred in high-security habitat distant from edges in OESF (412 of 523, Table 3.2A) and in low-security habitat near edges in SWWA (235 of 440, Table 3.3A). DNR-managed lands in OESF mirrored the trends of their surroundings, with the greatest increase in *K* predicted in high-security habitat (152 of 222, Table 3.4A). In SWWA, the trend predicted for DNR-managed lands differed from that of the analysis area at-large, *K* diminished in low-security habitat (from 104 to 81) and increased from 4 to 193 in high-security habitat (Table 3.5A).

Predicted nest-site security based on the multivariate landscape index to predation suggested a different distribution of risk across marbled murrelet habitat, however since I categorized security based on quartiles of predicted risk they can not be directly compared with those from empirical measurements of distance from edge. Rescaled indices suggested that OESF might be a slightly more risky nesting environment than SWWA as median index values were 22.6 and 18.5 in OESF compared to 25.7 and 19.4

in SWWA for the 2004 and 2067 landscapes respectively. Nearly all the predicted increase in *K* occurred in medium-security habitat in OESF (509 of 523, Table 3.2B). In SWWA, most of the predicted increase in *K* occurred in medium- and high-security habitat (378 of 440, Table 3.3B). Predicted trends in nest-site security on DNR-managed lands in OESF suggested a greater contribution to *K* from high-security habitat relative to the landscape at-large (46 of 222, Table 3.4B) but most of the increase in *K* was in medium-security habitat (145 of 222, Table 3.4B). All of the increased *K* predicted for DNR-managed lands in SWWA (175, Table 3.5B) occurred in medium- and high-security habitat.

Population projections -- Projections of the female portion of the murrelet population under the edge effects and landscape predation index models for nest-site security, and all 5 dispersal scenarios are presented in Figures 3.2A and 3.2B for the OESF and Figures 3.3A and 3.3B for SWWA. The declining trends depicted in all figures result from my assumptions that vital rate parameters for 6 of the 9 subpopulations (i.e., the low- and medium-security bins in the quality-security matrices) result in their experiencing negative population growth. Thus, under both nest-site security models, all dispersal scenarios, and in the current (2004) and predicted future landscapes (2067) resulting from implementation of DNR’s draft conservation strategy and other existing land-use policies, the metapopulations decline towards the *K* estimated only for their high-security sub-populations (Tables 3.2 and 3.3, OESF and SWWA respectively).

Projections of female murrelet populations in the OESF under the edge effects model for nest-site security are depicted in Figure 3.2A which illustrates parallel average trajectories under current and future landscape conditions. Ending populations are projected to be around 800 female murrelets for future landscape conditions compared to 500 for the current landscape (Table 3.6). Projections in OESF under the landscape predation index model for nest-site security (Figure 3.2B) suggest little long-term difference for murrelet populations between current and future landscape conditions as both trajectories converge around an ending population of approximately 550 female murrelets. Projections that reflect this view of the current and future landscapes overlap, with 2 of the 5 highest ending populations occurring in the 2004 landscape (Table 3.6). This reflects characteristics of the quality-security matrix predicted with the multivariate landscape index to predation, in which most of the *K* occurs in medium- or low-security situations where subpopulations decline (Table 3.2B). Although relatively small, differences between many of the dispersal scenarios are statistically significant. Differences between average ending population values of about 12-15 are statistically significant in OESF, with larger differences between means required for the larger standard deviations reported in Table 3.6 (to achieve $p < 0.05$ with 2-tailed *t*-tests, *d.f.* = 998).

Projections in SWWA under the edge effects model for nest-site security (Figure 3.3A) illustrate relatively steeper declines than in the OESF (Figure 3.2A), with a relatively wide range of ending populations all well below 100 female murrelets under current landscape conditions (Table 3.6). Projections under future landscape conditions all converge around an ending population of 100 female murrelets (Table 3.6).

Projections under the landscape predation index model in SWWA (Figure 3.3B) suggest similar relative responses of murrelet populations under current and future landscape conditions, however greater security predicted in the future (2067) relative to the current (2004) landscape result in ending populations averaging about 100 more female murrelets. The wide range of predicted ending populations under the various dispersal scenarios (Figure 3.3B, Table 3.6) reflect the interaction of different dispersal patterns with characteristics of the quality-security matrix derived with the landscape index to predation. Differences between average ending population values of about 2-6 are statistically significant in SWWA with larger differences between means required for larger standard deviations reported in Table 3.6 (to achieve $p < 0.05$ with 2-tailed *t*-tests, *d.f.* = 998). Thus many of the dispersal scenarios predict different population performance, particularly when nest-site security is based on the landscape index to predation.

Subpopulations -- All the metapopulation projections reported above summarize predicted numbers of female murrelets I characterized as 9 subpopulations occupying habitat represented by the appropriate quality-security matrices (Tables 3.2 and 3.3). Projections of those individual subpopulations are informative as to the potential for habitat in current and predicted future landscapes to support the metapopulations. Estimated ending population sizes under both models for nest-site security, all dispersal scenarios, current and predicted future landscapes in OESF and SWWA are depicted in Figures 3.4-8. Several features in these figures are prominent. Under the no dispersal scenario and both models for nest-site security (Figure 3.4), many of the ending subpopulations were extinct or nearly so, particularly in SWWA. Subpopulations were able to persist better when they could be rescued by dispersers, although many subpopulations ended with low numbers, very few were extinct in OESF where there was a large source population in high-quality/high-security habitat (Figures 3.4-8). Source populations were small in SWWA, particularly in the current (2004) landscape, and many ending subpopulations were extinct or nearly so under all dispersal scenarios (Figures 3.4-8). These local extinctions were more frequent in the 2004 landscape under all dispersal scenarios.

Subpopulations can become extirpated, then re-colonized by dispersers during these simulations, and although their ending abundance is informative, the amount of time they were unoccupied during the 100-year simulation period provides additional insight as to the conservation value of different habitat conditions. These "extinction durations" are presented in Table 3.7 and show that in OESF, subpopulations were rarely extirpated when dispersal occurred, and then only briefly. These patterns were similar in both the current and future landscape predicted to result from DNR's draft conservation strategy and other existing land-use policies (Table 3.7). Nearly all local populations were unoccupied at some time in SWWA, in the current and projected future landscapes, under both nest-site security models and under all dispersal scenarios (Table 3.7). These local extirpations were much briefer in the future landscape predicted to result from DNR's draft conservation strategy and other existing land-use policies (Table 3.7).

The abundance and quality of habitat available to subpopulations, i.e. *K* (Tables 3.2 and 3.3), was not directly related to their predicted abundances at the end of population projections (Figures 3.4-8) or the amount of time they were unoccupied (Table 3.7). For example, $K = 514$ for the subpopulation in the current high-quality/low-security (within 50 m of edge) habitat in OESF (H_L in Table 3.2A), but its ending abundance under all dispersal scenarios was 50 or less and it was briefly extirpated under several dispersal scenarios (Table 3.7). This same pattern occurred with the SWWA subpopulation in the current low-quality/low-security habitat ($K = 361$, Table 3.3A), with ending abundances less than 10 and substantial periods of extirpation (L_L in Table 3.7). Only the source subpopulations, i.e., those in high-security habitat, were predicted to have ending populations close to their predicted K. This feature of the source-sink, metapopulation structure helps elucidate differences in overall trends depicted in 3.2 and 3.3.

Dispersal -- Dispersal helped maintain occupancy in subpopulations with sink dynamics, but my dispersal scenarios did not support higher ending abundances in the metapopulation projections. In all projections, the highest ending abundances occurred under the no dispersal scenario (Figures 3.2, 3.3). I conducted a sensitivity analysis to evaluate population outcomes with increasing rates of dispersal. I simulated random, and 2 directed dispersal scenarios, toward nest-site security, and toward both stand-level habitat quality and nest-site security. I increased the base dispersal rates by 50%, 100%, 200%, and 400% and projected murrelet populations in the landscape with the best overall population performance, OESF 2067 with the edge effects model for nest-site security. Ending population sizes decreased as dispersal rates increased and the highest average ending population, 764 female murrelets, resulted from the dispersal to quality and security scenario with the lowest dispersal rate (Figure 3.9). The comparable base dispersal scenario resulted in an average ending population of 810 female murrelets (Table 3.6), significantly greater than the 764 from the best-performing high-dispersal scenario ($t = 4.87$, $d.f. = 998$, $p < 0.001$).

Alternative habitat configurations -- I projected murrelet populations under 4 hypothetical alternative management scenarios, 2 each in OESF and SWWA, that reflected different management approaches for marbled murrelet conservation on DNR-managed lands. After reviewing the results reported above, I revised the quality-security matrices based on the edge-effects model for nest-site security in the 2067 OESF and SWWA landscapes (Tables 3.2A, 3.3A) to reflect habitat configurations that might result from alternative management approaches that maintained DNR's objectives to increase the size and stability of marbled murrelet populations while providing greater economic efficiency. I considered results of projections based on the edge-effects model for those 2067 landscapes to reflect the baseline for comparing alternative management approaches.

The OESF alternatives reflected the large amounts of high-quality/high-security habitat there and the insensitivity of population projections to K in lower-security, i.e., sink habitat. I approximated an alternative management approach in which some lower quality habitat in low-security settings on DNR-managed land was removed with timber harvests so that K in those cells was also reduced from levels shown in Table 3.4A. This approach resulted in the revised estimates of K presented for OESF Trial 1, in which habitat in low- and medium-quality stands in low- and medium-security settings supported 47 fewer murrelets (Table 3.8). The other alternative was similar, except that it also represented an approach to improve the security of some high-quality, low- and medium-security habitat with intentional management to diminish edge effects. This alternative resulted in the revised estimates of *K* presented for OESF Trial 2 (Table 3.8). As in Trial 1, 47 fewer murrelets were supported by low- and medium-quality habitat in low- and medium-security settings, but Trial 2 also shifted *K* for 48 murrelets from high-quality habitat in low- and medium-security settings to high-security settings (Table 3.8). Alternative management under Trials 1 and 2 would result in approximately 22,000 fewer acres of low- and medium-quality murrelet habitat, thus increasing the capacity of that land base to achieve economic objectives. Intentional management to increase the security of some high-quality habitat under Trial 2 would diminish its economic efficiency relative to that of Trial 1.

Alternative management approaches in SWWA reflected the preponderance of habitat in low-security settings, including in small Marbled Murrelet Management Areas, and the insensitivity of population projections to *K* in those population sinks. One approach, similar to Trial 1 in the OESF, simulated management that identified low-security murrelet habitat and removed it with timber harvests so that *K* in those cells was reduced by amounts consistent with the abundance of those habitat conditions on DNR-managed land (Table 3.5A). I applied this approach to medium- and high-quality habitat in low- and medium-security settings and reduced overall *K* by 82 murrelets (SWWA Trial 1 in Table 3.8). The other approach built upon the Trial 1 scenario by simulating intentional management to reduce edge effects around low- and medium-security habitat which led to slight further reductions of *K* in low- and medium-security habitat with commensurate increases for *K* in high-security habitat (SWWA Trial 2 in Table 3.8). As in Trial 1, 82 fewer murrelets were supported by habitat in low- and medium-security settings, but Trial 2 also shifted *K* for 14 murrelets from high-quality habitat in low- and medium security settings to high-security settings (Table 3.8). Alternative management under Trials 1 and 2 would result in approximately 21,000 fewer acres of low- and medium-security murrelet habitat, thus increasing the capacity of that land base to achieve economic objectives. Intentional management to increase the security of some high-quality habitat under Trial 2 would diminish its economic efficiency relative to that of Trial 1.

Projections of female murrelet populations in the OESF under the alternative approaches are depicted in Figure 3.10A which illustrates basically identical trajectories under baseline and alternative management approaches. Ending populations were projected to average 788.9 female murrelets (standard deviation = 147.0) under Trial 1 and 811.1 (166.1) under Trial 2, compared to 809.7 (154.8) under the baseline approach. Trial 1 predicted significantly lower ending populations than the baseline ($t = 2.18$, *d.f.* = 998, $p = 0.03$), ending populations resulting from Trial 2 and the baseline were not different ($t = 0.89$, *d.f.* = 998, $p = 0.89$). Among the subpopulations, patterns of abundance and the duration of local extirpations, which were almost nonexistent, were virtually identical among Trials 1 and 2 and the baseline scenario (Figure 3.11A, Table 3.9).

Projections of female murrelet populations in SWWA under the alternative approaches are depicted in Figure 3.10B. Ending populations were projected to average 98.1 (23.6) female murrelets under Trial 1 and 113.8 (28.4) under Trial 2, compared to 97.1 (25.6) under the baseline approach. Ending populations from Trial 1 and the baseline were not different ($t = 0.52$, *d.f.* = 998, $p = 0.52$). Trial 2 predicted significantly larger ending populations than the baseline ($t = 9.76$, *d.f.* = 998, $p < 0.001$). The baseline scenario projected a larger ending subpopulation in high-quality, medium-security habitat than either of the alternatives ($t > 10.0$, *d.f.* = 998, $p < 0.001$). Trial 2 projected larger ending subpopulations in high-security habitat, regardless of its stand-level quality, than either the baseline scenario or Trial 1 ($t > 4.8$, *d.f.* = 998, $p < 0.001$). Local extirpations were more frequent under either alternative approach (Table 3.9), which intentionally reduced K for subpopulations in low-security habitat (Trials 1 and 2 in SWWA Table 3.8). There were small differences among the very low average durations of local extirpation in high-security habitat, most were not significant ($t \leq 1.7$, *d.f.* = 998, $p \geq 0.09$). These local extirpations were of shorter duration in low-quality habitat in the baseline scenario compared to either Trial 1 or Trial 2 ($t = 2.6$, *d.f.* = 998, $p = 0.01$).

Discussion

The models and their results described above provide a good basis for objective predictions of the performance of DNR’s draft marbled murrelet conservation strategy relative to its goals for population size and stability because they provide an explicit framework that integrates assumptions with available information on marbled murrelet biology and regional forest conditions. Models such as these are essential to credible predictions of population responses to management (Beissinger et al. 2006). Although the models appear to provide explicit predictions of carrying capacity and population growth, their outputs should be viewed as indices that allow qualitative evaluation of current and predicted future conditions, and management approaches to achieve them, in an objective, repeatable manner (Beissinger and Westphal 1998). These results do not provide an assessment of population viability, nor are they explicit predictions of current or future marbled murrelet abundance or vital rates. The replicated stochastic simulations allow easy statistical comparisons of results, but I suggest that in most cases where estimates resulting from these simulations are close enough to warrant statistical tests for significant differences, the uncertainties about marbled murrelet population biology render those differences biologically insignificant in light of our current knowledge. I propose that these results be viewed in a relative sense, in the context of marbled murrelet populations, habitat, and land-use patterns in Washington, in light of DNR's conservation objectives, and that they suggest management direction instead of explicit management prescriptions.

Current and predicted future habitat -- The striking differences between current habitat conditions in OESF and SWWA are the result of the land use patterns reviewed in the *Background* section. Historic patterns of timber harvests differed between those areas as well, with most of the timber harvest on the western Olympic Peninsula (OESF analysis area) occurring since 1960, while extensive timber harvesting has been ongoing since the early 20th century in southwest Washington (SWWA analysis area). That historic context explains why most of the increase in *K* predicted for OESF occurred in low quality habitat, the young second-growth forests regenerated following fairly recent timber harvests do not have time to develop characteristics of high-quality habitat, even with proactive silvicultural intervention (DNR 2007). The relatively abundant, older second-growth forests in SWWA are capable of developing those characteristics, particularly with intentional management (DNR 2007). DNR's high relative contribution to the predicted future *K* in SWWA resulted from a deliberate approach to provide habitat for a larger, hopefully more resilient regional murrelet population in a part of the state that would otherwise remain a fragile segment of the listed population (U.S. Fish and Wildlife Service 1997). Likewise the approach in OESF acknowledged the profoundly different regional context there.

The edge-effects model provides an easily interpreted perspective on nest-site security. The greatest increases in *K* were predicted to occur in high-security habitat in OESF, but in low- and medium-security habitat in SWWA. These disparities again resulted from the different regional contexts, with the increases in interior forest habitat (i.e., high-security) projected for OESF because of the generally increasing maturity of young, edge-creating forests projected for Late Successional Reserves on the Olympic National Forest (USDA and USDI 1994) and on much of the DNR-managed lands (DNR 2007). In SWWA most of the projected increases in low-security habitat near forest edges were due to assumptions regarding streamside buffers on private forest lands (DNR 2007) which predominate in SWWA, while much of the increase projected in higher-security habitat occured in proposed DNR Marbled Murrelet Management Areas (DNR 2007). Predictions of the landscape index to nest predation are more difficult to interpret, but a review of the different regional contexts in light of the multivariate model is informative. That model predicts predation risk increases as landscapes become more complex, with increased density of distinct cover-type patches and greater diversity in those cover types, with the abundance of high-contrast edges acting to diminish predation risk. The SWWA area is nearly all commercial forest land and industrial forestry is well known to simplify and homogenize landscapes (e.g., Lindenmayer and Franklin 2002), thus even though my approach of classifying risk by quartiles likely obscured some differences, predictions of current and future security and of the rescaled predation indices suggest somewhat less risk in SWWA than OESF from this perspective.

Population responses to habitat -- Under the assumptions I used to simulate marbled murrelet population responses to habitat, nest-site security was unequivocally more important than nest-site abundance, i.e. *K*. This suggests that my simulations were less sensitive to assumptions about *K* than to those about the influence of habitat conditions on nest success. Metapopulations always trended towards the *K* of source habitats, which I simulated as those that supported higher rates of nest success. Differences between starting and ending population sizes in my simulations were approximately equal to the *K* provided by low- and medium-security, i.e. sink habitat. High-quality habitat with abundant nest sites and sink dynamics was not able to maintain local populations anywhere near its predicted *K* even with simulated directed dispersal bringing in immigrants from source subpopulations. These findings are consistent with those from theoretical (Pulliam and Danielson 1991) and empirical studies (Donovan et al. 1995). These simulated source-sink dynamics may be occurring in real marbled murrelet habitat as well, much low-security habitat may only remain "occupied" (Evans Mack et al. 2003) by dispersing birds that rarely use it for breeding (Divoky and Horton 1995). It is clear that wildlife and land managers can not fully judge the value of marbled murrelet habitat without understanding its role in supporting their populations (Williams et al. 2002, Peery et al. 2004a, Sinclair et al. 2006, Zharikov et al. 2006).

Responses of vital rates to habitat conditions -- The assumptions I used to predict marbled murrelet demographic responses to habitat conditions were not derived from direct studies of their populations in Washington. Survival rates, which I assumed to be unrelated to forest conditions (Steventon et al. 2003), were based on empirical evidence from populations to the north and south and were probably fairly close to actual rates in the Washington population. Population growth is most sensitive to rates of adult survival in long-lived animals with low fecundities like marbled murrelets (Beissinger and Nur 1997). However, even with low rates of adult mortality, the murrelet population will decline if recruitment of juveniles is insufficient to replace that mortality as my projections demonstrate. It may be that recruitment rates in Washington murrelet populations are lower than I assumed, perhaps for reasons other than nest-site security as suggested by observations in central California (Peery et al. 2004a, Beissinger and Peery 2007). But that does not diminish the importance of the influence of forest habitat conditions on marbled murrelet populations. The cryptic alternate plumage and nesting behavior of marbled murrelets plainly reflect adaptations to diminish nest predation. The extent to which forest habitat conditions in Washington support a secure nesting environment will enable greater recruitment and a more resilient marbled murrelet population there.

The sensitivity of my population projections to the ability of forest habitat to support murrelets that nest successfully demonstrates the importance of increasing our understanding of the processes that influence this outcome (Marzluff et al. 2000). The edge-effects model of predation risk is easy to understand and manage for, but uncertainty in predicting actual recruitment rates by marbled murrelets can lead to less than effective conservation and lost opportunities to achieve other objectives of forest management. The multivariate landscape index to predation risk provides a different perspective and perhaps additional insights into this phenomenon. It is currently difficult to manage for particular index values in a predictable manner, but the experimental nature of the research that led to this index and its validation in follow-on studies (Marzluff et al. 2000, Raphael et al. 2002b, Marzluff et al. 2003) suggest it deserves further investigation in order to improve our ability to intentionally manage forest to improve nest-site security for marbled murrelets.

Dispersal -- In my metapopulation simulations, dispersal was critical to maintaining occupancy in sink habitat. While these sinks can not support growth or stability in the metapopulations I modeled, there are a variety of real-world reasons dispersal into sink habitat can improve individual fitness and overall population performance (Howe and Davis 1991, Dias 1996). Most important for marbled murrelet populations, if local habitat conditions change because of environmental fluctuations or intentional management to improve its security for nesting, sinks may become sources

(Dias 1996). Thus the ability of murrelets to colonize unoccupied habitat may be important to the success of conservation efforts, particularly in SWWA where DNR plans to increase the amount of murrelet habitat in an area where it currently is scarce. However, dispersal and apparent occupancy of sink habitat can confound interpretations of habitat quality and lead to decisions that are ineffective for both murrelet conservation and other objectives of forest management. Again, this reinforces the advisability of reducing our uncertainty around habitat conditions that support murrelet population growth.

Marbled murrelet conservation on DNR-managed lands -- My assessments of habitat conditions and murrelet population performance suggest that DNR's draft conservation strategy in both OESF and SWWA can be effective at meeting its goals for marbled murrelet conservation. While my analyses did not explore this directly, inspection of the quality-security matrices for all lands and DNR-managed lands in the OESF (Tables 3.2, 3.4) and population projections based on current and future OESF habitat conditions (Figures 3.2A, B) suggest this segment of the Washington population may be robust in the face of a reduced conservation effort from DNR. The cumulative effects of DNR's other conservation agreements and its draft murrelet strategy appear likely to provide the opportunity for a relatively large and stable population there. The situation in SWWA is quite different. Population simulations under current conditions suggest this segment of the population is much less likely than that in the OESF to be self-sustaining. Patterns of land ownership and land use in southwestern Washington preclude substantial habitat reserves such as those on the Olympic Peninsula. With this in mind, DNR's draft strategy took an aggressive approach towards increasing the abundance and security of murrelet habitat on state forests in SWWA. Although this approach, in concert with changes projected from other policies for state and private forests, resulted in a predicted doubling of regional *K*, projected population trajectories still suggested that the stability of this segment of the population is likely to be equivocal. The draft DNR strategy focused on those state forests judged most likely to meet its conservation goals (DNR 2007). Given existing patterns of land ownership, few additional opportunities remain there to improve the performance of the draft SWWA strategy.

Marbled murrelet conservation entails substantial tradeoffs in outcomes from managing state forests. Prominent among these tradeoffs is the opportunity to produce revenue from timber harvests to support the beneficiaries of these trust lands, in whose interest DNR is legally mandated to act with "undivided loyalty" (DNR 2006). While conservation of biodiversity in general as well as of threatened species with statutory protection is arguably part of that mandate, these tradeoffs are and will remain controversial. Thus it is prudent that DNR carefully evaluate and predict the effectiveness and efficiency of whatever marbled murrelet conservation strategy it adopts.

Alternative approaches to conservation -- The alternative approaches I explored were not based on spatially-explicit expressions of forest management practices and schedules across OESF and SWWA. Rather, they were fairly conservative approximations of how different approaches to marbled murrelet conservation might be implemented in those areas, based on my considerable experience with forest management planning and implementation. All the alternative approaches I devised resulted in lower estimates of *K* because they represented strategies to concentrate murrelet conservation in habitat that was more likely to support DNR's population goals, thus they allowed additional area to be managed for multiple objectives including commercial timber harvest. However, population projections suggested they provided similar murrelet conservation to DNR's draft strategy. Given the rather large acreages involved (> 20,000 acres in each analysis area), these alternative approaches could provide substantially increased efficiency in using state forests to achieve multiple objectives including effective marbled murrelet conservation. Thorough, spatially-explicit forest planning and analyses are required in order to actually propose, then conduct robust analyses of the effectiveness of alternative approaches to murrelet conservation.

Implications for forest management and marbled murrelet conservation -- A prominent implication of the results presented here is that the segment of Washington's marbled murrelet population in SWWA will likely continue to be at risk, regardless of whatever efforts DNR makes on behalf of their conservation. That suggests a continued focus on monitoring the effectiveness of those efforts. A corollary is that the population segment in the OESF appears to be fairly robust and its condition should allow application of adaptive management to improve our ability to manage for multiple objectives including marbled murrelet conservation. This type of experimental management often entails short-term losses of, for example timber harvest opportunities or wildlife conservation, in order to meet the long-term objective of increasing the effectiveness and efficiency of natural resources management (Walters and Holling 1990, Marzluff et al. 2000). In this case, the Olympic Experimental State Forest could live up to its name and serve as a laboratory to improve our ability to integrate marbled murrelet conservation with other objectives of forest management. The sensitivity of projected murrelet populations to variations in nest-site security demonstrated in my analyses suggest that understanding the mechanisms behind these variations could improve the effectiveness and efficiency of forest management to achieve DNR's goals for their population. Gaining this understanding is likely to be a lengthy and expensive endeavor though, and must be undertaken in due consideration of the broad range of mandates for management of state forests.

My exploration of alternative conservation scenarios suggest that a fairly broad range of alternatives may be competitive in terms of marbled murrelet conservation and that an evaluation of the tradeoffs between economic efficiency and conservation effectiveness may be productive. Forest management can increase the security of potential murrelet nesting habitat much more rapidly than it can increase the abundance of nest-sites (Malt and Lank 2007). At least to the extent the edge-effects model is a reliable predictor, this element of the influence of habitat conditions on population performance could prove to be critical in developing, evaluating, and possibly implementing an effective, efficient marbled murrelet conservation strategy.

Table 3.1. Vital rates (mean ± standard deviation) assumed for modeling populations of female marbled murrelets in high, medium, and low security nesting habitat. Juveniles are in their first year of life; $\text{Subadult}_{2,3,4}$ are in their second, third, and fourth years respectively; Adults are in their fifth year and beyond.

	Juvenile	Subadult_2	Subadult_3	Subadult_4	Adult
Survival	0.618 ± 0.069	0.882 ± 0.021	0.882 ± 0.021	0.882 ± 0.021	0.882 ± 0.021
Recruits-to-sea High security		0.016 ± 0.003	0.128 ± 0.023	0.192 ± 0.034	0.304 ± 0.055
Recruits-to-sea Medium security		0.011 ± 0.002	0.09 ± 0.0162	0.135 ± 0.024	0.214 ± 0.038
Recruits-to-sea Low security		0.008 ± 0.001	0.062 ± 0.011	0.093 ±0.017	0.147 ± 0.026

Table 3.2. Marbled murrelet carrying capacity estimates (predicted numbers of murrelets supported based on the abundance and quality of potential nesting habitat), cross-classified by estimated stand-level habitat quality and nest-site security for all lands in the Olympic Experimental State Forest (OESF). Nest-site security is estimated based on proximity to edges (Table A) and by the multivariate index to predation risk (Table B). Estimates are for current (2004) conditions and after projecting habitat development due to forest management under DNR's draft marbled murrelet conservation strategy and other existing land use policies (2067).

		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
A		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	84	10	514	608	171	17	509	697
	Medium	68	21	685	775	144	29	623	796
	High	27	25	610	663	226	19	830	1,075
	Total	179	57	1,809	2,045	540	65	1,962	2,568

		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
B		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	67	24	392	483	203	16	302	521
	Medium	84	23	743	850	271	33	1,056	1,359
	High	28	10	674	712	66	16	605	687
	Total	179	57	1,809	2,045	540	65	1,962	2,568

Table 3.3. Marbled murrelet carrying capacity estimates (predicted numbers of murrelets supported based on the abundance and quality of potential nesting habitat), cross-classified by estimated stand-level habitat quality and nest-site security for all lands in the Southwest Washington analysis area (SWWA). Nest-site security is estimated based on proximity to edges (Table A) and by the multivariate index to predation risk (Table B). Estimates are for current (2004) conditions and after projecting habitat development due to forest management under DNR's draft marbled murrelet conservation strategy and other existing land use policies (2067).

A

		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	173	11	1	185	361	20	39	420
	Medium	149	20	2	172	219	25	78	322
	High	61	21	3	85	45	16	78	139
	Total	383	52	6	441	625	60	196	881

B

		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	85	13	1	98	141	6	13	160
	Medium	190	23	4	217	287	25	96	409
	High	108	16	1	126	196	30	86	312
	Total	383	52	6	441	625	60	196	881

Table 3.4. Marbled murrelet carrying capacity estimates (predicted numbers of murrelets supported based on the abundance and quality of potential nesting habitat), cross-classified by estimated stand-level habitat quality and nest-site security for DNR-managed lands in the Olympic Experimental State Forest (OESF). Nest-site security is estimated based on proximity to edges (Table A) and by the multivariate index to predation risk (Table B). Estimates are for current (2004) conditions and after projecting habitat development due to forest management under DNR's draft marbled murrelet conservation strategy (2067).

A		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	6	10	18	35	27	17	40	85
	Medium	12	21	41	73	42	29	107	178
	High	15	25	69	110	25	19	133	177
	Total	34	57	128	218	94	65	280	440

B		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	11	24	64	100	36	16	79	131
	Medium	15	23	54	91	44	33	159	236
	High	7	10	10	27	14	16	43	73
	Total	34	57	128	218	94	65	280	440

Table 3.5. Marbled murrelet carrying capacity estimates (predicted numbers of murrelets supported based on the abundance and quality of potential nesting habitat), cross-classified by estimated stand-level habitat quality and nest-site security for DNR-managed lands in the Southwest Washington analysis area (SWWA). Nest-site security is estimated based on proximity to edges (Table A) and by the multivariate index to predation risk (Table B). Estimates are for current (2004) conditions and after projecting habitat development due to forest management under DNR's draft marbled murrelet conservation strategy (2067).

A

		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	19	10	1	31	31	20	39	89
	Medium	38	20	1	60	33	25	77	135
	High	46	21	2	69	18	16	77	111
	Total	104	52	4	160	81	60	193	335

B

		Stand-level habitat quality 2004				Stand-level habitat quality 2067			
		Low	Medium	High	2004 Total	Low	Medium	High	2067 Total
Nest-Site Security	Low	20	13	1	33	8	6	13	27
	Medium	50	23	2	76	34	25	94	153
	High	33	16	1	50	39	30	86	154
	Total	104	52	4	160	81	60	193	335

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Table 3.6. Population estimates (average ± 1 standard deviation) for the final year of 100-year stochastic simulations (N = 500) of female only marbled murrelet populations in the Olympic Experimental State Forest (OESF) and Southwest Washington analysis area (SWWA) under 2 models for nest-site security, edge effects (Edge) and the landscape predation index (Predation), and 5 dispersal scenarios. Rows labeled 2004 report results from simulations based on current landscapes, those labeled 2067 tabulate results from simulations based on projected future landscapes after implementation of DNR's draft marbled murrelet conservation strategy and other existing land-use policies.

			No Dispersal	Random Dispersal	Dispersal to Quality	Dispersal to Security	Dispersal to Quality and Security
OESF	Edge	2004	534.9 ± 100.3	475.3 ± 110.2	518.1 ± 120.9	464.8 ± 107.5	509.8 ± 108.2
		2067	810.0 ± 132.8	774.5 ± 163.0	776.5 ± 175.2	783.7 ± 149.4	809.7 ± 154.8
	Predation	2004	578.6 ± 109.7	515.7 ± 124.1	554.3 ± 129.2	512.3 ± 109.4	548.9 ± 114.5
		2067	645.5 ± 130.9	547.7 ± 130.8	599.9 ± 135.4	548.5 ± 112.8	589.6 ± 119.8
SWWA	Edge	2004	68.6 ± 22.9	53.7 ± 22.4	20.6 ± 12.6	53.8 ± 19.3	38.3 ± 16.4
		2067	113.2 ± 33.1	102.1 ± 30.2	105.2 ± 29.8	109.8 ± 27.2	97.1 ± 25.6
	Predation	2004	102.8 ± 28.5	78.8 ± 27.4	25.2 ± 15.9	81.4 ± 26.2	55.4 ± 24.0
		2067	250.0 ± 54.8	239.1 ± 53.4	145.6 ± 38.1	235.2 ± 49.0	201.7 ± 48.6

Table 3.7. Extinction durations (average years ± 1 standard deviation) recorded during 100-year stochastic simulations (N = 500) of female only marbled murrelet subpopulations in the Olympic Experimental State Forest (OESF) and Southwest Washington analysis area (SWWA). Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Estimates reflect 2 models for nest-site security, edge effects (Edge) and the landscape predation index (Predation), and 5 dispersal scenarios.

No Dispersal									
OESF					**SWWA**				
	Edge		**Predation**			**Edge**		**Predation**	
	2004	**2067**	**2004**	**2067**		**2004**	**2067**	**2004**	**2067**
L_L	25.7 ± 19.8	16.4 ± 15.5	29.9 ± 20.2	14.0 ± 15.1	**L_L**	15.3 ± 15.7	6.5 ± 9.8	26.0 ± 20.5	18.4 ± 16.4
M_L	68.0 ± 21.3	59.4 ± 23.7	50.9 ± 22.2	60.6 ± 22.7	**M_L**	67.4 ± 20.8	53.0 ± 22.5	64.7 ± 22.8	77.6 ± 17.2
H_L	4.3 ± 8.3	4.3 ± 8.6	5.7 ± 9.1	7.0 ± 10.5	**H_L**	98.4 ± 0.9	39.2 ± 23.0	98.4 ± 0.9	60.8 ± 22.9
L_M	4.9 ± 11.4	0.9 ± 4.4	3.3 ± 9.1	0.1 ± 1.0	**L_M**	0.5 ± 2.7	0.4 ± 2.6	0.6 ± 3.7	0.0 ± 0.4
M_M	31.7 ± 26.8	19.7 ± 23.2	27.1 ± 25.6	19.8 ± 23.5	**M_M**	33.9 ± 26.4	26.4 ± 25.3	27.8 ± 26.3	24.1 ± 24.5
H_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_M**	90.8 ± 9.2	91.1 ± 5.0	80.5 ± 16.7	3.5 ± 9.6
L_H	4.5 ± 14.0	0.0 ± 0.0	3.7 ± 12.7	0.0 ± 0.2	**L_H**	0.1 ± 1.1	0.4 ± 3.7	0.0 ± 0.0	0.0 ± 0.0
M_H	5.2 ± 15.3	7.7 ± 17.9	34.1 ± 31.7	17.9 ± 26.2	**M_H**	7.2 ± 16.8	18.1 ± 26.9	19.3 ± 28.6	3.2 ± 12.2
H_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_H**	88.9 ± 10.5	0.1 ± 1.4	88.9 ± 10.3	0.0 ± 0.0

Random Dispersal									
OESF					**SWWA**				
	Edge		**Predation**			**Edge**		**Predation**	
	2004	**2067**	**2004**	**2067**		**2004**	**2067**	**2004**	**2067**
L_L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	**L_L**	7.3 ± 9.0	1.9 ± 4.3	5.5 ± 7.5	0.2 ± 1.0
M_L	0.1 ± 0.7	0.0 ± 0.0	0.0 ± 0.2	0.0 ± 0.1	**M_L**	14.8 ± 11.5	4.1 ± 5.8	9.1 ± 8.6	2.5 ± 2.8
H_L	0.0 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1	**H_L**	43.5 ± 17.6	3.7 ± 6.0	30.8 ± 13.7	0.8 ± 2.0
L_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**L_M**	1.7 ± 4.7	0.4 ± 1.9	0.6 ± 2.7	0.0 ± 0.2
M_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**M_M**	7.9 ± 10.5	2.5 ± 5.5	3.8 ± 6.1	0.2 ± 1.3
H_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_M**	23.3 ± 11.9	18.2 ± 8.4	12.8 ± 8.6	0.1 ± 0.6
L_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**L_H**	0.6 ± 3.1	0.2 ± 1.5	0.1 ± 1.2	0.0 ± 0.0
M_H	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.2	0.0 ± 0.0	**M_H**	2.3 ± 5.9	1.1 ± 3.4	2.3 ± 5.9	0.0 ± 0.2
H_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_H**	21.8 ± 11.8	0.1 ± 1.1	16.2 ± 8.1	0.0 ± 0.0

Dispersal to Quality									
OESF					**SWWA**				
	Edge		**Predation**			**Edge**		**Predation**	
	2004	**2067**	**2004**	**2067**		**2004**	**2067**	**2004**	**2067**
L_L	0.1 ± 0.6	0.0 ± 0.1	0.0 ± 0.4	0.0 ± 0.2	**L_L**	22.7 ± 15.2	4.3 ± 5.7	22.4 ± 14.3	2.6 ± 3.8
M_L	0.1 ± 0.4	0.0 ± 0.0	0.0 ± 0.2	0.0 ± 0.1	**M_L**	20.1 ± 14.7	3.3 ± 5.1	15.4 ± 13.3	3.6 ± 3.9
H_L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_L**	32.2 ± 14.8	0.8 ± 2.7	26.8 ± 13.3	0.3 ± 1.1
L_M	0.0 ± 0.3	0.0 ± 0.0	0.0 ± 0.2	0.0 ± 0.0	**L_M**	14.4 ± 13.8	2.2 ± 4.3	10.9 ± 12.3	0.8 ± 2.8
M_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1	**M_M**	11.3 ± 12.3	1.5 ± 4.3	8.5 ± 11.5	0.5 ± 1.7
H_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_M**	17.2 ± 10.2	0.1 ± 0.9	10.7 ± 9.0	0.0 ± 0.1
L_H	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.3	**L_H**	8.2 ± 13.4	1.3 ± 4.1	4.6 ± 9.7	0.0 ± 0.4
M_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.3	0.0 ± 0.0	**M_H**	4.9 ± 10.5	0.8 ± 2.7	4.6 ± 8.9	0.1 ± 0.8
H_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_H**	16.8 ± 10.4	0.0 ± 0.0	14.7 ± 9.4	0.0 ± 0.0

Table 3.7. continued.

Dispersal to Security									
OESF					SWWA				
	Edge		Predation			Edge		Predation	
	2004	2067	2004	2067		2004	2067	2004	2067
L_L	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.3	0.0 ± 0.1	**L_L**	14.0 ± 12.1	5.3 ± 6.5	10.1 ± 10.2	0.7 ± 1.8
M_L	0.3 ± 1.0	0.0 ± 0.1	0.0 ± 0.5	0.1 ± 0.5	**M_L**	18.2 ± 12.4	7.3 ± 6.9	11.9 ± 9.7	3.0 ± 2.8
H_L	0.0 ± 0.4	0.0 ± 0.0	0.0 ± 0.3	0.0 ± 0.1	**H_L**	45.5 ± 17.2	7.5 ± 7.7	33.9 ± 14.2	1.3 ± 2.4
L_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**L_M**	2.8 ± 6.7	0.5 ± 2.3	0.9 ± 2.7	0.0 ± 0.2
M_M	0.0 ± 0.3	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	**M_M**	7.6 ± 9.9	2.4 ± 4.9	4.8 ± 7.5	0.2 ± 1.2
H_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_M**	21.8 ± 10.8	18.1 ± 8.6	12.6 ± 8.5	0.0 ± 0.2
L_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**L_H**	0.1 ± 0.9	0.1 ± 1.1	0.1 ± 1.2	0.0 ± 0.0
M_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1	**M_H**	1.3 ± 4.5	0.5 ± 2.3	0.9 ± 2.6	0.0 ± 0.1
H_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_H**	15.5 ± 8.4	0.0 ± 0.2	11.6 ± 6.6	0.0 ± 0.0

Dispersal to Quality and Security									
OESF					SWWA				
	Edge		Predation			Edge		Predation	
	2004	2067	2004	2067		2004	2067	2004	2067
L_L	0.1 ± 0.6	0.0 ± 0.3	0.1 ± 0.5	0.0 ± 0.4	**L_L**	22.3 ± 14.2	6.5 ± 6.5	19.4 ± 13.5	2.2 ± 3.4
M_L	0.2 ± 0.9	0.0 ± 0.1	0.0 ± 0.3	0.1 ± 0.6	**M_L**	24.3 ± 15.7	5.8 ± 6.3	18.4 ± 13.8	4.3 ± 3.5
H_L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_L**	47.7 ± 16.6	3.3 ± 4.7	39.3 ± 17.5	1.2 ± 2.2
L_M	0.0 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**L_M**	10.9 ± 11.6	1.6 ± 3.3	6.3 ± 8.8	0.3 ± 1.5
M_M	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**M_M**	12.3 ± 12.5	1.9 ± 3.7	7.7 ± 9.3	0.4 ± 1.4
H_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_M**	20.5 ± 10.7	0.2 ± 1.4	11.2 ± 8.3	0.0 ± 0.4
L_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**L_H**	0.8 ± 3.6	0.0 ± 0.4	0.2 ± 2.0	0.0 ± 0.0
M_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	**M_H**	0.9 ± 3.5	0.3 ± 1.3	1.0 ± 3.9	0.0 ± 0.1
H_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**H_H**	9.3 ± 5.8	0.0 ± 0.0	6.2 ± 4.4	0.0 ± 0.0

Table 3.8. Marbled murrelet carrying capacity estimates (predicted numbers of murrelets supported), cross-classified by estimated stand-level habitat quality and nest-site security for all lands in the Olympic Experimental State Forest (OESF) as defined by watersheds, and in the Southwest Washington analysis area (SWWA). Estimates are for landscapes projected after habitat development due to forest management under DNR's draft marbled murrelet conservation strategy and other existing land use policies (Baseline) and 2 alternative scenarios (Trials 1 and 2, see pp. 103-105). Nest-site security is estimated based on proximity to edges.

OESF		**Baseline**				**Trial 1**				**Trial 2**			
		Stand-level Habitat Quality											
		Low	**Medium**	**High**	**Total**	**Low**	**Medium**	**High**	**Total**	**Low**	**Medium**	**High**	**Total**
Nest Site Security	**Low**	171	17	509	697	164	8	509	681	164	8	486	658
	Medium	144	29	623	796	132	10	623	765	132	10	598	740
	High	226	19	830	1,075	226	19	830	1,075	226	19	878	1,123
	Total	540	65	1,962	2,568	522	37	1,962	2,521	522	37	1,962	2,521

SWWA		**Baseline**				**Trial 1**				**Trial 2**			
		Stand-level Habitat Quality											
		Low	**Medium**	**High**	**Total**	**Low**	**Medium**	**High**	**Total**	**Low**	**Medium**	**High**	**Total**
Nest Site Security	**Low**	361	20	39	420	361	10	20	391	361	6	15	382
	Medium	219	25	78	322	219	12	38	269	219	12	33	264
	High	45	16	78	139	45	16	78	139	45	20	88	153
	Total	625	60	196	881	625	38	136	799	625	38	136	799

Table 3.9. Extinction durations (average years ± 1 standard deviation) recorded during 100-year stochastic simulations (N = 500) of female only marbled murrelet subpopulations under the edge effects model for nest-site security, in landscapes projected after habitat development due to forest management under DNR's draft marbled murrelet conservation strategy and other existing land use policies (Baseline) and 2 alternative scenarios (Trials 1 and 2, see pp. 103-105), in the Olympic Experimental State Forest (OESF) and Southwest Washington analysis area (SWWA). Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3).

	OESF				**SWWA**		
	Baseline	**Trial 1**	**Trial 2**		**Baseline**	**Trial 1**	**Trial 2**
L_L	0.0 ± 0.3	0.0 ± 0.0	0.0 ± 0.2		6.5 ± 6.5	8.2 ± 7.6	6.4 ± 6.5
M_L	0.0 ± 0.1	0.0 ± 0.3	0.0 ± 0.3		5.8 ± 6.3	9.1 ± 7.3	8.6 ± 6.3
H_L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		3.3 ± 4.7	5.0 ± 6.5	4.1 ± 5.0
L_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		1.6 ± 3.3	2.6 ± 5.3	1.7 ± 3.8
M_M	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0		1.9 ± 3.7	4.4 ± 5.5	3.7 ± 5.8
H_M	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		0.2 ± 1.4	0.7 ± 2.5	0.3 ± 1.3
L_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		0.0 ± 0.4	0.2 ± 2.0	0.2 ± 1.7
M_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		0.3 ± 1.3	0.5 ± 2.3	0.2 ± 0.7
H_H	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

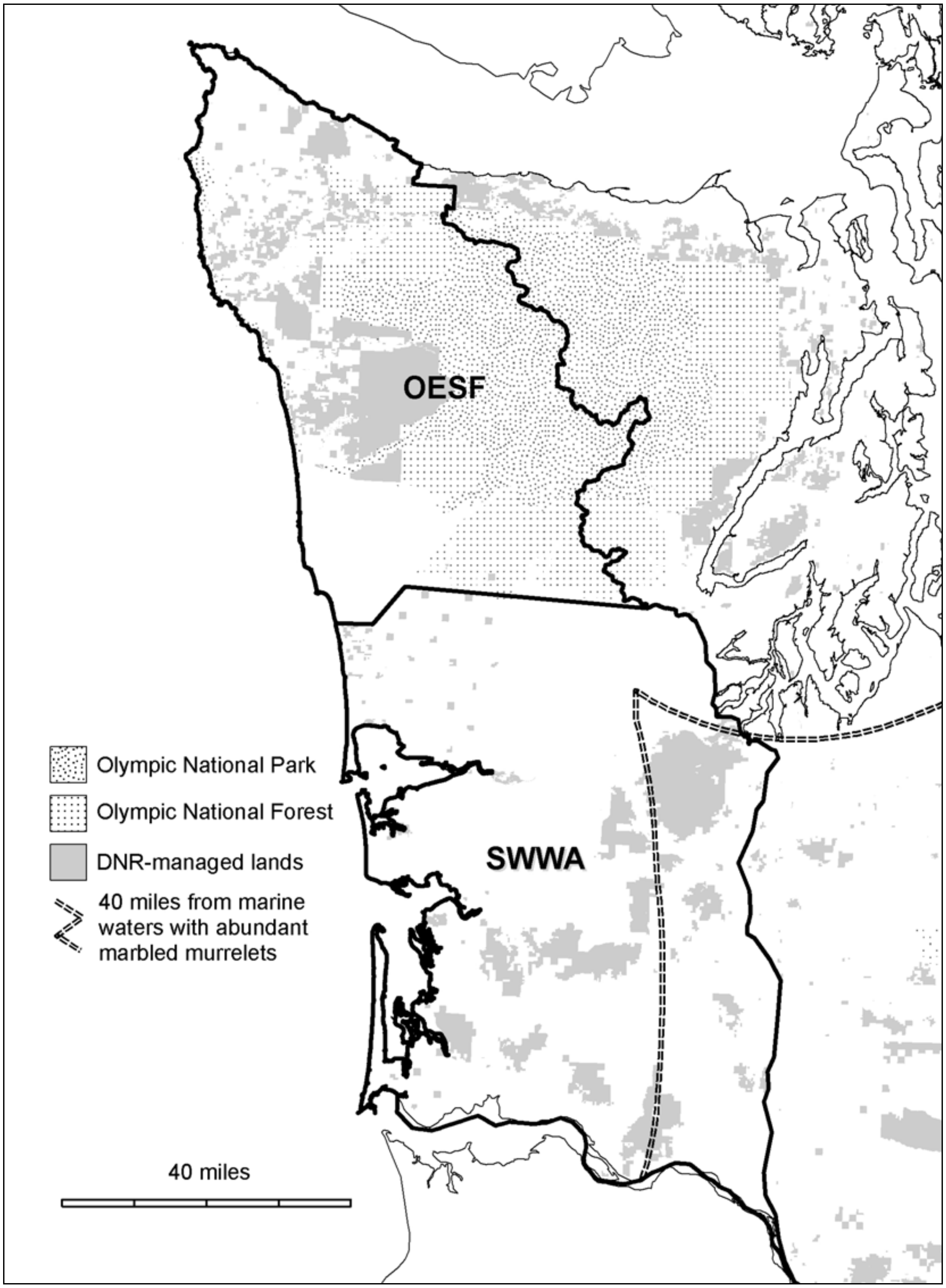

Figure 3.1. Map of the study area showing the Olympic Experimental State Forest (OESF) and Southwest Washington (SWWA) analysis areas outlined in bold black. DNR and federal forest lands are shaded, unshaded lands are managed by private landowners, tribal, or local governments.

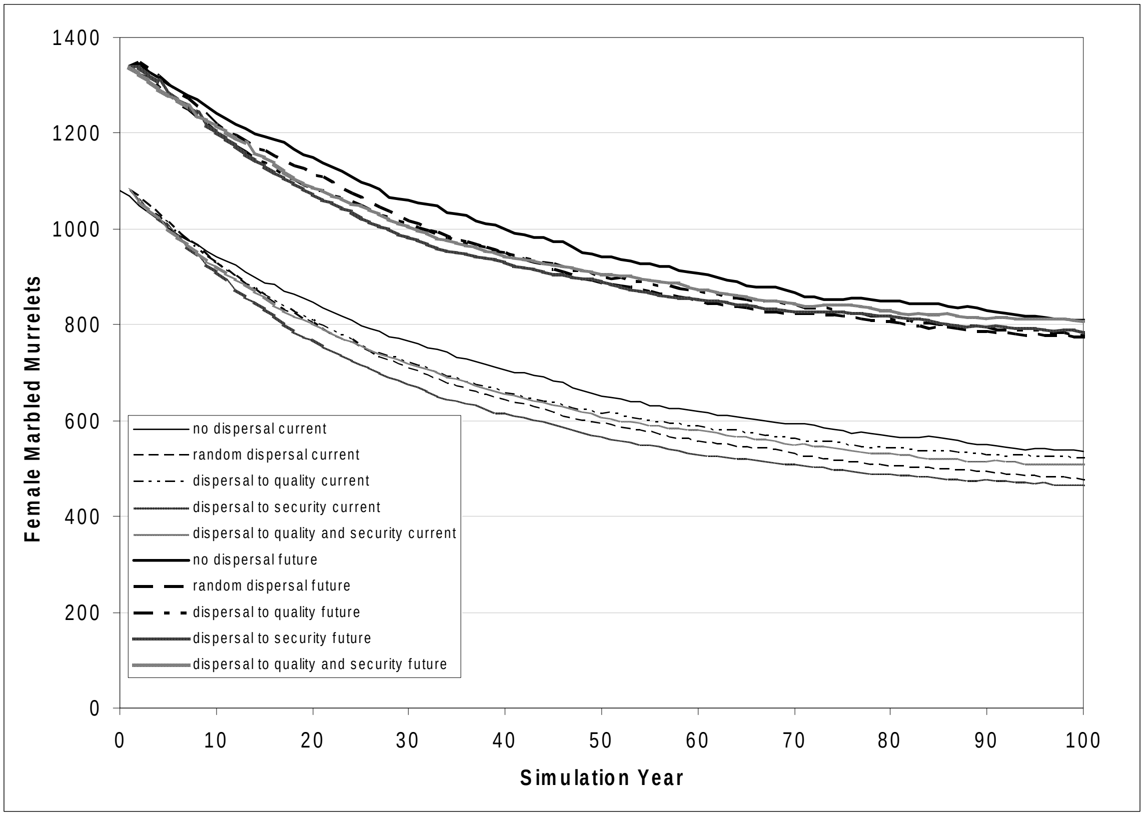

Figure 3.2A. Average trajectories over 100-year stochastic simulations (N = 500) of populations of female marbled murrelets in the Olympic Experimental State Forest under the edge effects model for nest-site security and 5 dispersal scenarios. Trajectories labeled "current" plot simulations based on 2004 landscapes, those labeled "future" plot simulations based on projected 2067 landscapes after implementation of DNR's draft marbled murrelet conservation strategy and other existing land-use policies.

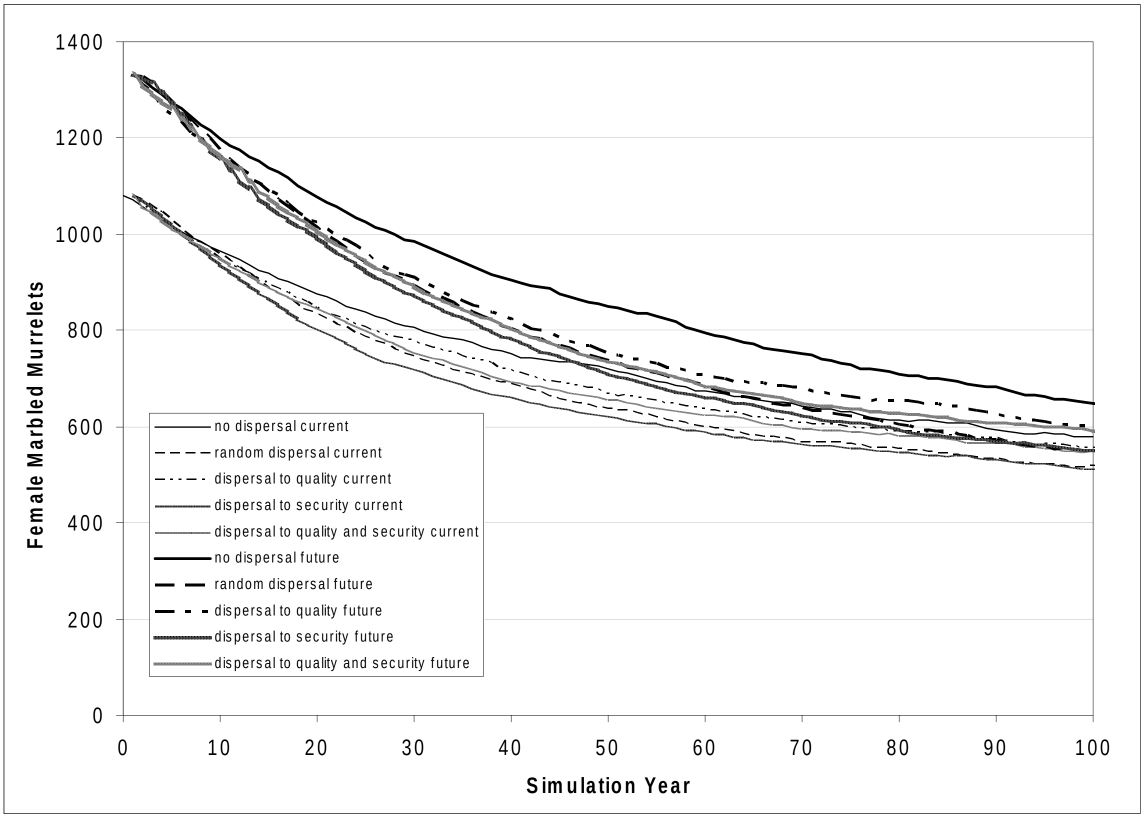

Figure 3.2B. Average trajectories over 100-year stochastic simulations (N = 500) of populations of female marbled murrelets in the Olympic Experimental State Forest under the landscape predation index model for nest-site security and 5 dispersal scenarios. Trajectories labeled "current" plot simulations based on 2004 landscapes, those labeled "future" plot simulations based on projected 2067 landscapes after implementation of DNR's draft marbled murrelet conservation strategy and other existing land-use policies.

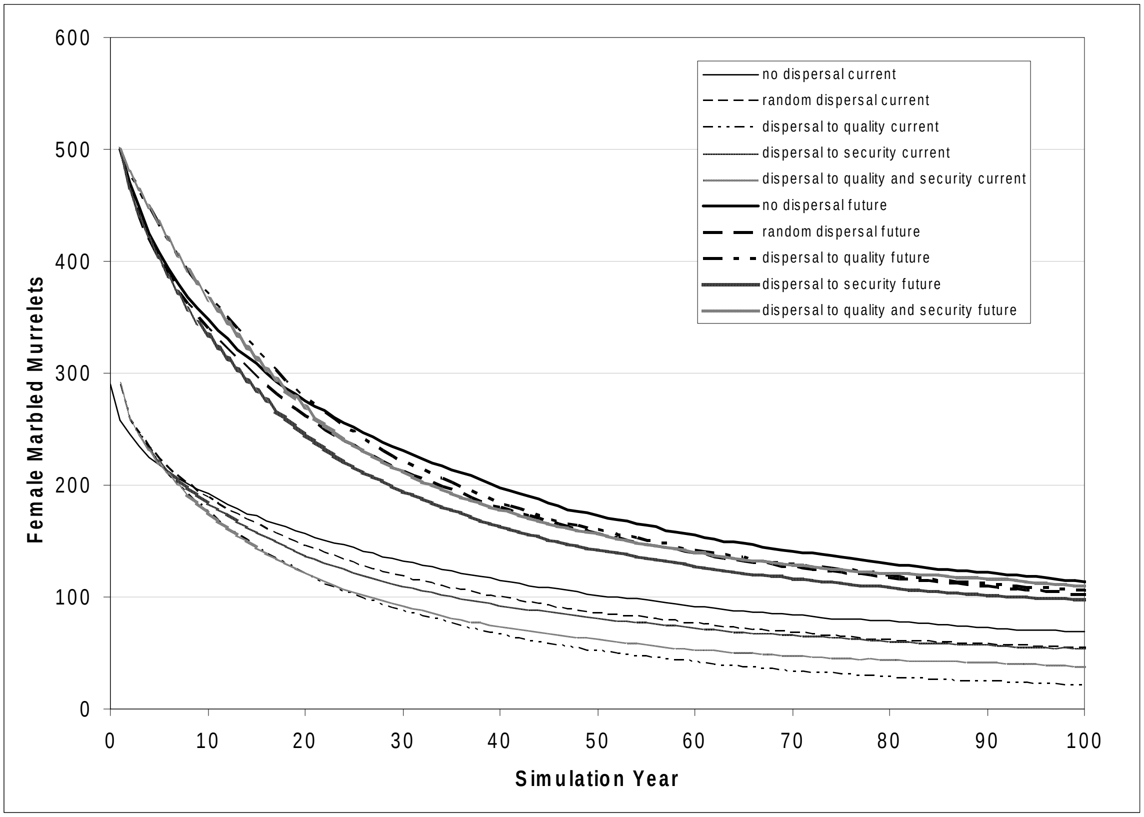

Figure 3.3A. Average trajectories over 100-year stochastic simulations (N = 500) of populations of female marbled murrelets in the Southwest Washington analysis area under the edge effects model for nest-site security and 5 dispersal scenarios. Trajectories labeled "current" plot simulations based on 2004 landscapes, those labeled "future" plot simulations based on projected 2067 landscapes after implementation of DNR's draft marbled murrelet conservation strategy and other existing land-use policies.

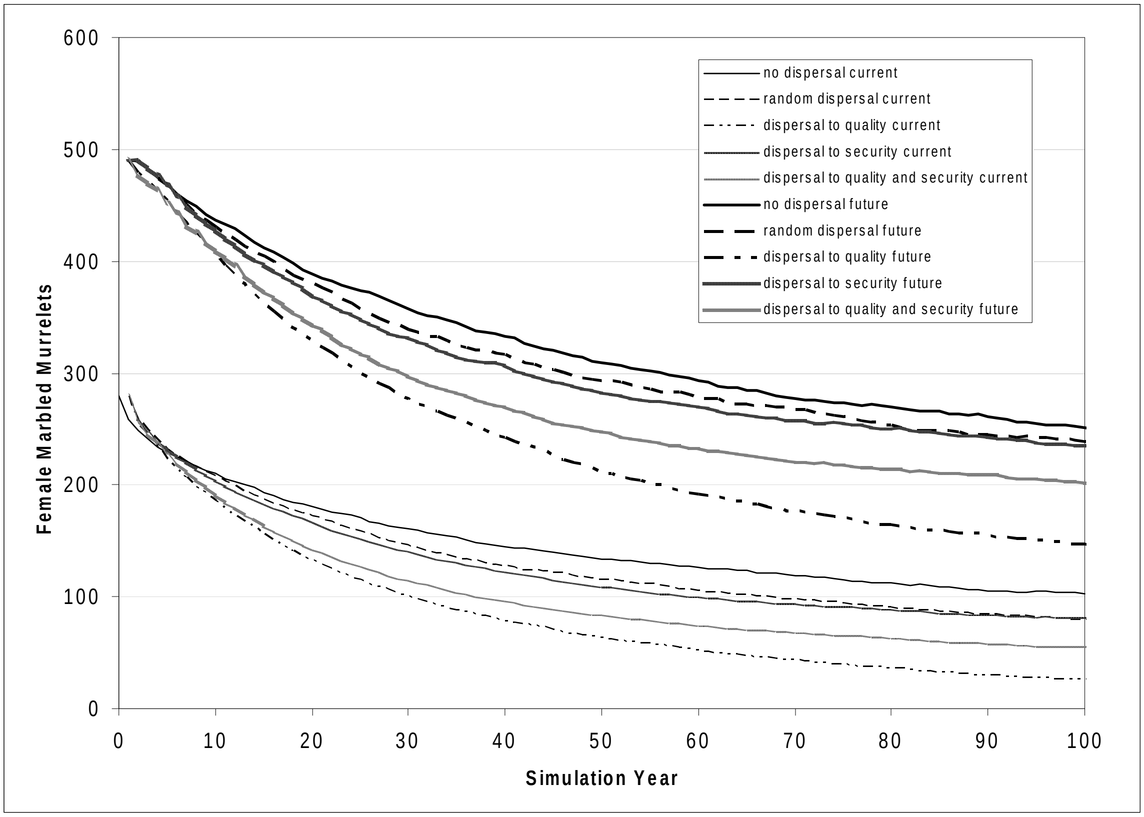

Figure 3.3B. Average trajectories over 100-year stochastic simulations (N = 500) of populations of female marbled murrelets in the Southwest Washington analysis area under the landscape predation index model for nest-site security and 5 dispersal scenarios. Trajectories labeled "current" plot simulations based on 2004 landscapes, those labeled "future" plot simulations based on projected 2067 landscapes after implementation of DNR's draft marbled murrelet conservation strategy and other existing land-use policies.

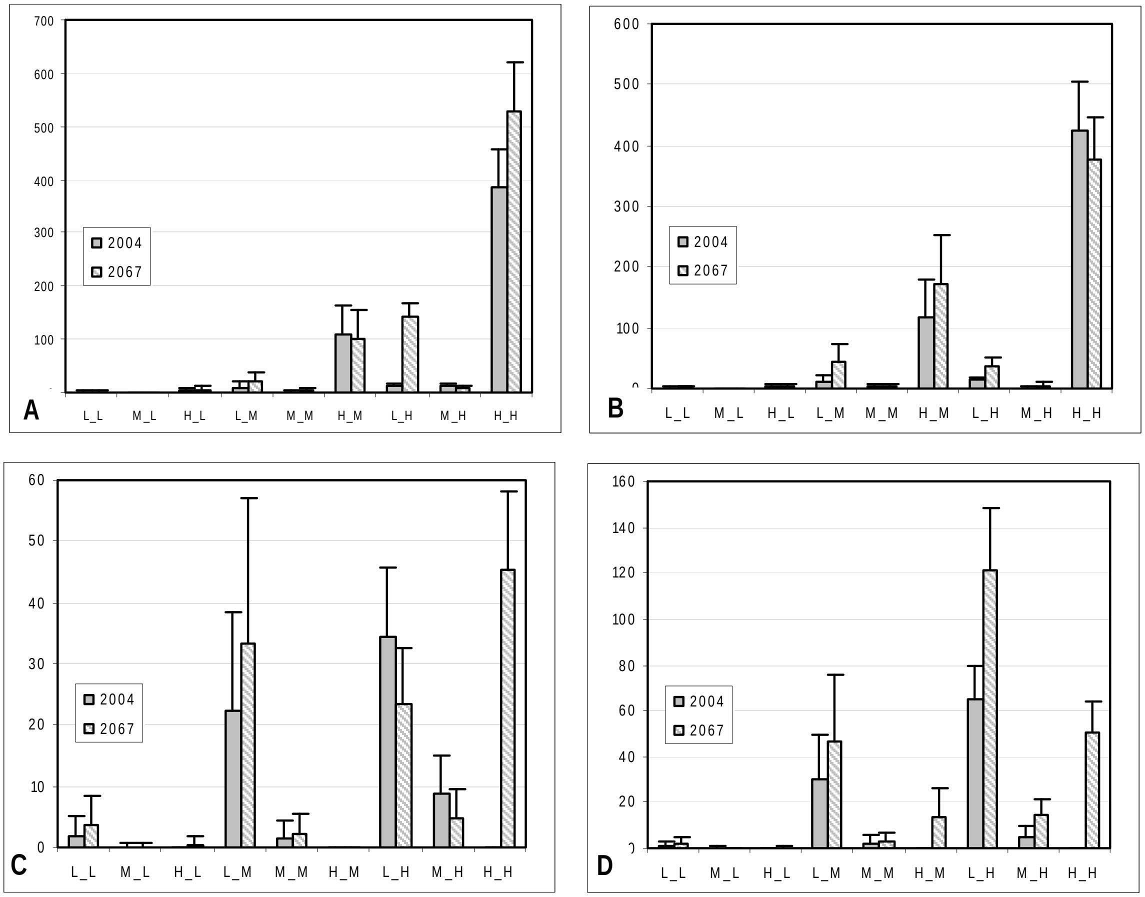

Figure 3.4. Population estimates (average ± 1 standard deviation) under the No Dispersal scenario for the final year of 100-year stochastic simulations (N = 500) of subpopulations of female marbled murrelets in the Olympic Experimental State Forest (panels A, B) and Southwest Washington (panels C, D) analysis areas. Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Panels A and C reflect estimates under the edge effects model for nest-site security. Panels B and D reflect estimates under the landscape predation index model for nest-site security. Note that the Y-axis scale differs among panels.

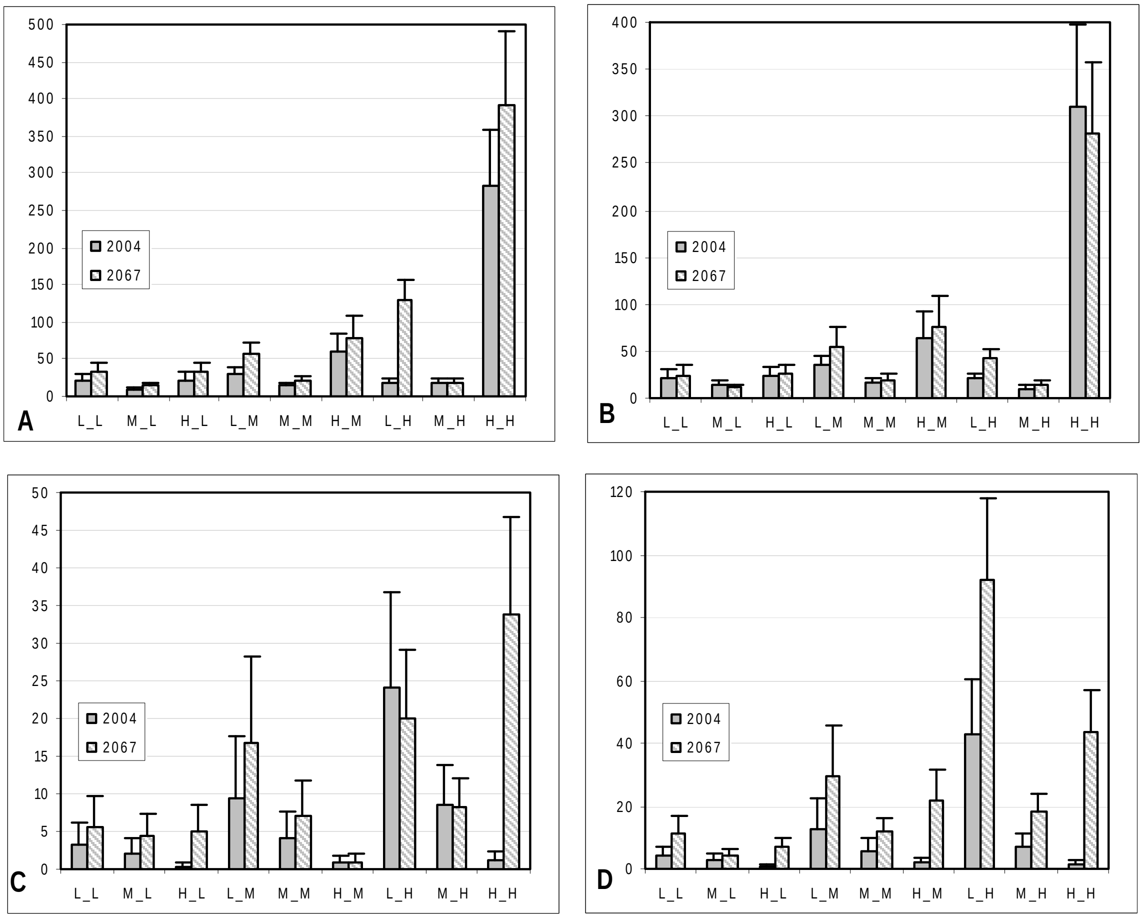

Figure 3.5. Population estimates (average ± 1 standard deviation) under the Random Dispersal scenario for the final year of 100-year stochastic simulations (N = 500) of subpopulations of female marbled murrelets in the Olympic Experimental State Forest (panels A, B) and Southwest Washington (panels C, D) analysis areas. Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Panels A and C reflect estimates under the edge effects model for nest-site security. Panels B and D reflect estimates under the landscape predation index model for nest-site security. Note that the Y-axis scale differs among panels.

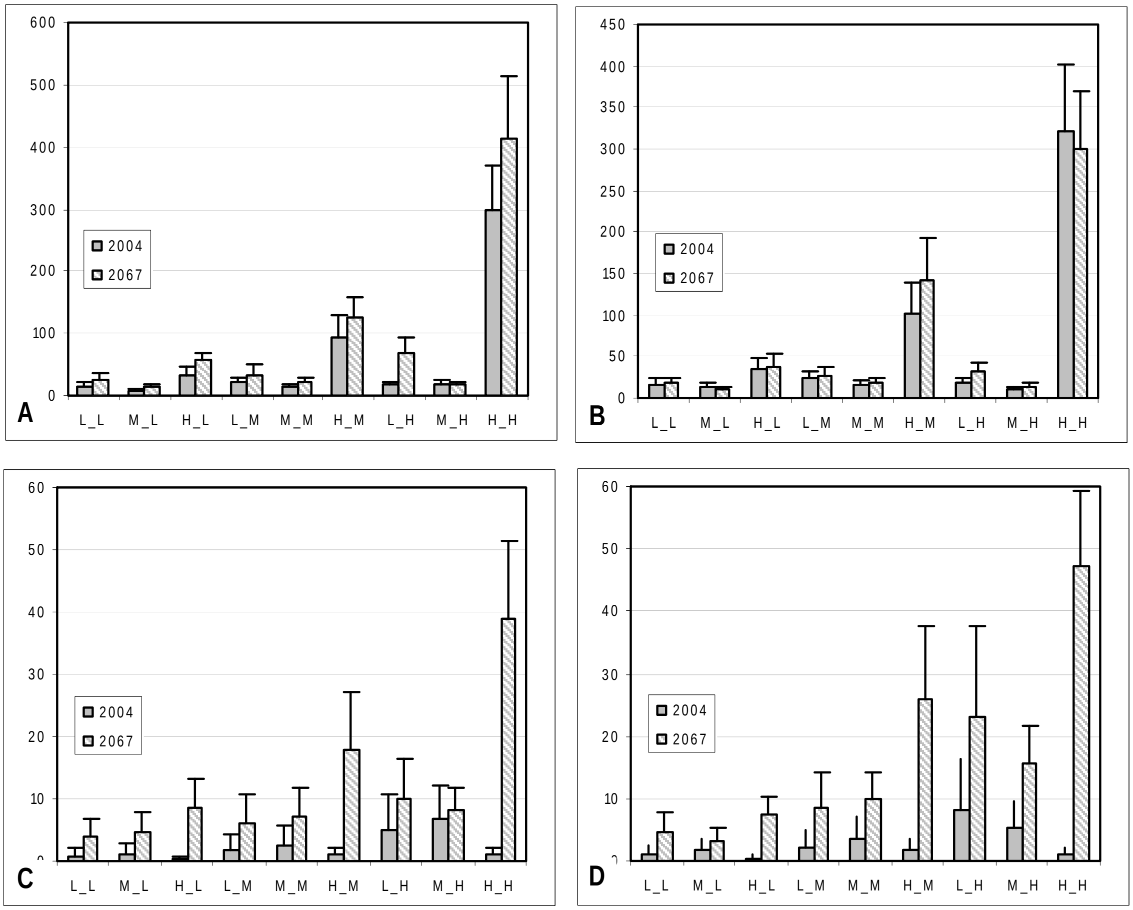

Figure 3.6. Population estimates (average ± 1 standard deviation) under the Dispersal to Stand-Level Habitat Quality scenario for the final year of 100-year stochastic simulations (N = 500) of subpopulations of female marbled murrelets in the Olympic Experimental State Forest (panels A, B) and Southwest Washington (panels C, D) analysis areas. Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Panels A and C reflect estimates under the edge effects model for nest-site security. Panels B and D reflect estimates under the landscape predation index model for nest-site security. Note that the Y-axis scale differs among panels.

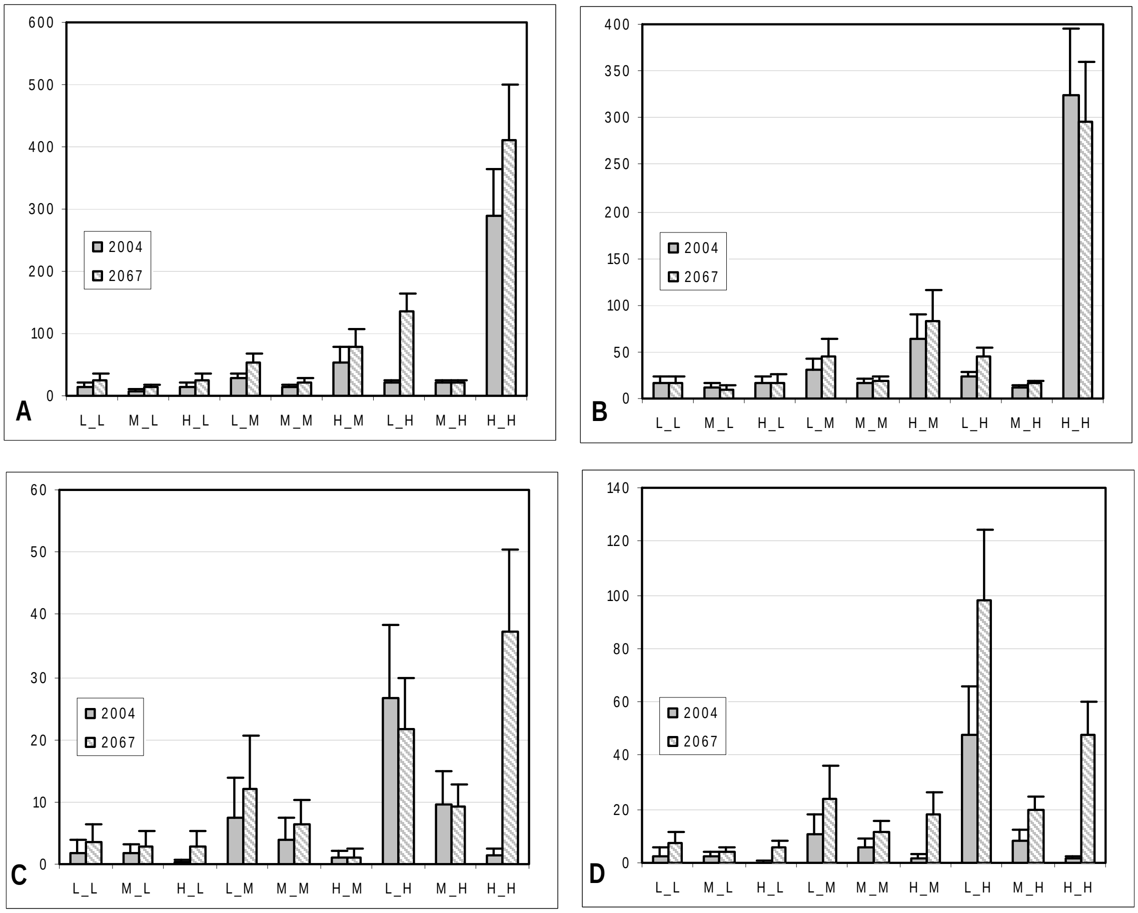

Figure 3.7. Population estimates (average ± 1 standard deviation) under the Dispersal to Landscape-level Nest-site Security scenario for the final year of 100-year stochastic simulations (N = 500) of subpopulations of female marbled murrelets in the Olympic Experimental State Forest (panels A, B) and Southwest Washington (panels C, D) analysis areas. Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Panels A and C reflect estimates under the edge effects model for nest-site security. Panels B and D reflect estimates under the landscape predation index model for nest-site security. Note that the Y-axis scale differs among panels.

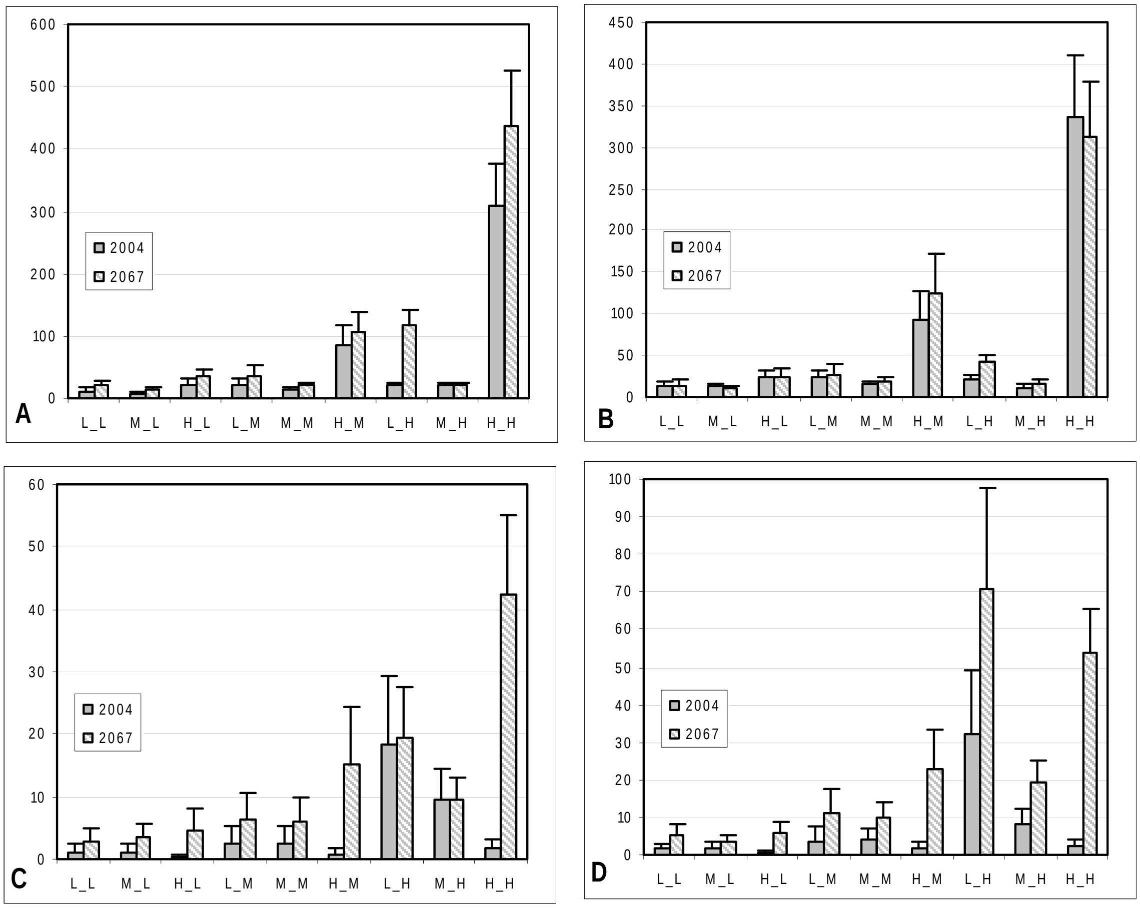

Figure 3.8. Population estimates (average ± 1 standard deviation) under the Dispersal to Stand-level Habitat Quality and Landscape-level Nest-site Security scenario for the final year of 100-year stochastic simulations (N = 500) of subpopulations of female marbled murrelets in the Olympic Experimental State Forest (panels A, B) and Southwest Washington (panels C, D) analysis areas. Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Panels A and C reflect estimates under the edge effects model for nest-site security. Panels B and D reflect estimates under the landscape predation index model for nest-site security. Note that the Y-axis scale differs among panels.

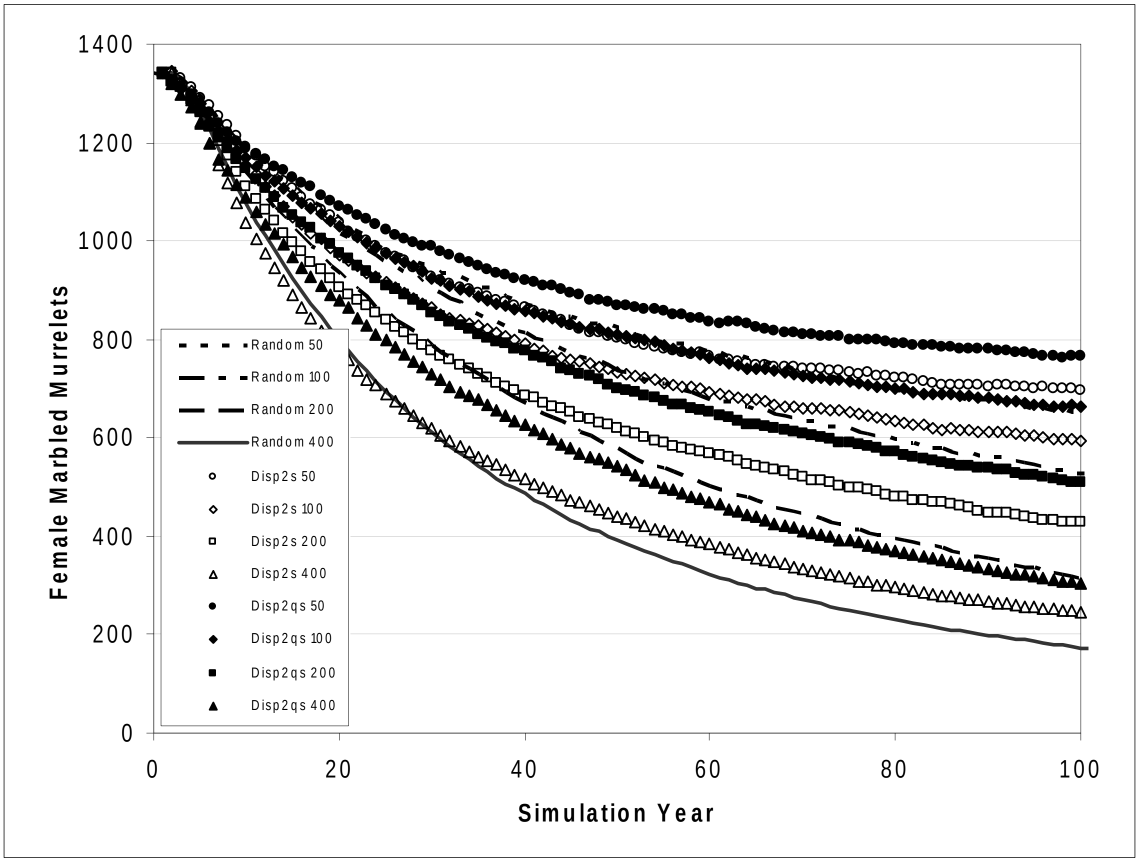

Figure 3.9. Sensitivity of projected populations of female marbled murrelets to varying, high rates of dispersal under 3 scenarios: random dispersal (Random) and directed dispersal to nest-site security (Disps2s) and to both stand-level habitat quality and nest-site security (Disps2qs). Dispersal rates were varied 50%, 100%, 200%, and 400% above baseline. Populations were projected with 100-year stochastic simulations (N = 500) in the Olympic Experimental State Forest future landscape predicted to result in 2067 from habitat development due to forest management under DNR's draft marbled murrelet conservation strategy and other existing land use policies.

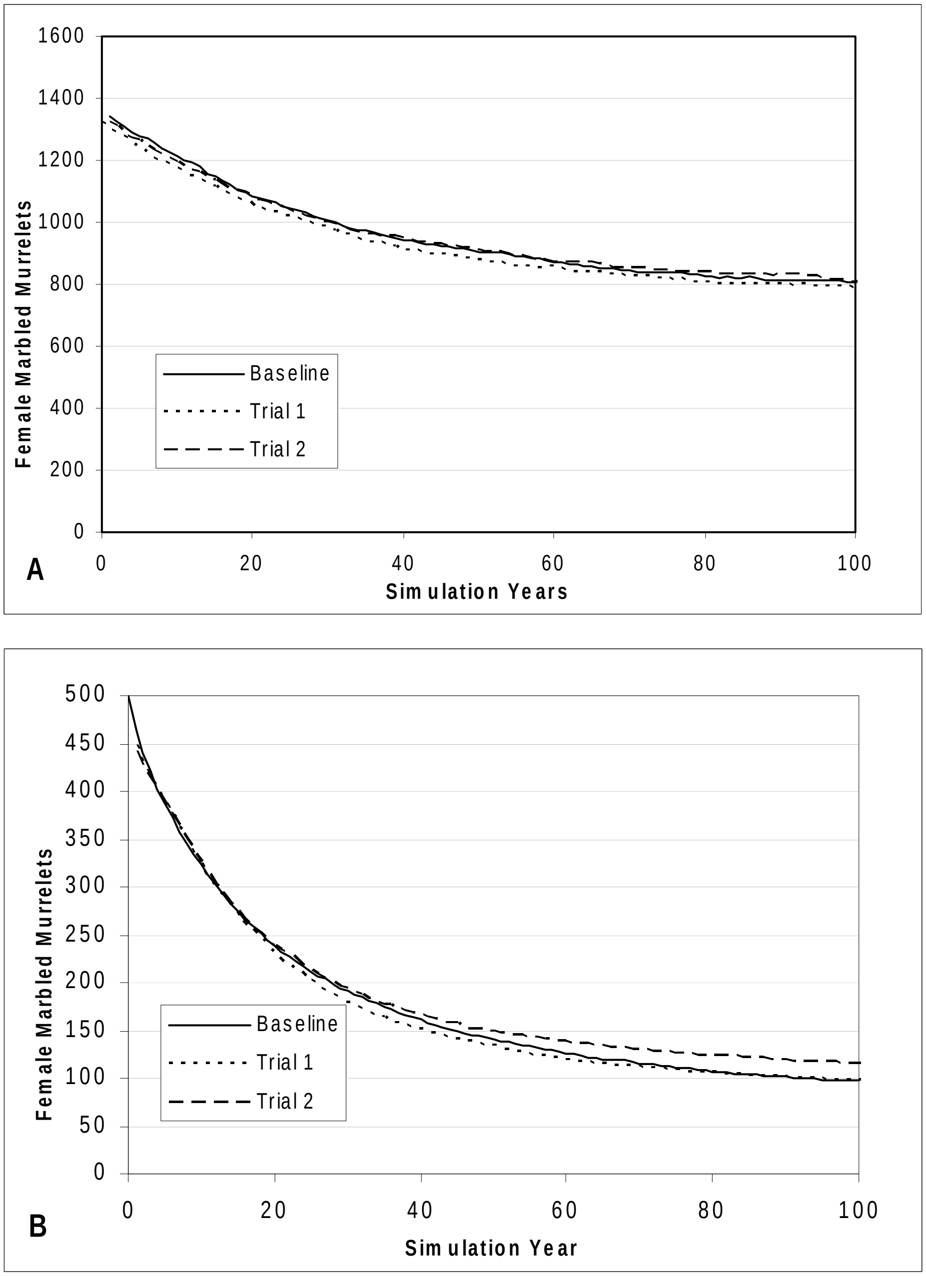

Figure 3.10. Average trajectories over 100-year stochastic simulations (N = 500) of female only marbled murrelet populations in the Olympic Experimental State Forest (A) and Southwest Washington analysis area (B) under the edge effects model for nest-site security and the dispersal to quality and security scenario. Trajectories labeled Baseline plot simulations based on projected future landscapes after implementation of DNR's draft marbled murrelet conservation strategy and other existing land-use policies, those labeled Trial 1 and Trial 2 are based on alternative scenarios for marbled murrelet conservation (see pp. 103-105). Note that the Y-axis scale differs among figures.

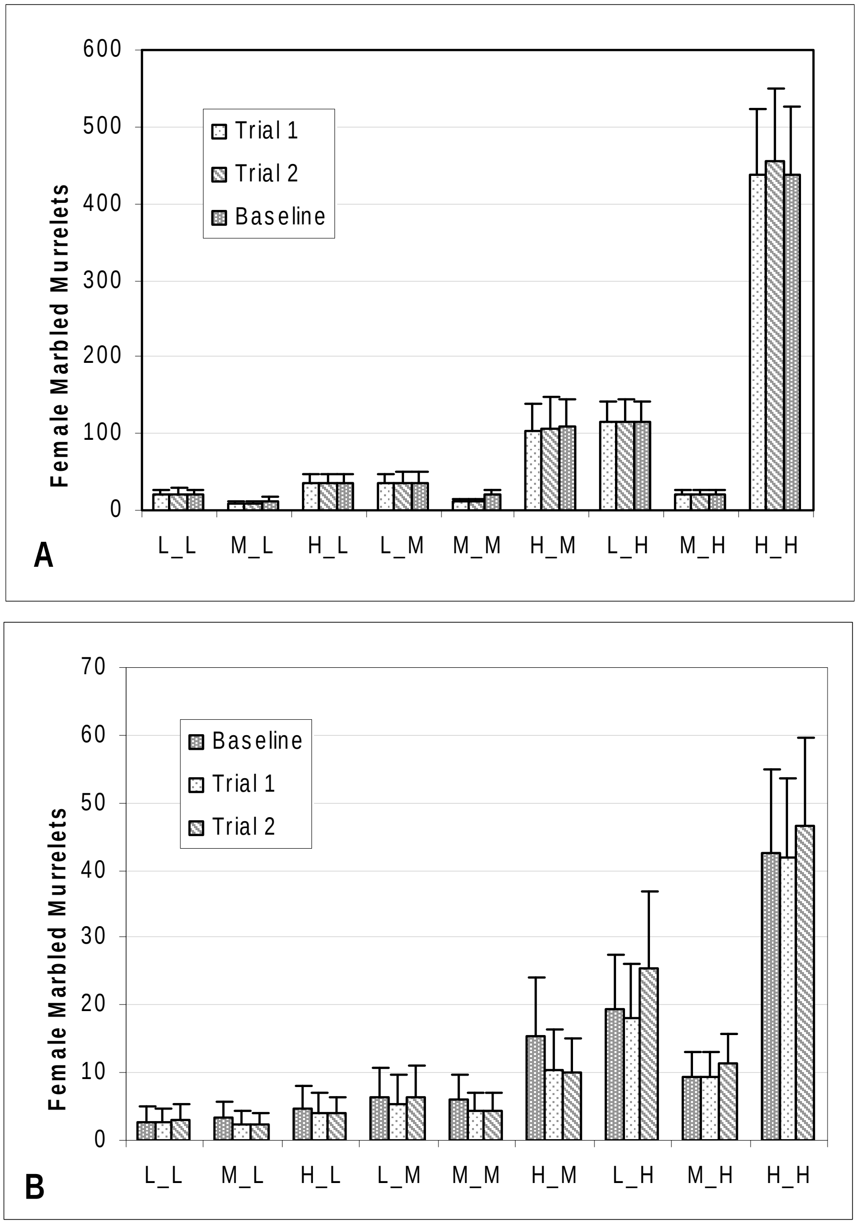

Figure 3.11. Population estimates (average ± 1 standard deviation) under the edge effects model for nest-site security, in landscapes projected after habitat development due to forest management under DNR's draft marbled murrelet conservation strategy and other existing land use policies (Baseline) and 2 alternative scenarios (Trials 1 and 2, see pp. 103-105), for the final year of 100-year stochastic simulations (N = 500) of female only marbled murrelet subpopulations in the Olympic Experimental State Forest (A) and Southwest Washington analysis area (B). Subpopulations are characterized by their position in the quality-security matrix with the first letter describing stand-level quality and the second letter describing landscape-level security (L low, M medium, H high, see Tables 3.2, 3.3). Note that the Y-axis scale differs between figures.

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Appendix A. Exploratory Analyses of Landscape Indices

A large variety of metrics are available for quantifying landscape pattern (Turner et al. 2001). These metrics may be defined at 3 levels: patch-level metrics quantify the spatial character and context of individual patches of a given cover type; class-level metrics are integrated across all patches of a cover type to quantify amounts and spatial distribution of that type, these may be interpreted as fragmentation indices; and landscape-level metrics are integrated across all patch-types or classes to quantify the spatial character of the entire analysis area or landscape (McGarigal et al. 2002). While the concept of a cover-type patch is intuitive, quantitative analyses based on patches are strongly influenced by a variety of somewhat arbitrary factors used to define the patches (Turner et al. 2001). For this reason, and because patch-level metrics are not appropriate for moving-window analyses (McGarigal et al. 2002) needed to provide continuous surfaces that describe landscape covariates, I used only class- and landscape-level metrics in these analyses.

Table A.1 itemizes class-level, landscape-level, and geographic metrics that were examined with correlation analyses. Initially, I evaluated correlations among class-level metrics for open, sapling, pole, small sawtimber, large sawtimber, and old-growth. An example of these correlations, calculated from 200 m radius plots, is provided in Table A.2. I evaluated correlations among additional class-level metrics for open, sapling, large sawtimber, old-growth, and "late-seral" (combined large sawtimber and old-growth) in subsequent analyses (exemplified in Table A.3). Correlations among old-growth class metrics, across scales are summarized in Table A.4 as an example of within-class correlations. Correlations among landscape metrics are summarized in Table A.5, and among geographic indices in Table A.6.

In total, I evaluated 460 univariate correlations of marbled murrelet activity with class- and landscape-level metrics (376 class and 84 landscape metrics) compiled for 200, 400, 800, 1600, 2400, and 3200 m radius circular plots. Of these, 126 (27%) showed significant correlations, $P \leq 0.05$. Correlations with open, sapling, large sawtimber, old-growth, and late seral comprised nearly 90% of those (Table A.7), while nearly 80% of those correlations were at the 200 - 800 m scales (Table A.7, Figure A.1). Among the strongest 25% of those correlations, 87% were at the 400 and 800 m scales (Figure A.1).

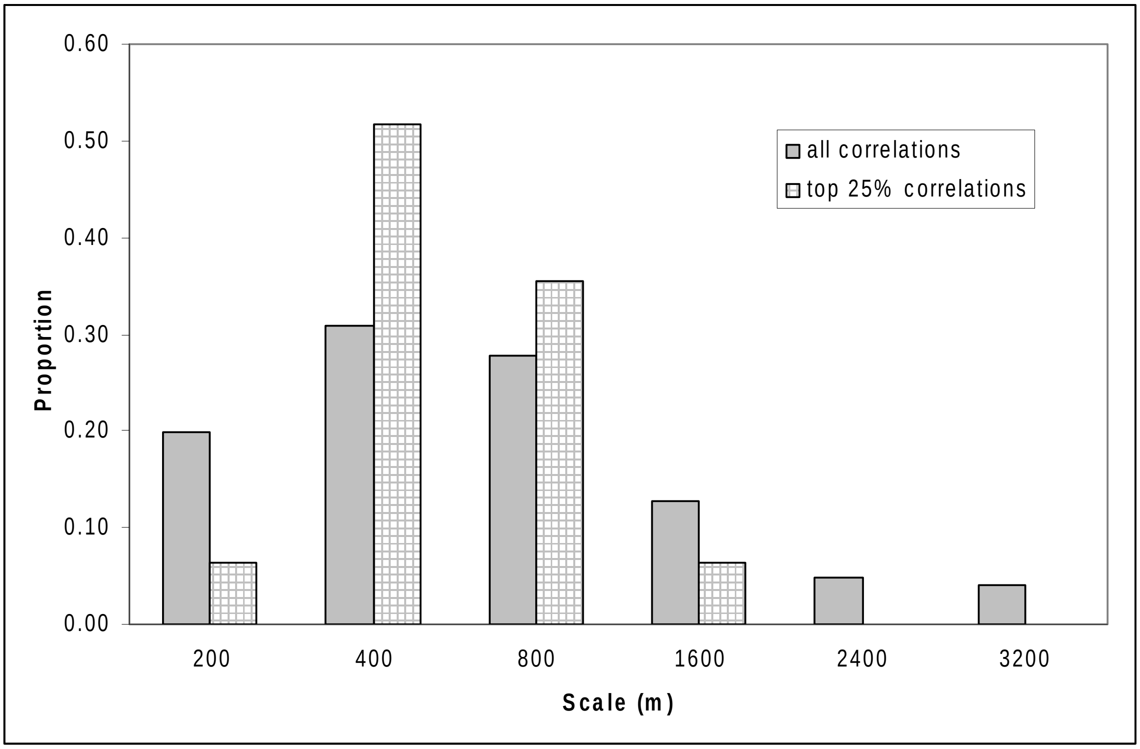

Figure A.1. Proportions of correlations between marbled murrelet activity and class- and landscape-level metrics, classified by the scale at which class and landscape metrics were calculated.

Table A.1. List of class-level, landscape-level, and geographic metrics examined with correlation analyses.

Metric Type	Metric	Abbreviation
	Class Metrics	
Open	Total class area	CA
(OP)	Area-weighted average patch size	AVAREA
	Landscape shape index	LSI
	Normalized landscape shape index	NLSI
	Total edge	TE
	Area-weighted average similarity index (100 m radius)	SIMI
	Total edge-contrast index	TECI
	Contrast-weighted edge density	CWED
Sapling	Total class area	CA
(SAP)	Area-weighted average patch size	AVAREA
	Landscape shape index	LSI
	Normalized landscape shape index	NLSI
	Total edge	TE
	Area-weighted average similarity index (100 m radius)	SIMI
	Total edge-contrast index	TECI
	Contrast-weighted edge density	CWED
Pole	Total class area	CA
(POL)	Area-weighted average patch size	AVAREA
	Landscape shape index	LSI
	Total edge	TE
Small Sawtimber	Total class area	CA
(SS)	Area-weighted average patch size	AVAREA
	Landscape shape index	LSI
	Total edge	TE
Large Sawtimber	Total class area	CA
(LS)	Area-weighted average patch size	AVAREA
	Number of patches	NP
	Core area as a percent of total class area	AVCAI
	Core area as a percent of total analysis area	CPLAND
	Area-weighted average similarity index (100 m radius)	SIMI
	Class-specific contagion	CLUMPY
	Landscape shape index	LSI
	Normalized landscape shape index	NLSI
	Total edge	TE
	Total edge-contrast index	TECI
	Contrast-weighted edge density	CWED

Table A.1. continued

Metric Type	Metric	Abbreviation
	Class Metrics (continued)	
Old-growth (OG)	Total class area	CA
	Area-weighted average patch size	AVAREA
	Number of patches	NP
	Core area as a percent of total class area	AVCAI
	Core area as a percent of total analysis area	CPLAND
	Area-weighted average similarity index (100 m radius)	SIMI
	Class-specific contagion	CLUMPY
	Landscape shape index	LSI
	Normalized landscape shape index	NLSI
	Total edge	TE
	Total edge-contrast index	TECI
	Contrast-weighted edge density	CWED
Late Seral (LT)	Total class area	CA
	Area-weighted average patch size	AVAREA
	Number of patches	NP
	Core area as a percent of total class area	AVCAI
	Core area as a percent of total analysis area	CPLAND
	Area-weighted average similarity index (100 m radius)	SIMI
	Class-specific contagion	CLUMPY
	Landscape shape index	LSI
	Normalized landscape shape index	NLSI
	Total edge	TE
	Total edge-contrast index	TECI
	Contrast-weighted edge density	CWED
	Total edge	TE

Table A.1. continued

Metric Type	Metric	Abbreviation
Landscape	Area-weighted average patch size	AVAREA
	Area-weighted average fractal dimension	AVFRAC
	Area-weighted average shape index	AVSHAPE
	Contagion index	CONTAG
	Contrast-weighted edge density	CWED
	Landscape shape index	LSI
	Modified Simpson's diversity index	MSIDI
	Number of patches	NP
	Shannon's diversity index	SHDI
	Shannon's evenness index	SHEI
	Simpson's diversity index	SIDI
	Simpson's evenness index	SIEI
	Total edge	TE
Geographic	Aspect (average)	ASPAV
	Aspect (standard deviation)	ASPSD
	Planform slope curvature (average)	CRVAV
	Planform slope curvature (standard deviation)	CRVSD
	Distance to fish-bearing streams (average)	D13AV
	Distance to fish-bearing streams (standard deviation)	D13SD
	Distance to all streams (average)	D19AV
	Distance to all streams (standard deviation)	D19SD
	Elevation (average)	DEMAV
	Elevation (standard deviation)	DEMSD
	Slope steepness (average)	SLPAV
	Slope steepness (standard deviation)	SLPSD
	Slope steepness * curvature (average)	SSAV
	Slope steepness * curvature (standard deviation)	SSSD

Table A.2. Correlations, calculated from 200 m radius plots, among class-level metrics for open, sapling, pole, small sawtimber, large sawtimber, and old-growth. Correlation coefficients are presented above *p*-values, ($p < 0.05$ are shaded). Metrics and their abbreviations are listed in Table A.1.

	OP_CA	OP_AREA	OP_NLSI	OP_TE	SAP_CA	SAP_AREA	SAP_LSI	SAP_TE	POL_CA	POL_AREA	POL_LSI	POL_TE	SS_CA	SS_AREA	SS_LSI	SS_TE	LS_CA	LS_AREA	LS_AVCAI	LS_SIMI
OP_AREA	0.98 0.00																			
OP_NLSI	-0.20 0.00	-0.25 0.00																		
OP_TE	0.68 0.00	0.58 0.00	0.15 0.02																	
SAP_CA	0.10 0.10	0.03 0.64	0.22 0.00	0.48 0.00																
SAP_AREA	0.04 0.57	-0.03 0.68	0.18 0.00	0.34 0.00	0.91 0.00															
SAP_LSI	0.25 0.00	0.18 0.01	0.23 0.00	0.53 0.00	0.70 0.00	0.50 0.00														
SAP_TE	0.18 0.01	0.09 0.16	0.24 0.00	0.56 0.00	0.92 0.00	0.75 0.00	0.88 0.00													
POL_CA	-0.17 0.01	-0.20 0.00	0.16 0.01	0.05 0.41	0.37 0.00	0.22 0.00	0.45 0.00	0.47 0.00												
POL_AREA	-0.13 0.03	-0.16 0.01	0.10 0.10	0.04 0.53	0.29 0.00	0.14 0.03	0.34 0.00	0.37 0.00	0.89 0.00											
POL_LSI	-0.15 0.01	-0.19 0.00	0.16 0.01	0.08 0.21	0.41 0.00	0.29 0.00	0.53 0.00	0.49 0.00	0.71 0.00	0.49 0.00										
POL_TE	-0.17 0.01	-0.21 0.00	0.18 0.00	0.07 0.25	0.44 0.00	0.30 0.00	0.53 0.00	0.55 0.00	0.91 0.00	0.69 0.00	0.89 0.00									
SS_CA	-0.25 0.00	-0.26 0.00	0.03 0.68	-0.14 0.03	0.19 0.00	0.15 0.02	0.20 0.00	0.21 0.00	0.28 0.00	0.14 0.03	0.39 0.00	0.36 0.00								
SS_AREA	-0.08 0.20	-0.11 0.08	0.01 0.86	0.00 0.99	0.16 0.01	0.16 0.01	0.10 0.13	0.13 0.04	0.09 0.14	0.02 0.71	0.21 0.00	0.15 0.01	0.77 0.00							
SS_LSI	-0.33 0.00	-0.34 0.00	0.08 0.22	-0.16 0.01	0.21 0.00	0.14 0.03	0.32 0.00	0.28 0.00	0.39 0.00	0.24 0.00	0.52 0.00	0.48 0.00	0.81 0.00	0.42 0.00						
SS_TE	-0.30 0.00	-0.30 0.00	0.05 0.47	-0.18 0.00	0.18 0.00	0.12 0.07	0.25 0.00	0.23 0.00	0.36 0.00	0.20 0.00	0.46 0.00	0.45 0.00	0.96 0.00	0.59 0.00	0.91 0.00					
LS_CA	-0.56 0.00	-0.52 0.00	-0.02 0.71	-0.57 0.00	-0.35 0.00	-0.27 0.00	-0.37 0.00	-0.38 0.00	-0.05 0.42	-0.07 0.28	0.03 0.59	-0.03 0.62	0.33 0.00	0.14 0.03	0.41 0.00	0.39 0.00				
LS_AREA	-0.37 0.00	-0.33 0.00	-0.04 0.48	-0.41 0.00	-0.26 0.00	-0.19 0.00	-0.33 0.00	-0.32 0.00	-0.06 0.37	-0.06 0.38	-0.02 0.76	-0.06 0.34	0.26 0.00	0.09 0.15	0.30 0.00	0.29 0.00	0.89 0.00			
LS_AVCAI	-0.51 0.00	-0.45 0.00	-0.07 0.26	-0.62 0.00	-0.46 0.00	-0.33 0.00	-0.58 0.00	-0.54 0.00	-0.22 0.00	-0.16 0.01	-0.29 0.00	-0.29 0.00	0.01 0.93	0.01 0.87	0.00 0.95	0.00 1.00	0.52 0.00	0.42 0.00		
LS_SIMI	-0.57 0.00	-0.53 0.00	0.01 0.89	-0.56 0.00	-0.45 0.00	-0.32 0.00	-0.54 0.00	-0.53 0.00	-0.27 0.00	-0.20 0.00	-0.31 0.00	-0.32 0.00	-0.29 0.00	-0.19 0.00	-0.32 0.00	-0.31 0.00	0.01 0.83	-0.09 0.17	0.53 0.00	
LS_CLUMP	0.02 0.70	0.01 0.88	0.04 0.54	0.04 0.49	0.02 0.76	0.03 0.65	0.05 0.46	0.03 0.60	0.11 0.09	0.09 0.16	0.11 0.09	0.12 0.06	0.06 0.35	0.06 0.38	0.11 0.10	0.06 0.36	0.17 0.01	0.22 0.00	-0.02 0.74	-0.12 0.06

Table A.2. continued

	OP_CA	OP_AREA	OP_NLSI	OP_TE	SAP_CA	SAP_AREA	SAP_LSI	SAP_TE	POL_CA	POL_AREA	POL_LSI	POL_TE	SS_CA	SS_AREA	SS_LSI	SS_TE	LS_CA	LS_AREA	LS_AVCAI	LS_SIMI
LS_CPLAN	-0.53	-0.48	-0.09	-0.60	-0.41	-0.29	-0.54	-0.49	-0.17	-0.13	-0.17	-0.21	0.19	0.09	0.22	0.20	0.86	0.79	0.79	0.21
	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.01	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00
LS_LSI	-0.61	-0.58	0.05	-0.58	-0.30	-0.25	-0.17	-0.24	0.05	0.00	0.18	0.10	0.21	0.02	0.39	0.30	0.52	0.23	0.35	0.29
	0.00	0.00	0.43	0.00	0.00	0.00	0.01	0.00	0.46	0.95	0.01	0.12	0.00	0.71	0.00	0.00	0.00	0.00	0.00	0.00
LS_NLSI	0.08	0.06	-0.02	0.05	0.09	0.08	0.14	0.13	0.00	0.02	0.03	0.01	-0.17	-0.15	-0.15	-0.16	-0.46	-0.50	-0.17	0.19
	0.23	0.32	0.72	0.44	0.15	0.20	0.03	0.04	0.94	0.76	0.67	0.92	0.01	0.02	0.02	0.01	0.00	0.00	0.01	0.00
LS_NP	-0.32	-0.32	0.11	-0.25	-0.06	-0.06	0.05	0.00	0.04	0.02	0.10	0.07	-0.04	-0.06	0.03	0.00	-0.18	-0.44	0.06	0.37
	0.00	0.00	0.08	0.00	0.35	0.36	0.40	0.99	0.50	0.74	0.10	0.26	0.56	0.35	0.59	0.95	0.01	0.00	0.38	0.00
LS_TE	-0.66	-0.62	0.04	-0.63	-0.34	-0.28	-0.26	-0.32	0.00	-0.05	0.14	0.05	0.33	0.12	0.48	0.41	0.85	0.61	0.46	0.16
	0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.98	0.41	0.02	0.40	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.01
LS_TECI	0.34	0.28	0.03	0.43	0.48	0.39	0.55	0.54	0.32	0.23	0.41	0.40	0.25	0.18	0.24	0.24	-0.24	-0.15	-0.77	-0.56
	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
OG_CA	-0.49	-0.45	0.04	-0.44	-0.45	-0.33	-0.52	-0.51	-0.32	-0.24	-0.36	-0.36	-0.46	-0.33	-0.43	-0.46	-0.10	-0.21	0.45	0.94
	0.00	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
OG_AREA	-0.37	-0.34	0.00	-0.35	-0.34	-0.24	-0.44	-0.41	-0.29	-0.20	-0.35	-0.33	-0.45	-0.30	-0.47	-0.47	-0.25	-0.33	0.37	0.92
	0.00	0.00	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OG_AVCAI	-0.59	-0.53	-0.10	-0.66	-0.40	-0.29	-0.50	-0.46	-0.11	-0.07	-0.13	-0.14	-0.08	-0.08	-0.05	-0.08	0.41	0.27	0.62	0.64
	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.08	0.26	0.04	0.03	0.19	0.20	0.39	0.20	0.00	0.00	0.00	0.00
OG_SIMI	-0.52	-0.48	0.00	-0.55	-0.34	-0.26	-0.39	-0.40	-0.07	-0.07	0.00	-0.07	0.23	0.04	0.35	0.29	0.94	0.88	0.53	0.06
	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.27	0.28	0.95	0.26	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.38
OG_CLUMPY	0.11	0.11	0.04	0.08	-0.10	-0.12	0.01	-0.09	-0.04	-0.06	0.02	0.00	-0.31	-0.20	-0.29	-0.30	-0.28	-0.26	-0.07	0.18
	0.10	0.08	0.56	0.20	0.10	0.06	0.82	0.17	0.49	0.36	0.70	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
OG_CPLAND	-0.53	-0.48	-0.09	-0.57	-0.41	-0.28	-0.58	-0.50	-0.27	-0.19	-0.34	-0.32	-0.35	-0.23	-0.34	-0.36	0.05	-0.07	0.57	0.91
	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.45	0.25	0.00	0.00
OG_LSI	-0.43	-0.39	0.07	-0.43	-0.42	-0.40	-0.25	-0.35	-0.10	-0.09	-0.04	-0.10	-0.01	-0.20	0.22	0.11	0.67	0.49	0.43	0.10
	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.11	0.17	0.56	0.12	0.84	0.00	0.00	0.10	0.00	0.00	0.00	0.12
OG_NLSI	0.01	0.02	-0.08	-0.09	-0.05	-0.11	0.00	0.01	0.13	0.16	0.02	0.06	0.25	0.02	0.33	0.31	0.37	0.38	0.05	-0.31
	0.94	0.73	0.21	0.14	0.40	0.08	0.94	0.87	0.05	0.01	0.75	0.32	0.00	0.80	0.00	0.00	0.00	0.00	0.45	0.00
OG_NP	-0.25	-0.24	0.05	-0.19	-0.17	-0.19	-0.02	-0.09	0.12	0.08	0.13	0.12	0.27	0.01	0.41	0.37	0.62	0.53	0.10	-0.27
	0.00	0.00	0.47	0.00	0.01	0.00	0.80	0.17	0.07	0.19	0.04	0.05	0.00	0.89	0.00	0.00	0.00	0.00	0.13	0.00
OG_TE	-0.57	-0.54	0.12	-0.52	-0.46	-0.39	-0.40	-0.46	-0.23	-0.19	-0.16	-0.23	-0.18	-0.24	0.02	-0.09	0.53	0.30	0.55	0.44
	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.72	0.14	0.00	0.00	0.00	0.00
OG_TECI	0.53	0.49	0.09	0.56	0.20	0.12	0.29	0.25	0.02	0.04	-0.07	-0.01	-0.11	-0.12	-0.15	-0.11	-0.49	-0.33	-0.51	-0.38
	0.00	0.00	0.16	0.00	0.00	0.06	0.00	0.00	0.74	0.49	0.25	0.82	0.07	0.05	0.02	0.07	0.00	0.00	0.00	0.00

Table A.2 continued

	LS_CLUMPY	LS_CPLAND	LS_LSI	LS_NLSI	LS_NP	LS_TE	LS_TECI	OG_CA	OG_AREA	OG_AVCAI	OG_SIMI	OG_CLUMPY	OG_CPLAND	OG_LSI	OG_NLSI	OG_NP	OG_TE
LS_CPLAN	0.06 0.33																
LS_LSI	**-0.18** **0.01**	**0.40** **0.00**															
LS_NLSI	**-0.65** **0.00**	**-0.36** **0.00**	**0.23** **0.00**														
LS_NP	**-0.25** **0.00**	**-0.17** **0.01**	**0.51** **0.00**	**0.51** **0.00**													
LS_TE	-0.02 0.77	**0.68** **0.00**	**0.85** **0.00**	**-0.19** **0.00**	**0.16** **0.01**												
LS_TECI	**0.15** **0.02**	**-0.51** **0.00**	**-0.22** **0.00**	0.11 0.08	-0.09 0.15	**-0.27** **0.00**											
OG_CA	**-0.18** **0.01**	0.12 0.06	**0.23** **0.00**	**0.23** **0.00**	**0.43** **0.00**	0.06 0.34	**-0.60** **0.00**										
OG_AREA	**-0.18** **0.00**	-0.01 0.91	0.10 0.13	**0.29** **0.00**	**0.43** **0.00**	-0.11 0.08	**-0.51** **0.00**	**0.95** **0.00**									
OG_AVCAI	-0.01 0.83	**0.53** **0.00**	**0.42** **0.00**	-0.07 0.29	**0.12** **0.05**	**0.47** **0.00**	**-0.53** **0.00**	**0.57** **0.00**	**0.50** **0.00**								
OG_SIMI	0.12 0.06	**0.85** **0.00**	**0.48** **0.00**	**-0.39** **0.00**	**-0.18** **0.00**	**0.79** **0.00**	**-0.30** **0.00**	-0.05 0.41	**-0.19** **0.00**	**0.42** **0.00**							
OG_CLUMPY	-0.07 0.24	**-0.20** **0.00**	**-0.15** **0.01**	**0.21** **0.00**	0.12 0.06	**-0.25** **0.00**	-0.07 0.27	**0.27** **0.00**	**0.30** **0.00**	**0.13** **0.03**	**-0.16** **0.01**						
OG_CPLAND	**-0.13** **0.05**	**0.28** **0.00**	**0.28** **0.00**	**0.16** **0.01**	**0.33** **0.00**	**0.17** **0.01**	**-0.61** **0.00**	**0.90** **0.00**	**0.86** **0.00**	**0.77** **0.00**	0.06 0.31	**0.14** **0.03**					
OG_LSI	-0.05 0.44	**0.58** **0.00**	**0.66** **0.00**	**-0.16** **0.01**	0.11 0.09	**0.79** **0.00**	**-0.44** **0.00**	0.11 0.07	-0.09 0.15	**0.32** **0.00**	**0.68** **0.00**	**-0.20** **0.00**	0.10 0.11				
OG_NLSI	0.11 0.09	**0.22** **0.00**	**0.15** **0.02**	**-0.20** **0.00**	**-0.21** **0.00**	**0.27** **0.00**	0.12 0.07	**-0.39** **0.00**	**-0.43** **0.00**	**-0.13** **0.04**	**0.27** **0.00**	**-0.72** **0.00**	**-0.27** **0.00**	**0.37** **0.00**			
OG_NP	0.05 0.40	**0.40** **0.00**	**0.40** **0.00**	**-0.25** **0.00**	**-0.16** **0.01**	**0.59** **0.00**	0.02 0.80	**-0.29** **0.00**	**-0.48** **0.00**	0.03 0.68	**0.51** **0.00**	**-0.31** **0.00**	**-0.25** **0.00**	**0.64** **0.00**	**0.53** **0.00**		
OG_TE	**-0.15** **0.02**	**0.56** **0.00**	**0.70** **0.00**	-0.02 0.71	**0.31** **0.00**	**0.73** **0.00**	**-0.65** **0.00**	**0.49** **0.00**	**0.30** **0.00**	**0.47** **0.00**	**0.57** **0.00**	-0.04 0.54	**0.43** **0.00**	**0.86** **0.00**	0.01 0.93	**0.35** **0.00**	
OG_TECI	-0.08 0.22	**-0.50** **0.00**	**-0.51** **0.00**	**0.14** **0.03**	-0.10 0.10	**-0.57** **0.00**	**0.39** **0.00**	**-0.28** **0.00**	**-0.20** **0.00**	**-0.77** **0.00**	**-0.42** **0.00**	0.03 0.64	**-0.52** **0.00**	**-0.30** **0.00**	0.04 0.48	**-0.13** **0.05**	**-0.38** **0.00**

Table A.3. Additional correlations, calculated from 200 m radius plots, among class-level metrics for open, sapling, pole, small sawtimber, large sawtimber, and old-growth. Correlation coefficients are presented above *p*-values, ($p < 0.05$ are shaded). Metrics and their abbreviations are listed in Table A.1.

	OG_LSI	OG_NLSI	OG_SIMI	OG_TECI	OG_CWED	LS_LSI	LS_NLSI	LS_SIMI	LS_TECI	LS_CWED	LT_LSI	LT_NLSI	LT_SIMI	LT_TECI	LT_CWED	OP_LSI	OP_NLSI
OG_NLSI	0.38 0.00																
OG_SIMI	0.60 0.00	0.35 0.00															
OG_TECI	-0.30 0.00	0.09 0.32	-0.45 0.00														
OG_CWED	0.15 0.12	-0.10 0.30	-0.28 0.00	0.69 0.00													
LS_LSI	0.61 0.00	0.09 0.34	0.38 0.00	-0.59 0.00	-0.19 0.04												
LS_NLSI	-0.19 0.04	-0.20 0.03	-0.41 0.00	0.17 0.07	0.16 0.08	0.22 0.02											
LS_SIMI	0.13 0.17	-0.36 0.00	0.11 0.26	-0.44 0.00	-0.03 0.72	0.38 0.00	0.20 0.03										
LS_TECI	-0.50 0.00	0.12 0.19	-0.34 0.00	0.39 0.00	0.00 1.00	-0.29 0.00	0.14 0.15	-0.50 0.00									
LS_CWED	0.16 0.08	0.34 0.00	0.31 0.00	-0.14 0.12	-0.15 0.10	0.42 0.00	-0.11 0.26	-0.32 0.00	0.52 0.00								
LT_LSI	0.12 0.22	0.40 0.00	0.02 0.85	0.23 0.01	0.23 0.01	0.24 0.01	0.03 0.77	-0.41 0.00	0.45 0.00	0.73 0.00							
LT_NLSI	0.29 0.00	0.25 0.01	0.27 0.00	-0.26 0.00	-0.20 0.03	0.30 0.00	0.01 0.92	0.33 0.00	-0.32 0.00	-0.10 0.27	0.12 0.21						
LT_SIMI	-0.20 0.03	0.26 0.00	-0.06 0.53	0.20 0.03	0.00 0.96	-0.02 0.81	-0.01 0.89	-0.53 0.00	0.52 0.00	0.61 0.00	0.66 0.00	-0.35 0.00					
LT_TECI	-0.25 0.01	0.08 0.39	-0.38 0.00	0.73 0.00	0.51 0.00	-0.36 0.00	0.15 0.11	-0.64 0.00	0.67 0.00	0.30 0.00	0.34 0.00	-0.56 0.00	0.46 0.00				
LT_CWED	0.24 0.01	0.22 0.02	0.07 0.48	0.36 0.00	0.56 0.00	0.23 0.01	0.02 0.81	-0.29 0.00	0.43 0.00	0.73 0.00	0.77 0.00	-0.22 0.02	0.51 0.00	0.60 0.00			
OP_LSI	-0.33 0.00	-0.08 0.37	-0.41 0.00	0.47 0.00	0.34 0.00	-0.41 0.00	-0.02 0.82	-0.45 0.00	0.42 0.00	0.04 0.65	0.07 0.44	-0.60 0.00	0.21 0.02	0.64 0.00	0.27 0.00		
OP_NLSI	0.09 0.35	-0.06 0.49	0.02 0.85	0.03 0.71	0.23 0.01	0.07 0.44	-0.05 0.63	0.03 0.72	-0.02 0.86	0.06 0.49	0.00 0.97	-0.20 0.03	0.08 0.42	0.18 0.05	0.21 0.02	0.48 0.00	
OP_SIMI	-0.44 0.00	-0.04 0.65	-0.43 0.00	0.38 0.00	0.14 0.13	-0.53 0.00	-0.01 0.95	-0.38 0.00	0.41 0.00	-0.07 0.43	0.04 0.67	-0.52 0.00	0.23 0.01	0.48 0.00	0.03 0.71	0.71 0.00	0.23 0.01

Table A.3 continued

	OG_LSI	OG_NLSI	OG_SIMI	OG_TECI	OG_CWED	LS_LSI	LS_NLSI	LS_SIMI	LS_TECI	LS_CWED	LT_LSI	LT_NLSI	LT_SIMI	LT_TECI	LT_CWED	OP_LSI	OP_NLSI
OP_TECI	-0.13	0.03	-0.10	0.25	0.28	-0.17	-0.07	-0.23	0.35	0.28	0.15	-0.55	0.31	0.47	0.42	0.65	0.46
	0.17	0.78	0.29	0.01	0.00	0.06	0.45	0.01	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
OP_CWED	-0.40	-0.04	-0.55	0.63	0.35	-0.58	0.00	-0.58	0.46	-0.13	0.07	-0.42	0.12	0.66	0.14	0.83	0.11
	0.00	0.67	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.18	0.47	0.00	0.19	0.00	0.14	0.00	0.23
SAP_LSI	-0.27	-0.01	-0.46	0.32	0.15	-0.17	0.13	-0.51	0.53	0.28	0.29	-0.52	0.51	0.60	0.33	0.60	0.20
	0.00	0.92	0.00	0.00	0.12	0.07	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
SAP_NLSI	-0.18	-0.01	-0.48	0.41	0.35	-0.17	0.15	-0.30	0.36	0.14	0.27	-0.42	0.32	0.49	0.35	0.41	0.05
	0.05	0.91	0.00	0.00	0.00	0.06	0.12	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.58
SAP_SIMI	-0.48	0.03	-0.55	0.50	0.05	-0.59	0.13	-0.55	0.40	-0.18	0.01	-0.40	0.30	0.50	-0.12	0.36	-0.09
	0.00	0.74	0.00	0.00	0.61	0.00	0.17	0.00	0.00	0.05	0.91	0.00	0.00	0.00	0.21	0.00	0.34
SAP_TECI	-0.07	0.03	-0.24	0.21	0.14	0.00	0.09	-0.34	0.37	0.36	0.36	-0.42	0.44	0.42	0.39	0.36	0.08
	0.48	0.77	0.01	0.02	0.15	0.98	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.37
SAP_CWED	-0.25	0.05	-0.40	0.22	0.03	-0.15	0.08	-0.48	0.47	0.22	0.22	-0.38	0.43	0.49	0.20	0.55	0.23
	0.01	0.56	0.00	0.02	0.78	0.11	0.39	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.03	0.00	0.01

	OP_SIMI	OP_TECI	OP_CWED	SAP_LSI	SAP_NLSI	SAP_SIMI	SAP_TEC
OP_TECI	0.56						
	0.00						
OP_CWED	0.64	0.34					
	0.00	0.00					
SAP_LSI	0.55	0.43	0.52				
	0.00	0.00	0.00				
SAP_NLSI	0.24	0.25	0.41	0.55			
	0.01	0.01	0.00	0.00			
SAP_SIMI	0.47	0.12	0.52	0.50	0.43		
	0.00	0.20	0.00	0.00	0.00		
SAP_TECI	0.26	0.34	0.28	0.68	0.55	0.48	
	0.00	0.00	0.00	0.00	0.00	0.00	
SAP_CWED	0.57	0.36	0.50	0.90	0.28	0.37	0.43
	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A.4. Correlations among old-growth class metrics, across scales. Correlation coefficients are presented above *p*-values, (*p* < 0.05 are shaded). The scale at which metrics were calculated is indicated by numbers appended to the index abbreviation: 1, 200 m; 2, 400 m; 3, 800 m, 4, 1600 m. Metrics and their abbreviations are listed in Table A.1.

	AVAREA1	CA1	CPLAND1	CWED1	NLSI1	SIMI1	AVAREA2	CA2	CPLAND2	CWED2	NLSI2	SIMI2	AVAREA3	CA3	CPLAND3	CWED3	NLSI3
CA1	0.95																
	0.00																
CPLAND1	0.85	0.90															
	0.00	0.00															
CWED1	0.13	0.18	-0.20														
	0.04	0.00	0.00														
NLSI1	-0.50	-0.48	-0.33	-0.18													
	0.00	0.00	0.00	0.01													
SIMI1	-0.20	-0.10	0.04	-0.23	0.22												
	0.00	0.12	0.53	0.00	0.00												
AVAREA2	0.83	0.83	0.79	0.04	-0.42	-0.17											
	0.00	0.00	0.00	0.53	0.00	0.01											
CA2	0.76	0.85	0.80	0.08	-0.39	-0.04	0.90										
	0.00	0.00	0.00	0.22	0.00	0.50	0.00										
CPLAND2	0.68	0.76	0.82	-0.14	-0.30	0.08	0.86	0.93									
	0.00	0.00	0.00	0.02	0.00	0.23	0.00	0.00									
CWED2	0.24	0.31	0.04	0.68	-0.22	-0.21	0.17	0.28	-0.04								
	0.00	0.00	0.49	0.00	0.00	0.00	0.01	0.00	0.52								
NLSI2	-0.61	-0.62	-0.50	-0.14	0.68	0.25	-0.66	-0.62	-0.51	-0.28							
	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00							
SIMI2	0.14	0.24	0.36	-0.22	0.07	0.72	0.15	0.31	0.42	-0.20	0.05						
	0.03	0.00	0.00	0.00	0.31	0.00	0.02	0.00	0.00	0.00	0.46						
AVAREA3	0.52	0.56	0.57	-0.05	-0.27	0.00	0.76	0.77	0.80	0.01	-0.45	0.30					
	0.00	0.00	0.00	0.45	0.00	0.98	0.00	0.00	0.00	0.89	0.00	0.00					
CA3	0.48	0.55	0.54	-0.01	-0.28	0.09	0.67	0.81	0.80	0.09	-0.44	0.41	0.86				
	0.00	0.00	0.00	0.90	0.00	0.16	0.00	0.00	0.00	0.14	0.00	0.00	0.00				
CPLAND3	0.43	0.49	0.53	-0.12	-0.22	0.15	0.61	0.74	0.81	-0.09	-0.36	0.46	0.86	0.96			
	0.00	0.00	0.00	0.06	0.00	0.02	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00			
CWED3	0.28	0.35	0.21	0.37	-0.24	-0.09	0.34	0.46	0.24	0.71	-0.34	0.02	0.25	0.43	0.20		
	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	0.00		
NLSI3	-0.52	-0.55	-0.44	-0.17	0.58	0.13	-0.60	-0.62	-0.51	-0.30	0.83	-0.06	-0.57	-0.59	-0.52	-0.40	
	0.00	0.00	0.00	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	
SIMI3	0.29	0.38	0.47	-0.16	-0.03	0.43	0.46	0.58	0.67	-0.13	-0.16	0.78	0.67	0.71	0.76	0.11	-0.28
	0.00	0.00	0.00	0.01	0.64	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.00	0.00	0.00	0.08	0.00

Table A.4. continued

	AVAREA1	CA1	CPLAND1	CWED1	NLSI1	SIMI1	AVAREA2	CA2	CPLAND2	CWED2	NLSI2	SIMI2	AVAREA3	CA3	CPLAND3	CWED3	NLSI3
AVAREA4	0.26	0.29	0.28	-0.01	-0.17	0.04	0.40	0.47	0.48	-0.03	-0.26	0.22	0.73	0.73	0.73	0.20	-0.38
	0.00	0.00	0.00	0.90	0.01	0.51	0.00	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CA4	0.32	0.38	0.34	0.06	-0.24	0.08	0.46	0.60	0.56	0.13	-0.35	0.31	0.69	0.86	0.81	0.41	-0.48
	0.00	0.00	0.00	0.39	0.00	0.19	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CPLAND4	0.28	0.33	0.32	0.00	-0.18	0.13	0.41	0.55	0.54	0.04	-0.28	0.36	0.69	0.85	0.83	0.29	-0.43
	0.00	0.00	0.00	0.97	0.00	0.04	0.00	0.00	0.00	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NLSI4	-0.48	-0.52	-0.42	-0.18	0.50	0.08	-0.57	-0.63	-0.52	-0.31	0.67	-0.12	-0.58	-0.66	-0.57	-0.48	0.84
	0.00	0.00	0.00	0.01	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
SIMI4	0.21	0.25	0.29	-0.06	-0.05	0.28	0.35	0.43	0.49	-0.10	-0.12	0.52	0.65	0.71	0.74	0.13	-0.30
	0.00	0.00	0.00	0.36	0.44	0.00	0.00	0.00	0.00	0.10	0.06	0.00	0.00	0.00	0.00	0.04	0.00

	SIMI3	AVAREA4	CA4	CPLAND4	NLSI4
AVAREA4	0.45				
	0.00				
CA4	0.54	0.83			
	0.00	0.00			
CPLAND4	0.57	0.86	0.98		
	0.00	0.00	0.00		
NLSI4	-0.32	-0.53	-0.67	-0.61	
	0.00	0.00	0.00	0.00	
SIMI4	0.75	0.76	0.75	0.79	-0.42
	0.00	0.00	0.00	0.00	0.00

Table A.5. Correlations among landscape metrics, calculated from 200 m radius plots. Correlation coefficients are presented above *p*-values, ($p < 0.05$ are shaded). Metrics and their abbreviations are listed in Table A.1.

	AVAREA	AVFRAC	AVSHAPE	CONTAG	CWED	LSI	MSIDI	MSIEI	NP	SHDI	SHEI	SIDI	SIEI	TE
AVFRAC	-0.05 0.58													
AVSHAPE	0.12 0.22	0.97 0.00												
CONTAG	0.90 0.00	-0.12 0.19	0.03 0.78											
CWED	-0.68 0.00	-0.32 0.00	-0.42 0.00	-0.74 0.00										
LSI	-0.81 0.00	0.37 0.00	0.26 0.00	-0.86 0.00	0.61 0.00									
MSIDI	-0.93 0.00	-0.08 0.37	-0.24 0.01	-0.91 0.00	0.79 0.00	0.73 0.00								
MSIEI	-0.86 0.00	0.03 0.75	-0.13 0.15	-0.90 0.00	0.66 0.00	0.67 0.00	0.93 0.00							
NP	-0.68 0.00	-0.11 0.24	-0.17 0.06	-0.76 0.00	0.77 0.00	0.82 0.00	0.67 0.00	0.53 0.00						
SHDI	-0.89 0.00	-0.18 0.05	-0.32 0.00	-0.87 0.00	0.84 0.00	0.71 0.00	0.97 0.00	0.84 0.00	0.73 0.00					
SHEI	-0.85 0.00	-0.06 0.50	-0.22 0.02	-0.90 0.00	0.72 0.00	0.67 0.00	0.93 0.00	0.98 0.00	0.60 0.00	0.88 0.00				
SIDI	-0.95 0.00	-0.04 0.64	-0.20 0.03	-0.90 0.00	0.76 0.00	0.72 0.00	0.98 0.00	0.91 0.00	0.64 0.00	0.97 0.00	0.91 0.00			
SIEI	-0.92 0.00	0.04 0.68	-0.12 0.18	-0.91 0.00	0.68 0.00	0.70 0.00	0.96 0.00	0.98 0.00	0.57 0.00	0.89 0.00	0.96 0.00	0.96 0.00		
TE	-0.78 0.00	0.37 0.00	0.26 0.00	-0.84 0.00	0.60 0.00	0.99 0.00	0.70 0.00	0.64 0.00	0.83 0.00	0.68 0.00	0.64 0.00	0.69 0.00	0.67 0.00	
TECI	-0.40 0.00	-0.58 0.00	-0.64 0.00	-0.42 0.00	0.89 0.00	0.21 0.03	0.56 0.00	0.41 0.00	0.48 0.00	0.65 0.00	0.50 0.00	0.54 0.00	0.44 0.00	0.20 0.03

Table A.6. Correlations among geographic metrics, calculated from 200 m radius plots. Correlation coefficients are presented above *p*-values, ($p < 0.05$ are shaded). Metrics and their abbreviations are listed in Table A.1.

	ASPAV	ASPSD	CRVAV	CRVSD	D13AV	D13SD	D19AV	D19SD	DEMAV	DEMSD	SLPAV	SLPSD	SSAV
ASPSD	0.13 0.05												
CRVAV	-0.02 0.77	0.06 0.35											
CRVSD	0.07 0.28	0.00 0.99	0.13 0.04										
D13AV	0.09 0.15	-0.06 0.37	0.22 0.00	0.47 0.00									
D13SD	0.02 0.72	-0.21 0.00	0.24 0.00	0.22 0.00	0.40 0.00								
D19AV	0.11 0.07	-0.11 0.09	0.07 0.29	-0.22 0.00	0.17 0.01	0.15 0.02							
D19SD	-0.05 0.47	-0.02 0.71	0.12 0.06	-0.30 0.00	0.05 0.41	0.11 0.10	0.50 0.00						
DEMAV	0.11 0.08	-0.07 0.25	0.29 0.00	0.77 0.00	0.68 0.00	0.31 0.00	-0.10 0.10	-0.09 0.17					
DEMSD	0.10 0.11	-0.22 0.00	0.18 0.00	0.81 0.00	0.47 0.00	0.35 0.00	-0.23 0.00	-0.24 0.00	0.78 0.00				
SLPAV	0.10 0.11	-0.12 0.06	0.21 0.00	0.89 0.00	0.51 0.00	0.30 0.00	-0.24 0.00	-0.28 0.00	0.83 0.00	0.96 0.00			
SLPSD	0.12 0.06	0.08 0.20	0.15 0.02	0.77 0.00	0.37 0.00	0.15 0.02	-0.24 0.00	-0.21 0.00	0.67 0.00	0.76 0.00	0.82 0.00		
SSAV	-0.03 0.65	0.02 0.74	0.89 0.00	0.24 0.00	0.15 0.02	0.24 0.00	0.00 0.95	0.00 1.00	0.28 0.00	0.29 0.00	0.32 0.00	0.21 0.00	
SSSD	0.09 0.14	-0.05 0.40	0.17 0.01	0.94 0.00	0.51 0.00	0.28 0.00	-0.23 0.00	-0.29 0.00	0.82 0.00	0.91 0.00	0.97 0.00	0.83 0.00	0.28 0.00

Table A.7. Numbers and percentages, in parentheses, of correlations ($p \leq 0.05$) between marbled murrelet activity and landscape- and class-level metrics, tabulated by scale.

	Metric Type									
Scale (m)	Geographic	Landscape	Open	Sapling	Pole	Small Sawtimber	Large Sawtimber	Old-growth	Late Seral	Row Total
200		4		2		3	4	3	9	25 (20)
400		2	6	5	1		7	7	11	39 (31)
800		1	6	3			9	10	6	35 (28)
1600			3				4	7	2	16 (13)
2400					1		2	2	1	6 (5)
3200					1		2	2		5 (4)
Column Total	0 (0)	7 (6)	15 (12)	10 (8)	3 (2)	3 (2)	28 (22)	31 (25)	29 (23)	126