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Long-term Risks to Marbled Murrelet (*Brachyramphus marmoratus*) Populations: Assessing Alternative Forest Management Policies in Coastal British Columbia

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Ministry of Forests Forest Science Program

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J. Douglas Steventon, Glenn D. Sutherland, and Peter Arcese

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PREFACE

This risk assessment is Part C of a three-part Conservation Assessment that was initiated by the Canadian Marbled Murrelet Recovery Team (CMMRT). Part A provides a review of biology (Burger 2002) and Part B provides recommendations for conservation and management (CMMRT 2003). This assessment follows an earlier report (Arcese and Sutherland 2001) that reviewed alternative approaches to conducting ecological risk assessments, using Marbled Murrelet as an example. The key policy implications of this assessment are also summarized by Steventon et al. (2003).

We conducted an analysis of conservation risk—or, alternatively, of the confidence of success—associated with nesting habitat management strategies for the Marbled Murrelet (MAMU) in British Columbia. The goal was to provide decision support to the B.C. Ministry of Forests, Ministry of Water, Land and Air Protection, and the Canadian Marbled Murrelet Recovery Team (CMMRT) in evaluating regional and coast-wide conservation strategies.

The framework for the analysis was a habitat-linked population viability analysis. We used an integrated package of models of MAMU demography, habitat associations, habitat management, and environmental change to project relative population size and persistence probability, applying various forest management assumptions.

We focused on changes in persistence probability as an unambiguous measure of risk, applied primarily at the scale of the MAMU Conservation Regions proposed by the CMMRT. We also assessed coast-wide risk using a "bet hedging" probability theory approach to combining regional risks.

A key component of our analysis was the inclusion of uncertainty. Uncertainty arose from: (1) lack of information about some relationships linking MAMU populations to the environment; (2) unpredictability of future environmental conditions; (3) incomplete information about starting conditions of populations and habitats; and (4) the possibility that chance events could affect population numbers, nesting habitat, at-sea conditions, and future forest harvest policy. Because of those uncertainties, it was not possible to confidently predict future MAMU populations. Instead, we examined how robust different management strategies might be in light of those uncertainties. The models and resulting analyses should be considered our current hypotheses of future risks to MAMU, subject to improvement through research and adaptive management.

We found that gross habitat supply and its quality in terms of nesting density, combined with survival and reproductive rates as affected by future at-sea conditions, are the dominant predictors of projected outcomes. Edge effects (representing habitat configuration) were minor, declining in importance with increasing habitat amount. The rate of habitat decline (when separated from final habitat amount) had only a weak effect.

A nesting population objective of ≥2000 pairs within a Conservation Region, or a coast-wide objective of maintaining ≥12 000 nesting pairs (~36 000+ total birds), appeared robust to the uncertainties we modelled. Based on mean nesting densities inferred from recent radar-based surveys, a nesting capacity of 2000 translates into a habitat target of 100 000–400 000 ha of habitat per Conservation Region (600 000–2.4 million ha coast-wide). Given these habitat amounts, estimated expected persistence value for regional MAMU populations was in the 80–90% range (Figure 1) and 90–99% at the coast-wide scale.

Applying Bayesian decision analysis, we found that the optimal choice of habitat amount to set aside for conserving regional MAMU populations was sensitive to three key factors: habitat quality (nesting density); the proportion of habitat located within the operable landbase; and the MAMU vs. timber policy emphasis. Policy decisions were not sensitive to hypothesized effects of forest edges on MAMU survival.

As a result of historical patterns of timber harvesting, the risks and opportunities associated with protecting habitat vary among Conservation Regions. There is no compelling reason to apply equal conservation emphasis to all of them, and we recommend further development of the decision analysis to aid in assessing emphasis options among regions. This will require specific mapping of MAMU nesting habitat in relation to the timber harvesting landbase, the acquisition of region-specific nesting habitat data, and explicit weighting of MAMU vs. timber values.

In summary, our conclusions are as follows:

- The long-term risk to MAMU persistence is sensitive to the amount and quality of nesting habitat available. This relationship is a non-linear one of diminishing incremental benefit as amount of habitat increases. Outcome is also sensitive to the spatial scale of application—Conservation Region or coast-wide.
- Edge effects influence persistence much less than availability of nesting habitat does. Nevertheless, policies that reduce forest fragmentation remain a useful goal for MAMU conservation, as it would be difficult to reverse fragmentation if further research confirmed that it significantly compromises survival.
- Decision analysis has the potential to help resource managers and decision-makers determine habitat priorities among Conservation Regions, and to set research and adaptive management priorities.

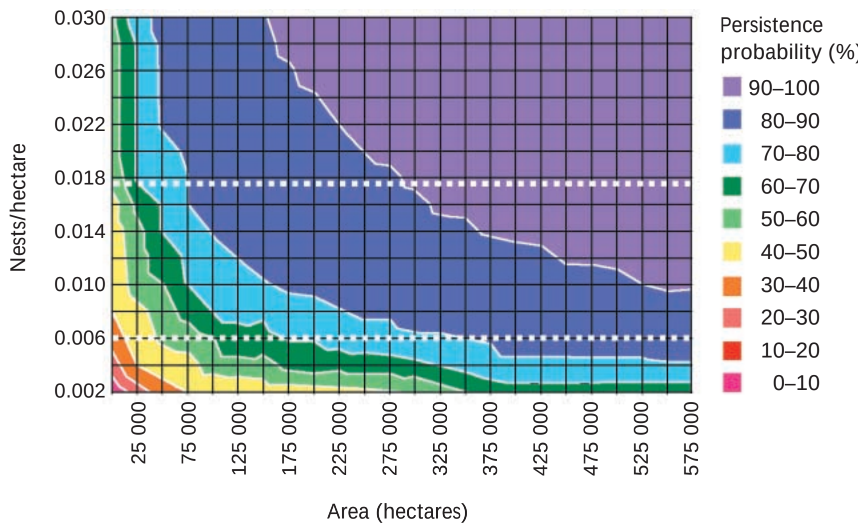

FIGURE 1 *Expected probability of persistence (≥100 years) as a function of total area of nesting habitat and habitat quality (equal weighting given to all patch sizes). White horizontal lines represent range of mean density estimates (nests/ha) inferred from recent British Columbia studies (Burger 2002).*

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1 INTRODUCTION

1.1 Background

Marbled Murrelets (MAMU) are designated as "threatened" in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2001), and in Washington, Oregon, and California.

Most of the world's population of MAMU are found in Alaska, where estimates range from 280 000 to >1 million (Burger 2002). Recent estimates of total numbers in Washington, Oregon, and California (excluding the area south of San Francisco) include 18 100 in 2000 and 21 200 in 2001, although confidence intervals are wide (Burger 2002). The current population of MAMU in British Columbia is estimated to be between 54 000 and 78 000 (Burger 2002).

We do not clearly know the extent or significance of population changes of MAMU in the province during the last century, mainly because of insufficient data (Burger 2002). Anecdotal evidence, as well as much of the available quantitative data, indicates that many populations in British Columbia have declined. Some populations in Alaska also appear to be declining, although these trends (except in the Prince William Sound area) have been disputed (Burger 2002). Major declines have been reported in Washington, Oregon, and California as well (Ralph et al. 1995; U.S. Fish and Wildlife Service 1997), although there are few actual count data with which to assess historical changes in those states (Burger 2002).

Loss of MAMU nesting habitat from timber harvesting, combined with possible increases in predation due to the creation of forest edge, is thought to have contributed to population declines (Beissinger and Nur 1997; Burger 2002). As well, direct effects of human activities (e.g., oil spills, fishing by-catch) on survival of MAMU at sea, and indirect effects of both human activities and oceanic conditions (e.g., fluctuating ocean temperature effects on prey availability) on survival and reproductive success, may be important (Boulanger et al. 1999; Burger 2002).

Although recent research has greatly added to our knowledge of MAMU demography and nesting behaviour (Burger 2002), substantial uncertainties remain about nesting habitat requirements, historical rates of nesting habitat losses, present amount and quality of nesting habitat, reproductive rates, and factors influencing mortality. These gaps in scientific knowledge, combined with controversies over management options, have hindered development of sound habitat protection policies for the MAMU Conservation Regions proposed for coastal British Columbia (Figure 2).

1.2 Objectives

Our general objective was to assess forest habitat management policies for MAMU in terms of relative population size and persistence at multiple time and spatial scales (CMMRT Conservation Regions and coast-wide). Including various types of uncertainty (e.g., scientific uncertainties about MAMU ecology, long-term environmental trends, and the effects of short-term chance events and environmental fluctuations on MAMU) was a key component of our approach (see Ludwig et al. 2001; Ludwig and Walters 2002).

The specific objectives were:

1. to develop a general framework for analyzing potential MAMU population responses to forest management policies at coast-wide, regional, sub-regional, or landscape unit / watershed scales. In this report, we focus on the regional and coast-wide scales.

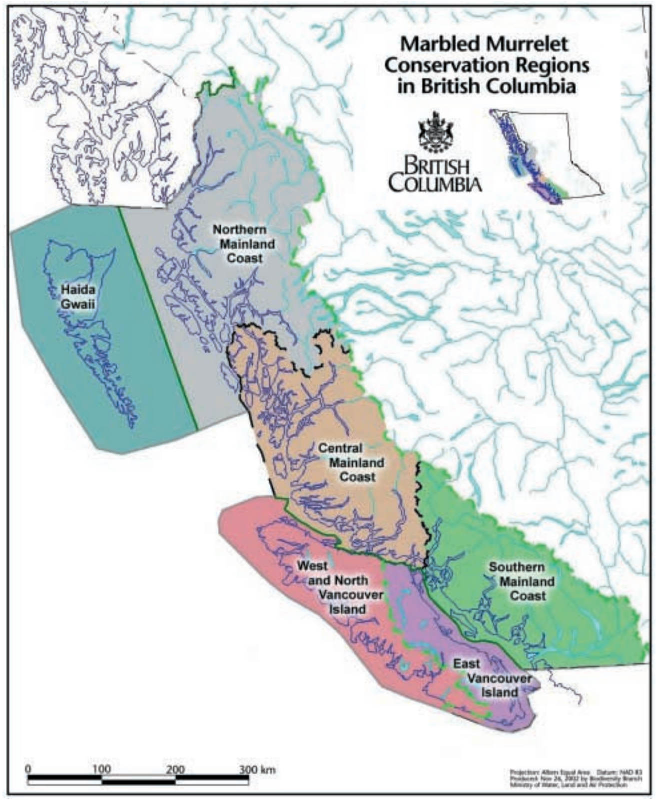

FIGURE 2 *Proposed Marbled Murrelet Conservation Regions (CMMRT 2003).*

2. to provide a means of explicitly representing present views and assumptions of MAMU biology and management issues over a geographically diverse area. The resulting framework is a tool for exploring consequences of uncertainty in knowledge, known geographic differences in MAMU ecology, and divergent opinions about the interpretation of empirical data. Models provide a formal basis for updating our understanding as new data become available.
3. to assess the potential effects of currently proposed MAMU nesting habitat management strategies on MAMU populations. The management questions addressed in this report are:
   - What is the probability that a regional MAMU population could persist over the long term and that selected population targets could be achieved, depending on the amount and quality (i.e., nesting density) of forest habitat retained in the landscape?
   - How does the proportion of high-contrast edge in nesting habitat influence the probability of persistence?

The forest management policy parameters we examined were: (1) long-term amount (in hectares) of nesting habitat; (2) the length of time to reach that amount; (3) nesting habitat quality (as reflected by nesting density of MAMUs); and (4) edge effects on reproductive success and survival of breeding adults. These are the same key policy components being considered by the Canadian Marbled Murrelet Recovery Team (CMMRT) in Part B of the Conservation Assessment process (CMMRT 2003). Uncertainties—in future on-shore and oceanic conditions, in our understanding of MAMU biology, and in the future course of timber management in coastal areas of British Columbia—are also elements of this analysis.

In Section 2, we describe the purpose of each of the component models and their information requirements; and in Section 3, we present the main results of the risk analysis. Section 4 contains our conclusions and recommendations. Further details on the sub-models used in this assessment, their parameterization, and supplemental results are presented in the appendices.

2.1 Risk Assessment Methodology

We carried out a habitat-linked Population Viability Analysis (PVA) using a Bayesian belief network (BBN) framework (Appendix 1). Extending the PVA approach to apply Bayesian decision analysis methods enabled us to integrate risk estimates with social values and to choose among adaptive management options.

The advantages and disadvantages of using PVA for conservation assessments are reviewed by Beissinger and McCullough (2002). Other examples of PVA and related approaches are discussed by Beissinger and Westphal (1998), Ludwig (1999), Ellner et al. (2002), Brook et al. (2002), and Reed et al. (2002).

We chose the BBN framework because it is a flexible, transparent, and structured way of integrating both biological data and expert opinion with potential management policy scenarios. It also allows explicit and flexible inclusion of uncertainties into model relationships and outcomes. Within the BBN we assigned belief weightings to each uncertain life-history parameter value, and to many of the relationships among parameters (e.g., relationship of habitat quality to nesting density). This resulted in a range of possible population outcomes, each with a resultant probability (plausibility) weighting. Several authors (Reckhow 1999; Marcot et al. 2001; Raphael et al. 2001; Riemen et al. 2001) provide good background and examples of using BBNs in natural resource management problems. Theory and example applications of Bayesian decision analysis in resource management are described by Bergerud and Reed (1998), Conroy and Noon (1996), Peterman and Peters (1998), and Wade (2000). We used the Netica BBN software to develop the framework (Norsys Software Corp; see www.norsys.com).

We developed a set of three component models to structure the BBN framework (Figure 3):

1. **Nesting habitat sub-models** (Appendix 2). This model predicts regional forest nesting capacity (maximum number of nesting pairs) and the proportion of the nesting capacity potentially subject to increased mortality due to edge effects. Forest older than 120 years, and height-class 2 or greater, is considered possible nesting habitat. MAMU nesting density is then modelled as a function of the forest and landscape characteristics (distance to sea, forest inventory attributes, biogeoclimatic variant, slope, elevation, amount of high-contrast edge) that affect nest platform abundance and MAMU access to those platforms. Edge influence is modelled as the proportion of nesting capacity within 50 m of forest <40 years of age.
2. **Demography model** (Appendix 3). We used a stochastic, stage-structured, females-only population projection model (developed externally in Excel) to project future populations under varying habitat and demography assumptions. Three life stages were included: juveniles (recruits-to-sea that survive their first fall/winter), 2- and 3-year-old sub-adults, and breeding adults. Immigration was applied as a proportion of the sub-adult population. Model parameters represent recruits-to-sea (representing the combined probability of nesting success and fecundity), overall survival of each stage (combining local survival with emigration), immigration, and correlation between these rates among regions and among years. Edge effects are applied as an uncertain effect on mortality rates, separately for breeding-age individuals and recruits-to-sea.

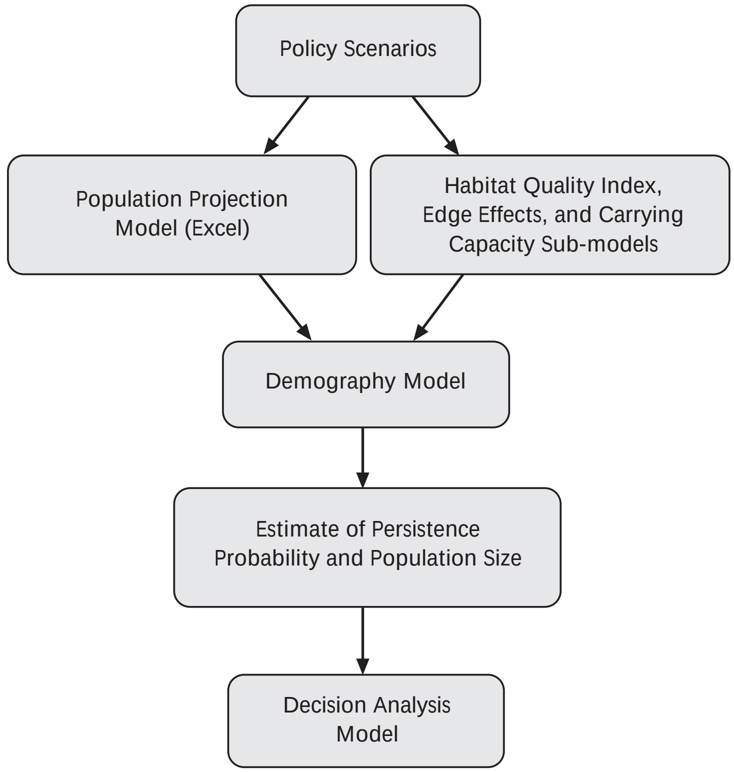

FIGURE 3 *Risk analysis framework.*

Because of many uncertainties in our knowledge of basic MAMU ecology, we modelled a wide range (89 000+ combinations) of plausible population and habitat parameter values.

For each set of parameter values, we projected the demography model 200 times generating probability distributions of future persistence probability and median population size (all age classes). For the purpose of this analysis, we defined a threshold population size of 50 females >1 year of age. Populations remaining above this threshold were considered to persist, while those falling below it were considered not to persist. We chose 100 years as our primary time period benchmark, and 300 years as an additional benchmark (see Section 2.2.3).

The results of the simulations we then applied to the BBN via a case file database. The BBN is then queried to conduct sensitivity analysis and to assess specific management policy scenarios.

3. **Decision analysis model** (Appendix 4). A preliminary decision model was developed to assess the trade-offs associated with retaining differing amounts and quality of MAMU habitat in terms of the forest harvesting landbase. We developed simple utility functions for both risk to MAMU and reduced timber harvest volume. By explicitly incorporating uncertainties in both types of utility, this model helped us identify the most effective (and robust) options for regional forest management policy, given the evidence in the model and the management emphasis.

We did not attempt to explicitly model interactions among regions, but we did include such effects in the range of demographic assumptions (Appendix 3). To examine coast-wide implications, we applied the "bet hedging" probability theory approach of Boyce et al. (2002). Both coast-wide and regional persistence would be expected to decrease with greater correlation among regions (as a result of synchrony of fluctuations), and with perfect correlation would be equal to the most persistent individual region. With total independence among regions, coast-wide risk would be the product of multiplying all the individual region risks. Because we do not know the strength of demographic correlation among regions, we applied a correlation range of 0.25–0.75 for estimating coast-wide persistence.

We emphasize that our approach was intended primarily to rank proposed MAMU nesting habitat management strategies in terms of their relative effects on indicators of MAMU population status—not to predict actual future MAMU populations.

Our data sources were a combination of published literature, unpublished data from ongoing research, the results of an intensive modelling workshop, and numerous discussions at CMMRT meetings.

2.2 Assessing Risk and Characterizing Outcomes

2.2.1 Defining "risk" "Risk" is an expression of the probability of an undesirable outcome occurring over a specified time period. To understand how risky a set of management actions might be, we need to ask three questions: What can happen? How likely is it to happen? and What are the consequences if it does happen? (to paraphrase Kaplan 1997).

In the context of our analysis, we considered irreversible declines or loss of MAMU populations (as described below) to be undesirable outcomes. If the analysis determined that particular management actions would contribute to an increasing probability of an undesirable outcome, those actions would be viewed as increasing risk.

Assessing the risks of particular policy choices includes considering the effects of uncertain future environmental conditions beyond the control of managers (e.g., climate change), uncertainty in MAMU biology, uncertainty of future forest management practices, and choice of assessment time horizon. Our goal was to examine the influence of forest management policy parameters (amount, type, and spatial pattern of old-growth forest) on the resilience of MAMU populations in the face of those uncertainties.

2.2.2 Population outcomes To assess the risks that the MAMU population in British Columbia (or a regional sub-population) could become non-self-sustaining, we used the persistence probability estimates as our indicator of resilience. A decreasing probability of persistence is an undesirable outcome; an increasing probability of persistence is a desirable outcome. As nesting habitat abundance (and thus potential population size) decreases, the population may become more susceptible (less resilient) to fluctuations in survival at sea and its probability of persistence may decline.

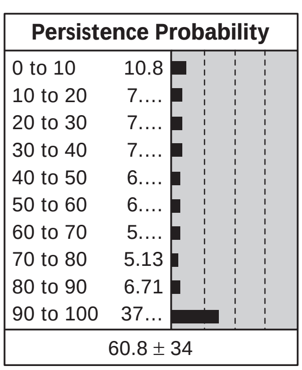

FIGURE 4 *Example distribution of probabilities of persistence for one management scenario.*

The example at the left (Figure 4) indicates the resulting distribution of probabilities of persistence for one management scenario. The length of the horizontal bars (expressed as a percentage) is the likelihood of each persistence outcome. In this example, there is a small chance (10.8%) of a low (<10%) probability of persistence. The greatest chance (37%) is for a persistence probability >90%. Without uncertainty of the correct input parameter values, there would only be one outcome (only one horizontal bar in the illustration).

The value at the bottom of the box is the "expected" value, our primary index of risk. It is the percentage of total population simulations that persisted for that management scenario. It is also the weighted-mean of the probability distribution of all possible outcomes. The expected value combines both "real" risk (the persistence probability for a given set of parameter values if they were correct) and knowledge uncertainty, represented by the range and weighting of input parameter values. An increasing value of the index indicates a shift towards higher probability of persistence, and thus resilience to uncertainty, while a decreasing value indicates a shift towards lower persistence.

2.2.3 Projection time period for assessing outcomes Statements about risk are usually expressed for a specific time period (e.g., the next decade or the next 100 years). The chances of an undesirable outcome occurring (such as loss of a population) increase with lengthening time horizon, all else held constant (see Ludwig 1999 and Lande 2002 for discussion of this point). Uncertainty also increases as the time horizon lengthens due to the compounding of both parameter uncertainty and structural errors in the models. While the effect of parameter uncertainty is accounted for in our model framework, the effect of structural error is not. The persistence criteria adopted by the International Union for the Conservation of Nature (IUCN 2001) and the COSEWIC use a reference of 100 years. For consistency, we also used 100 years as our primary benchmark period for comparing projected outcomes.

In terms of evaluating land management policies for MAMU nesting habitat, however, longer time horizons are required because MAMU nesting habitat, once logged, potentially takes 200–300 years to recover (i.e., to recruit trees of sufficient size to develop large branches with epiphytes suitable for nesting). Policy-makers generally want assurance that resource decisions are sustainable well into the future and that economic investment is not placed unduly at risk. Thus, we also examined outcomes at 300 years, seeking management options that are robust at both 100- and 300-year time frames.

3 RESULTS AND DISCUSSION

3.1 Sensitivity Analysis

Sensitivity analysis was used to examine the influence of model variables on the predicted outcome. Assumptions of future demographic rates had the greatest influence on expected value of population persistence, followed by on-shore nesting capacity (Table 1). Of the parameters that can be controlled by forest policy, the time period of assessment, habitat quality (potential nesting density), and area of old growth maintained had the greatest influence. Patch size and shape had minimal influence (1–4% difference in persistence probability).

The sensitivity results can also be useful for prioritizing research efforts by directing them to variables with the most influence. Aside from demographic rates, the presumption of a linear relationship of murrelet nesting capacity with amount of habitat had the greatest influence, while the degree of selection for edges had the least influence.

3.2 At-sea Demographics and Resulting Population Growth Rate

Our focus in this assessment was on nesting habitat. However, much of the MAMU life cycle is spent at sea. Potential at-sea effects were captured in our base vital rates scenarios (see Appendix 3), with both persistence probability and population size sensitive to the weighting of those scenarios.

Consistent with what has occurred in other demographic analyses for MAMU (Beissinger and Nur 1997; Cam et al. 2003), the range of plausible demographic rates we applied resulted in a wide range of annual population growth rate (λ) estimates (Table 2). We found that even in the absence of

TABLE 1 *Sensitivity of expected persistence probability to findings for 18 variables. Variables in **bold** are those that are potentially controlled by forest management policy. See appendices for further descriptions of variables. Variance reduction is a measure of relative influence on the results (see Glossary).*

Assessment variable	Variance reduction
Demographic rates scenario	664.6
Nesting capacity (number of nesting pairs)	306.9
Linear vs. non-linear response to amount of old growth	188.0
Time period (100 vs. 300 years)	125.8
Nesting density (0.002/ha to 0.03/ha)	103.0
Area of old growth (hectares)	100.8
Percent old growth remaining today (regional context)	86.8
Radar-based mean density estimate	32.1
Precision of radar estimates	11.0
Correlation of immigration rate with population size	6.4
Final percentage of habitat influenced by edge	5.8
Effect of edge on recruits-to-sea (RS)	3.5
Conversion of radar estimate to nesting density	3.1
Effect of edge on adult survival (Sa)	3.1
Immigration rate (1% or 2% of sub-adult population)	2.4
Patch size (10, 50, 250 ha)	1.7
Do MAMU select edges (true = 2× preference for edge)?	0.9
Patch perimeter/area ratio	0.3

density dependence and other on-shore nesting habitat effects, long-term declines or increases are possible (modified by the degree of annual environmental variation). Mean λ in the absence of nesting habitat limitations was a 1.2% average annual potential population increase (left side of Table 2). Realized rates of population growth (including density-dependence and the effects of edge on vital rates) were lower, averaging a slow decline (right side of Table 2).

We cannot directly compare our projected average λ to the empirical estimates presented in Cam et al. (2003) (the latter include measurement and sampling error, and were for a small number of years), but our realized rates were generally consistent with those empirical estimates.

We also found a strong interaction between the effects of the marine environment (represented by the demographic rate scenarios) and nesting habitat capacity. With highly pessimistic demographic assumptions, nesting habitat was rarely limiting because populations remained below carrying capacity. With highly optimistic scenarios, nesting habitat limited population size but maintained high persistence probability except at very low nesting capacity values. Persistence was most sensitive to nesting capacity for mean lambda ~ 1.0 in combination with higher environmental variation (demographic scenario 4; see Appendix 3).

3.3 Effect of Habitat Amount and Quality on Population Size and Persistence Probability

The likelihood of achieving a particular at-sea population size was a non-linear function of both habitat amount and quality (Figure 5). While available nesting habitat set an upper limit on population size of nesting females, at-sea demographic assumptions largely determined the likelihood of achieving it.

We also found a trade-off between the density of nesting MAMU (quality of nesting habitat) and the amount (in hectares) of old growth in terms of expected probability of persistence (Figure 6). Given that forest management can affect both the amount and quality of habitat, the data in Figure 6 allow comparison of policies advocating different amounts or quality of nesting

TABLE 2 *Average annual population growth rate (λ) outcomes generated by the demographic model. Estimates for each demographic scenario reflect base vital rates combined with environmental variation (left-hand portion of the table) and the added effects of density dependence and habitat effects on vital rates (right-hand section).*

Lambda applied in absence of carrying capacity effects, immigration, or edge effects				Lambda "realized" across all simulations			
Demographic scenario	**Median**	**Mean**	**Standard deviation**	**Demographic scenario**	**Median**	**Mean**	**Standard deviation**
Higher environmental variation							
1	0.999	0.996	0.076	1	0.989	0.984	0.082
2	0.987	0.983	0.075	2	0.976	0.970	0.081
3	0.983	0.977	0.079	3	0.999	0.991	0.082
4	1.057	1.051	0.083	4	1.010	1.003	0.086
Lower environmental variation							
5	1.029	1.027	0.053	5	1.003	1.001	0.057
6	0.991	0.989	0.051	6	0.992	0.989	0.056
7	0.998	0.995	0.054	7	0.988	0.983	0.057
8	1.078	1.076	0.057	8	1.006	1.002	0.057
Mean	1.015	1.012	0.066	Mean	0.995	0.990	0.070

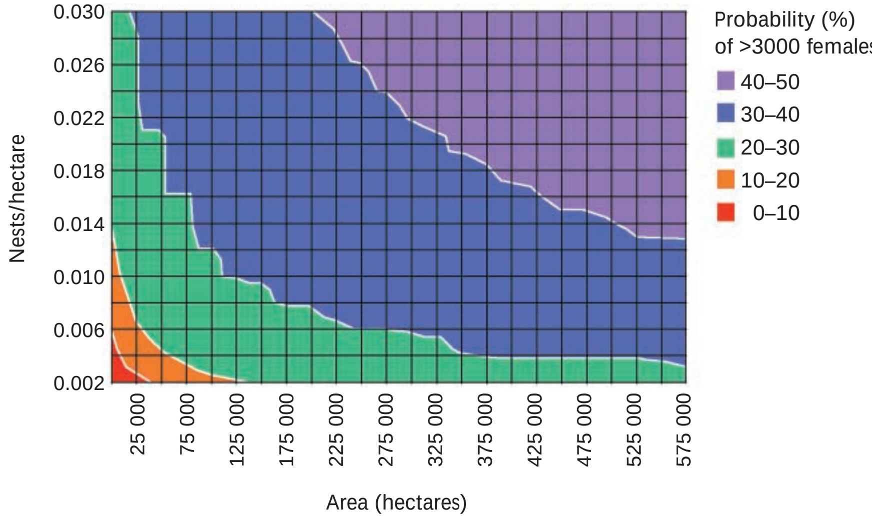

FIGURE 5 *Likelihood of achieving a female population (all ages) of 3000 at 100 years.*

habitat. Examining the full probability distribution of outcomes (Figure 7) is the most informative approach, but impractical for a large number of scenarios. A nesting capacity of 1000 pairs, for example, provides an expected value of persistence of 64% and a most likely outcome of 95% persistence or better.

To interpret Figure 6, consider, for example, the change in risk if the density of MAMU is held constant at 0.006 nests per hectare. With 100 000 ha of habitat of this quality, our assessment predicted an expected value of persistence of 50–60% to 100 years. If 175 000 ha, 250 000 ha, or 400 000 ha of habitat of this same quality were available, the expected value rose to 60–70%, 70–80%, and 80–90%, respectively. Above 400 000 ha of habitat of this quality, our assessment predicted no further substantive increase unless the quality of the habitat (nesting density) also increases.

We found that to achieve >80% expected probability of persistence required >2000 nesting pairs, while >90% required >5500 nesting pairs. Thus, a 10% improvement in persistence required more than a doubling of nesting capacity.

Not all old growth is equally suitable for nesting by MAMU, but scientific debate continues about the relative suitability of forest types. The CMMRT has defined general attributes of "most," "moderately," and "least preferred" habitats (CMMRT 2003). Explicit assessment of risk associated with specific land management plans, however, requires assigning estimates of nesting density (including statistical uncertainty) to mapped areas of available habitats (e.g., Steventon 2003; Appendix 2).

The IUCN (2001) classifies as "vulnerable" ("threatened" in the COSEWIC system) those species likely to experience >10% risk of extinction in the next 100 years. This classification implies that a level of risk commensurate with 90% or better odds of persistence will prevent a species from being listed as "vulnerable."

As was the case for the expected value of persistence, the likelihood (certainty) of achieving the IUCN 90% persistence probability threshold was a non-linear function of amount and quality of nesting habitat (Figure 8). This likelihood reflects the uncertainty of actual persistence probability as a result of the uncertainties associated with murrelet biology—notably, those tied to

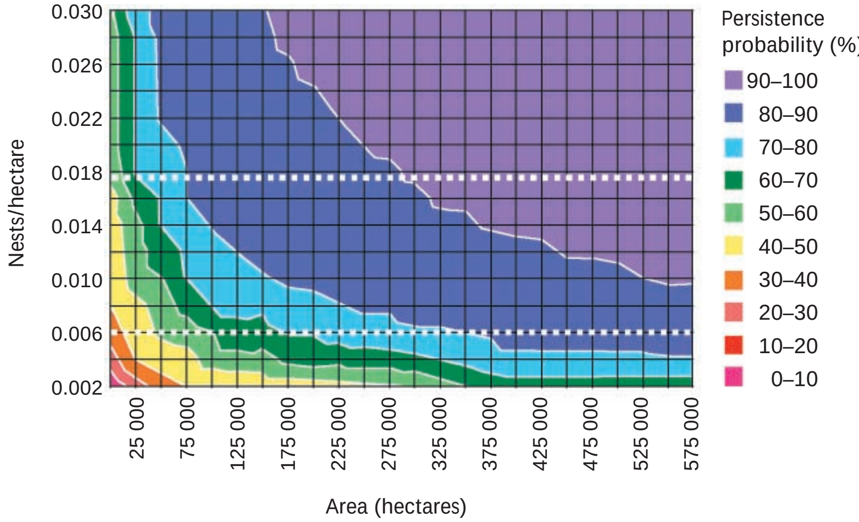

FIGURE 6 *Expected probability of persistence (≥100 years) as a function of total area of nesting habitat and habitat quality (equal weighting given to all patch sizes). White horizontal lines represent range of mean density estimates (nests/ha) inferred from recent British Columbia studies (Burger 2002).*

	1000 pairs	2000 pairs	5000 pairs
	Persistence 100 yr	Persistence 100 yr	Persistence 100 yr
0 to 5	7.11	0.19	.004
5 to 10	1.52	0.11	.025
10 to 15	1.32	0.23	.063
15 to 20	1.86	0.55	0.17
20 to 25	2.20	0.78	0.24
25 to 30	2.85	1.20	0.37
30 to 35	3.38	1.60	0.50
35 to 40	4.94	2.45	0.78
40 to 45	5.41	2.83	1.00
45 to 50	5.12	2.89	1.18
50 to 55	5.37	3.37	1.62
55 to 60	4.89	3.48	1.97
60 to 65	3.87	3.45	2.39
65 to 70	3.55	3.67	2.78
70 to 75	3.40	4.04	3.25
75 to 80	2.65	4.41	3.63
80 to 85	1.56	5.00	3.93
85 to 90	1.04	6.32	4.82
90 to 95	0.43	7.03	9.05
95 to 100	37.5	46.4	62.2
	63.9 ± 32	80.8 ± 22	88.7 ± 16

FIGURE 7 *Persistence probability distributions for nesting capacities of 1000, 2000, and 5000 pairs. The three categories of nesting pairs (1000, 2000, 5000) correspond to the expected value of persistence equal to 64, 81, and 89%, respectively (Figure 6).*

the demographic assumptions. Given the effect of demographic uncertainty, we were unable to exceed 80–90% likelihood of at least 90% persistence through increased amount or quality of nesting habitat. We concluded that a high likelihood of achieving the IUCN standard (or better) is feasible coast-wide, but will be difficult to demonstrate at the regional scale. This further illustrates the importance of achieving better understanding of the at-sea component of the MAMU life cycle.

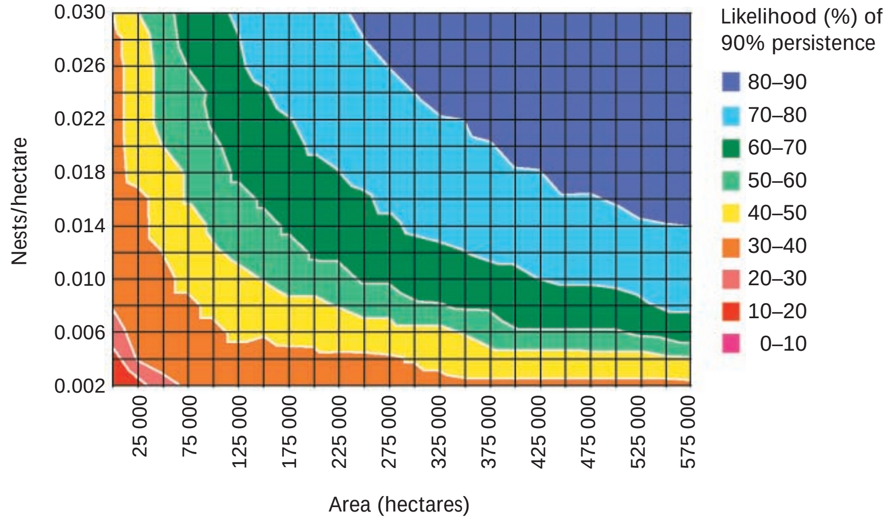

FIGURE 8 *Likelihood of achieving 90% persistence probability at 100 years.*

3.4 Assessing Risk Associated with Present Population Sizes, Proposed CMMRT and IUCN/COSEWIC Population Size Threshold

At the largest spatial scale (coast-wide), the risk that MAMU will not persist in British Columbia is low, given current estimated population sizes and amounts of nesting habitat (Table 3). At the regional scale, only one Conservation Region—East Vancouver Island—is at high risk of failing to persist as a viable, independent population.

The CMMRT thresholds resulted in 94–99% expected probability of persistence coast-wide. Individual Conservation Regions (Table 3) varied from a potential low of 38% expected value of persistence for East Vancouver Island to 90% expected value with optimistic population assumptions for West and North Vancouver Island.

Depending on whether optimistic or pessimistic population estimates are applied, and the strength of environmental correlation among regions, IUCN/COSEWIC thresholds based on rates of decline (e.g., populations allowed to decline to 50–65% of current size) are somewhat less likely to achieve coast-wide persistence (Table 3). Risks to individual regions—especially East Vancouver Island, the Southern Mainland Coast, and Haida Gwaii (Queen Charlotte Islands)—increased markedly, the magnitude being greatest with pessimistic demographic assumptions.

As it may take up to 300 years for nesting habitat to recover after harvest, assessment time horizons longer than 100 years (the IUCN/COSEWIC standard) may be appropriate. We found that simulations providing an expected persistence probability of 95% or greater at 100 years also maintained high expected persistence probability at 300 years. Given present parameter uncertainty, assuring 95% probability was not possible at the regional scale, but was readily achieved at the coast-wide scale.

3.5 Decision Analysis and Acceptable Risk

An acceptable level of risk depends on the nature of the risk (such as its reversibility and the severity of outcome), the tolerance of risk by decision-makers, the spatial scale under assessment (region vs. coast-wide), and the incremental costs of reducing risk. If minimizing risk to MAMU populations was the sole forest management objective within the MAMU Conservation Regions, regardless of cost, then the best decision would simply be to preserve all potential MAMU nesting habitat. Yet, as noted above, we found that reducing risk to nesting capacity (habitat amount and quality) yielded

TABLE 3 *Confidence of persistence, by MAMU Conservation Region, for long-term population size targets (total birds) as a percentage of estimated present populations*

Conservation Region	Present population estimate (2002)		Expected value of probability of persistence			
	Optimistic	Pessimistic	Present	CMMRT [a]	50% decline	65% decline
Northern Mainland Coast	14 700	10 100	84–89	80–84	71–81	64–71
Haida Gwaii (Queen Charlotte Islands)	9 500	8 500	83–84	77–79	70–71	62–64
Central Mainland Coast	21 000	10 000	84–91	80–88	71–84	64–78
Southern Mainland Coast	7 000	6 000	78–80	65–78	64–64	55–56
West and North Vancouver Island	24 500	19 400	90–92	87–90	84–86	80–83
East Vancouver Island	1 000	700	38–41	38–40	20–25	15–20
Coast-wide	77 700	54 700	95–99[b]	94–99	92–99	90–99

a Estimates of population sizes by Conservation Region are taken from Part B – Conservation and Management (CMMRT 2003). Decrements from present population estimates represent decrements of ~30% of the preceding value as suggested by the COSEWIC maximum decline rate criteria.
b Range represents correlation coefficients of 0.25–0.75 for demographic fluctuations among regions.

diminishing returns. Realistic decision-making includes considering the potential economic costs (e.g., foregone timber harvest values) and other societal objectives and values.

Formal decision analysis (e.g., Buongiorno and Gilless 2003) allows rational examination of questions such as "What decisions about managing forests containing MAMU nesting habitat are feasible, given the objectives of sustaining both timber harvesting and MAMU populations?" Because good quality MAMU nesting habitat often occurs in productive forests, the potential for conflict between management objectives is high. It is also useful to ask whether different stakeholders (e.g., conservationists, government agencies, forest products companies) might view different decisions as either under-protecting or over-protecting habitat, or whether these differing views may converge on a common solution. The management choice with the highest utility is considered "optimal," given the evidence and emphasis weightings represented in the model (Wade 2000).

Conducting an effective decision analysis requires direct involvement of decision-makers to ensure that the model represents decision criteria correctly. Region-specific nesting habitat data and further development of the utility functions are also needed. Also key is that decision-makers need to weigh the MAMU and timber emphasis to be applied in each Conservation Region—a subjective decision process. However, even without consensus on the MAMU vs. timber emphasis, decision models can clarify the range of plausible decision choices and trade-offs.

An example of a decision analysis is provided in Appendix 4.

3.6 Opportunities for Adaptive Management

Adaptive management (AM) is a process that explicitly recognizes the intertwining of research and management, and seeks to blend methods of scientific investigation with ongoing manipulation of managed systems (Walters 1986; Nyberg 1998). To reduce uncertainties about system interactions—uncertainties that inhibit the making of informed management decisions—AM treats actions as learning opportunities, applying designed tests and monitoring results. Adaptive management is especially useful for large spatial-scale and long-term questions that cannot readily be addressed at specialized experimental sites.

Both research and AM should use principles of rigorous experimental design (e.g., randomization) to assure reliability of findings. Our modelling framework offers a useful means of assessing priorities for AM research to improve conservation options for MAMU, and of comparing specific experimental designs in particular coastal watersheds. In principle, given an available pool of financial resources, priority should go to projects that minimize decision uncertainty or decision risk.

Already clear is that habitat amount, nesting density assumptions, movement rates between populations, and the apparent linear relationship between murrelet abundance and amount of old growth remain the most important uncertainties. Other questions include whether it is more effective to concentrate habitat in fewer watersheds or to disperse it (the CMMRT "core area" concept), and whether partial cutting or other management practices can maintain sufficient habitat or restore already degraded habitat.

3.7 Further Assessment Work

Our recommended priorities for further assessment work include the following:

- Explore methods of increasing the ease and flexibility of modifying and setting parameters in the assessment model. One option, for example, is to directly include difference equations for predicting relative persistence in the BBN. This would remove the delays involved in running the Excel simulations for revised sets of parameter values.
- Complete the parameterization of the habitat sub-model to allow it to be applied to real-life land use scenarios. This has been done for the Northern Mainland Coast as part of the North Coast Land and Resource Management Plan (LRMP) process, but this sub-model could be extended and applied elsewhere on the coast.
- Conduct a more complete analysis of the potential cost/benefit trade-offs for habitat management and conservation strategies within and among MAMU Conservation Regions.
- Extend the decision analysis to incorporate stakeholder estimates of management costs and utility values.
- Formalize procedures for assessing adaptive management and research options for maximizing "information" return on investment.

Setting priorities for further assessment work requires interaction with decision-makers. There would be little value, for instance, in conducting the analysis of a trade-off among regions if decision-makers had no interest in varying land use objectives by region.

4 CONCLUSIONS AND RECOMMENDATIONS

Despite uncertainty, our analyses indicated substantial change in risk to MAMU persistence in response to plausible ranges of key demographic and habitat parameters. While we cannot confidently predict future populations of MAMU, we can make useful inferences to guide habitat protection policies, subject to the life history traits of MAMU being within the ranges we applied.

Our main conclusions are:

1. The long-term risk to MAMU is sensitive to the amount and quality of nesting habitat. This relationship is non-linear, with diminishing incremental benefit in reducing risk as amount of habitat increases. Although the acceptable level of risk is a subjective decision, it appears that the risk accelerates below a nesting capacity of 2000 pairs in each region (12 000 coast-wide, or a total population of ~36 000 MAMU). Risk continues to decrease above 2000 pairs per region, but at a slower rate.
   This threshold is higher than the generic COSEWIC thresholds, but lower for some regions than the 30-year thresholds suggested by the CMMRT. Using nesting densities inferred from recent radar-based surveys and uncertainty of habitat quality models, we calculate that this would equate to about 100 000–400 000 ha of average value nesting habitat per region, or 600 000–2.4 million ha coast-wide.
2. The rate of habitat decline has less influence on long-term risk to MAMU persistence than does the actual level at which the rate of the habitat decline eventually stabilizes.
3. Future conditions at sea will play a profound role in maintaining MAMU populations. Uncertainty about basic vital rates, and about how marine conditions (such as climate change and fisheries management) may affect these rates, was at least as important as nesting habitat in terms of influencing the outcome. Our weighting of the vital rate scenarios results in an average long-term mean lambda (λ: realized population growth rate) of close to 1.0 (stability), but with an increased chance of poor years (λ<1.0) rather than better years (λ>1.0). Making this weighting too pessimistic results in over-estimating the amount of nesting habitat required. Given the potential length of time (2–3 centuries) for nesting habitat to recover once it is harvested, until better understanding of at-sea effects is achieved, applying conservative demographic assumptions is recommended.
4. Population size and relative persistence outcomes are only modestly sensitive to the details of patch shape and size (i.e., habitat configuration). Thus, while reducing fragmentation of forested habitats remains a useful means of reducing MAMU conservation risk, doing so is much less important than maintaining the amount and quality of habitat (expressed as nesting probability or relative density).
5. There is no reason for all six MAMU Conservation Regions to be treated identically in terms of risk or to be assigned the same habitat objectives. Decision analysis techniques should be used to assess trade-offs among forest management and land-use objectives in each region.
   We recommend further analysis of management options among regions, including estimates of economic cost. Some trade-off among regions may be the most rational approach for achieving a high level of certainty coast-wide while maintaining acceptable risk at regional scales with acceptable

economic costs. Nevertheless, increased risk in one region can only be partly offset by decreased risk in another (because of the diminishing persistence improvement with increasing amount of habitat).
Similarly, trade-offs in objectives across spatial scales (coast-wide, region, landscape unit, watershed) could be examined further.

6. High priority should be given to research aimed at refining assumptions about nesting density and associated habitat selection and estimates of immigration/emigration rates between regions. Studies to monitor population trends by Conservation Region and to determine the relative influence of at-sea conditions vs. nesting habitat effects on populations are also important. The radar survey method appears to have the greatest potential for reducing many of the key uncertainties. Continued use of radio-tagging in a variety of locations would be the most effective method to confirm nesting habitat preferences.
7. Adaptive management offers considerable potential as a method of prioritizing MAMU conservation issues and improving the risk assessment process. In regions where habitat amount and quality appear limiting, the use of partial cutting or variable retention harvesting could be tested as a provisional habitat maintenance and recruitment strategy. Similarly, watersheds could be logged in a variety of patterns to test some of the habitat suitability assumptions (e.g., varying patch size). With additional refinements, the assessment model could also be used as a tool to examine the relative efficacy and cost of various potential adaptive management strategies.

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The first step in designing a Bayesian belief network (BBN) is to create a conceptual box and arrows model of the study system. Boxes represent nodes (variables); arrows (links) represent a relationship between nodes.

The second step is to quantify the relationships between the nodes, using data, expert opinion, or a combination of the two. Each possible state for a node is given both a value and a probability of being true (an expression of uncertainty) based on the values of the nodes feeding into it (called the parent nodes). These probabilities are represented in a conditional probability table (CPT) for each node. The relationship of a node to its parents can be manually entered into the CPT, expressed as equations (which are converted by Netica into a CPT), or read into the BBN model as "case files." In our models we use all three methods at various nodes.

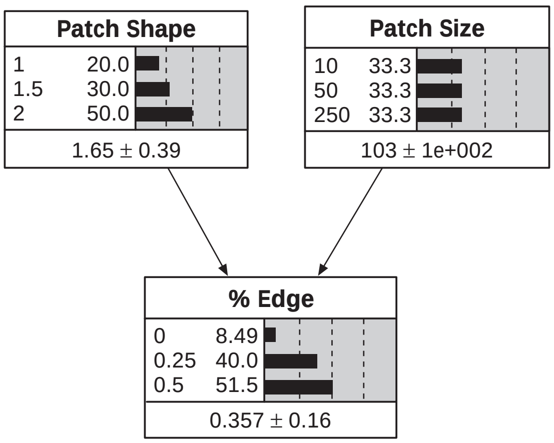

FIGURE A1.1 *Example BBN model.*

The categories within a box represent the values the node can assume based on the values of parent nodes feeding into it. In the example to the left (Figure A1.1), the bars represent "strength of belief" (probabilities expressed as a percentage) for each value in the node. In this example, the node "% Edge" is the edge effect multiplier to be used in the demographic model (Appendix 3) for changing one of the vital rates (annual number of recruits-to-sea per female [RS]). The black bars show the weightings (degree of belief) in each multiplier value. This node is conditional on patch size and shape. A "no edge effect" (multiplier=0) receives a 8.5 % weighting, while the greater edge effects represented by multipliers of 0.25 and 0.5 receive 40% and 52% weightings, respectively. The overall "expected value" (mean of the probability distribution) is 0.357 with a standard deviation of 0.16.

Any of the node values or belief probabilities can be changed to allow examination of effects elsewhere in the network. Nodes whose values and beliefs remain static or have little influence on outcomes can be "absorbed" to create a simpler model that maintains the influence of the eliminated nodes. We applied greater uncertainty and ranges for base vital rates (survival and recruitment) than those estimated from current data to account for potential (but unknown) effects of climate change, given the long time frame of model projections.

The results of the external demographic model were used to parameterize parts of the BBN via a "case file." A case file is a database of findings (e.g., observations) that can be used to initialize the conditional probability tables (CPTs) for the demographic nodes in the network. Once that is done, the population model is no longer needed unless parameterization is required for a broader range of node values.

The nesting habitat sub-models (Figures A2.1–A2.3) predict habitat carrying capacity in terms of female nesting density, and the proportion of the nesting population potentially subject to edge effects. The latter effects are due mostly to forest edges, but also represent slope and elevation influences.

These models are used to explore how changes in landscape composition through forest management may affect population outcomes. They have only been applied to-date (in a customized version) to the North Coast Land and Resource Management Plan (LRMP) area (Steventon 2003).

Structure and parameterization of the models are based on: Burger (2002); the modelling workshop held in September 2001 and a follow-up workshop with A. Burger and L. Waterhouse; our review of the literature; and analyses of platform density data from the Queen Charlotte Islands (Haida Gwaii) (D. McLennan and I. Manley, unpubl. data) and northern Vancouver Island (J. Deal, unpubl. data).

We hypothesize that potential MAMU nesting density is a function of forest and landscape characteristics (distance to sea, forest inventory attributes, slope, elevation, and edge) affecting platform abundance and access to those platforms. A Habitat Quality Index (HQI) is scored from 0 to 1, with 0 representing no habitat value and 1 representing maximum habitat value. Edge effects are also scored from 0 to 1, representing the proportion of the nesting population affected.

The expected value of HQI for each landscape (e.g., watershed or landscape unit) and the amount of habitat (in hectares) in the landscape are then applied in the carrying capacity sub-model.

Habitat Quality Index sub-model

The model parameters shown in Figure A2.1 include:

% Slope, Elevation, Canopy Complexity, Canopy Closure Class, Age Class, Height Class, and Biogeoclimatic Variant: These are all standard forest inventory attributes (B.C. Ministry of Sustainable Resources, unpubl. data) from GIS or spatial model projections. Arrows between them indicate significant correlations (e.g., canopy closure and height class are correlated with age class).

% Edge: The proportion of nesting habitat within 50 m of forest <40 years of age.

Platform Abundance: Directly parameterized from two field data sets: Queen Charlotte Islands (McLennan et al. 2000), and northern Vancouver Island (J. Deal, Canfor Ltd., pers. comm.). Both of those studies involved applying sample transects to estimate platform abundance in forest inventory polygons, using Resource Inventory Committee standard definitions. The two data sets were read into the BBN model as a case file with very high weighting to override the uniform prior distribution. There were very few samples from age-class 7 stands, so those probabilities were set subjectively as being very low.

Distance to Sea: Distance in kilometres from nearest salt water (20-km intervals).

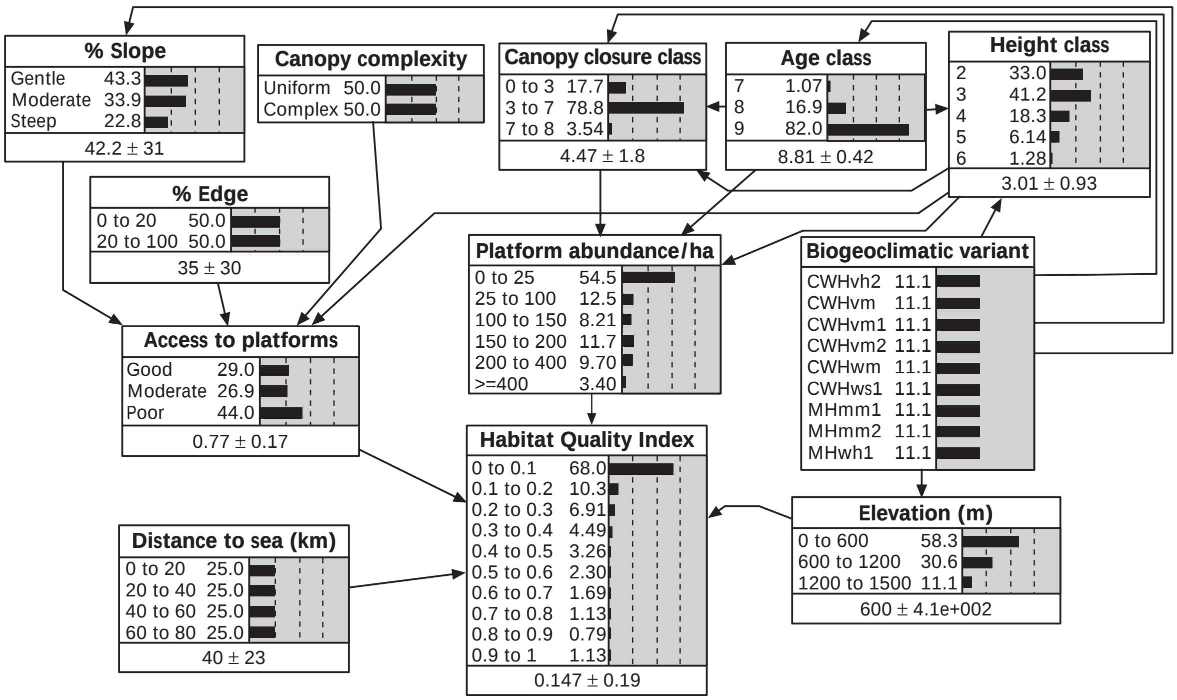

FIGURE A2.1 *Habitat Quality Index sub-model BBN.*

Habitat Quality Index: A function of platform density, modified by access, elevation, and distance to salt water. Range is 0 to 1, with 1 being highest quality and 0 being no value as habitat.

The index is first calculated as a Weibull function of platform density: (1-exp(-20*Platforms/800)$^{1.5}$. The Weibull distribution is a generalization of the exponential distribution, and is an appropriate distribution to use when a number of roughly equivalent factors are competing to determine the probability of an event occurring. This may be the case for the suite of habitat factors that determine the probability of suitable nesting platforms for MAMU occurring in a landscape.

Nesting probability rises rapidly with platform abundance above 25 per hectare, with no further improvement above 200 per hectare. Estimated platform abundance is reduced by 40% for elevations above 600 m. The resulting value is then multiplied by the access value, and distance to sea is applied as a negative exponential function for distances beyond 20 km: {exp(-(Distance-10)/40)}.

Access to Platforms: This node was subjectively parameterized. The underlying hypothesis is that greater stand height, more complex canopy structure, and steeper slopes combine to provide easier access to platforms and thus greater chance of use (Burger 2002; Waterhouse et al. 2002; Huetteman et al.[2]). It has only a minor effect on the HQI compared to platform abundance.

2 Huettmann, F., E. Cam, D.B. Lank, R. Bradley, L. Lougheed, L. McFarlane Tranquilla, C. Lougheed, Y. Zharikov, P. Yen, N. Parker, and F. Cooke. In review. Breeding habitat selectivity for large-scale habitat features by Marbled Murrelets in fragmented and virgin old-growth forest landscapes. Submitted to Wildlife Monographs.

Edge effects sub-model

The other hypothesized influence on nesting habitat is edge. High-contrast, management-induced edge (defined as old growth adjacent to <40-year-old forest) has been hypothesized to increase predation risk to nests and adults (Burger 2002), although this theory has not been accepted by all MAMU ecologists.

The model parameters shown in Figure A2.2 include:

% Edge: High-contrast edge (forest <40 years of age) is calculated in the node "% Edge" (Figure A2.2) as a function of patch size and shape, assuming a 50-m edge effect zone (Burger 2002). Modelling effects of high-contrast edge this way is a simple, albeit indirect way of representing the patch size distribution of the forest. A number of shape issues confound analyses of patch size (see Perry et al. 2002 for a recent discussion), particularly in highly dissected landscapes such as those on the coast. Expressing percentages of habitat area influenced by edge as a probability distribution for the study area as a whole avoids having to account for these shape issues for all patches.

Based on the results of recent analyses of nests located by telemetry on the province's South Coast and Clayoquot Sound, we moderate "% Edge" with increasing elevation and slope. However, given uncertainty about the generality of those results when applied elsewhere, we do not apply as strong a slope effect as implied by those particular analyses. Since steep slopes are less likely to be harvested, this, effectively, is a conservative assumption. Nonetheless, it represents a shift and expansion of the paradigm defining "good MAMU habitat."

BEC Variant: Biogeoclimatic Ecosystem Classification variant nodes (Banner et al. 1993). BEC variants influence the model through the elevation and slope.

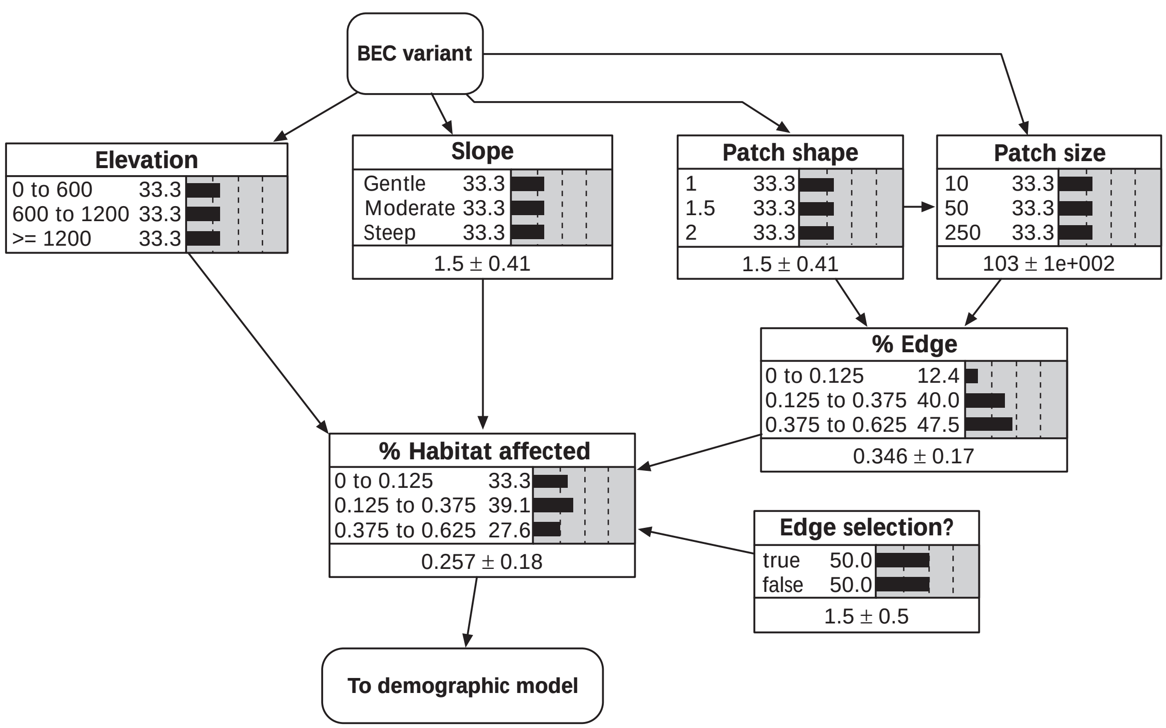

FIGURE A2.2 *Edge influence sub-model.*

Elevation: Elevation classes (as shown in BBN).

Slope: Slope classes. Passed to "% Habitat Affected" as a value of 1,2, or 3.

Patch Shape: Perimeter to area ratio.

Patch Size: 10, 50, or 250 ha.

Edge Selection: A node that weights two alternative hypotheses of nesting distribution relative to edge. Node state "true" represents the hypothesis that MAMU preferentially nest within 50 m of distinct edges at double the density seen in areas away from edges. "False" represents a hypothesis of no preference for edges. The former hypothesis was put forward based on telemetry-located nests in Desolation Sound, but has not yet received general acceptance. If nesting survival is reduced at edges, then nest site selection for edges (or, by extension, smaller patches) will increase risk (Donovan and Lamberson 2001).

% Habitat Affected: The combined effect of edge, slope, and elevation, represented by the equation:
P (Effected_Pop | Edge_select, Elev, slope1, Edge) =
(Elev == #0) ? NormalDist(Effected_Pop,Edge_select*(Edge) / slope1, 0.05) :
(Elev == #1) ? NormalDist(Effected_Pop,Edge_select*(Edge)/ 1.2 / slope1, 0.05) :
NormalDist(Effected_Pop,Edge_select*(Edge) / 4 / slope1, 0.05)

Nesting carrying capacity sub-model

Nesting carrying capacity is a function of average Habitat Quality Index (HQI), hectares of habitat, density estimates from radar-based inventory of birds accessing watersheds, estimates of the proportion of those birds that are breeding females, and the regional context (Figure A2.3). To date, the relationship of our HQI to density has only been examined for the northern mainland coast (Steventon and Holmes 2002). In that study, the best-fit relationship was an exponential function, applied in the BBN as a log-Normal distribution with mean $\{HQI \times 4.968 – 6.3456\}$ and standard deviation of 0.791. In the North Coast Land and Resource Management Plan (LRMP) assessment, three plausible regression models were applied using three assumptions of minimal usable forest inventory height class (Steventon 2003).

The BBNs can also be used "in reverse" to generate scenarios consistent with a desired management objective. Figure A2.5 provides two examples from the North Coast LRMP (Steventon 2003) of two landscape composition scenarios consistent with a nesting capacity of 3500 pairs.

Model parameters as shown in Figure A2.3:

- ***Regional Context:*** Combinations of murrelet radar estimates and percentage of old growth remaining in a region. Used in conjunction with the "Constant Density Assumption" node (below). Not applied except for sensitivity analysis.
- ***Mean Habitat Quality Index:*** The mean HQI for a landscape.
- ***Proportion Nesting Females:*** Converts radar estimates to estimates of nesting females (pairs). Of the birds accessing a watershed, the proportion that is nesting females is not known. Thus, a probability distribution (see Figure A2.3) was applied.
- ***% Habitat Remaining:*** The percentage of original old growth remaining in the landscape.

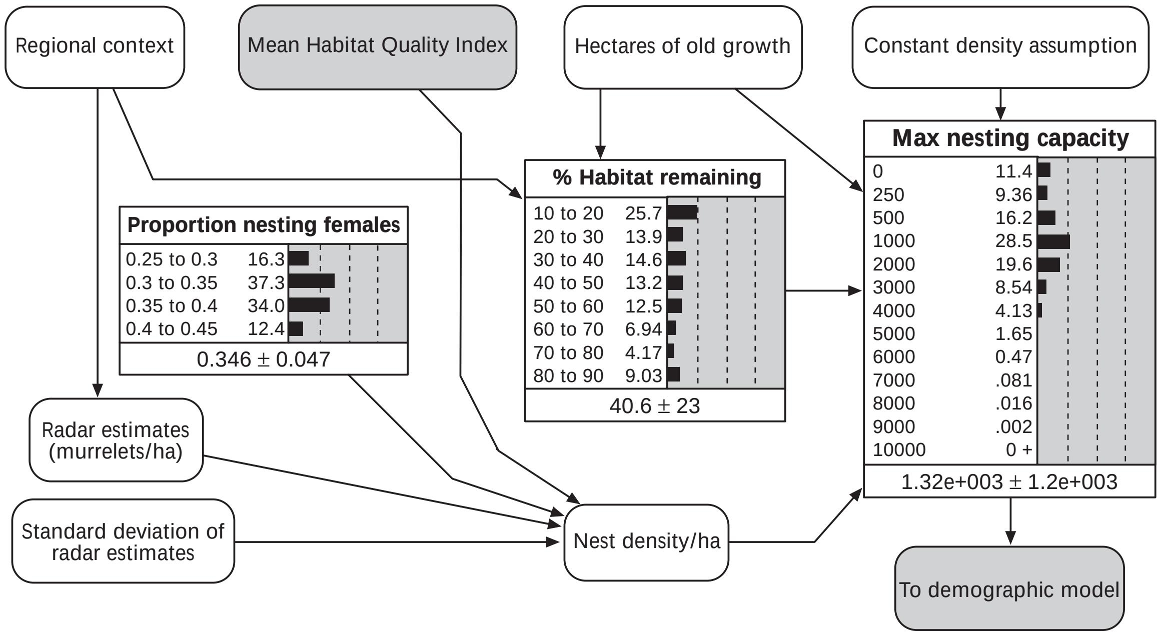

FIGURE A2.3 *Nesting carrying capacity sub-model.*

- ***Radar Density Estimates:*** Density estimates from radar studies.
- ***Standard Deviation of Radar Estimates:*** Standard error estimates from radar studies.
- ***Nest Density/ha:*** Resulting nesting density estimate.
- ***Max. Nesting Capacity:*** The resulting nesting population ceiling applied in demographic model.
- ***Hectares of Old Growth:*** Area of potential murrelet habitat.
- ***Constant Density Assumption:*** If this node is set to "true," density is dependent only on the HQI. If false, density is modelled as a power function (Figure A2.4) based on percentage of old-growth forest remaining in the landscape. The latter hypothesis is that murrelets can initially "pack" into remaining habitat as old growth is removed, but only to some maximum amount. Except for sensitivity analyses, this parameter was set to "true."

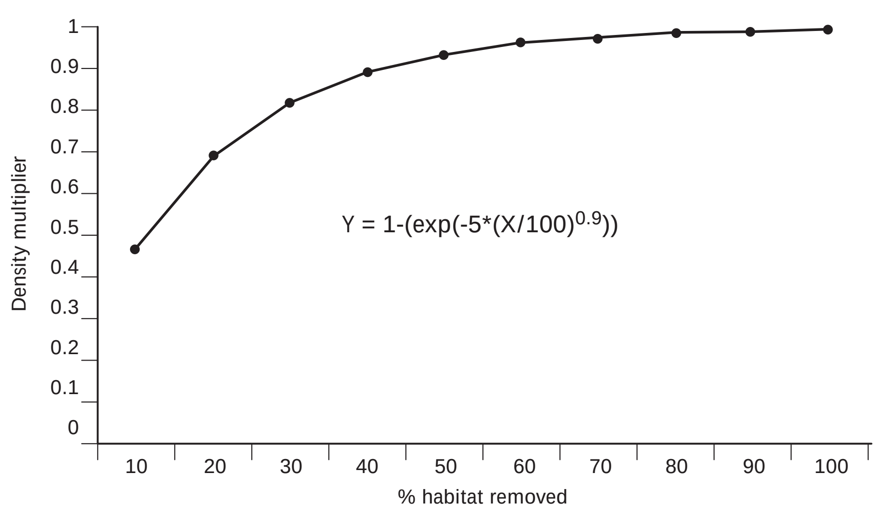

FIGURE A2.4 *Maximum population density as a function of % habitat removed.*

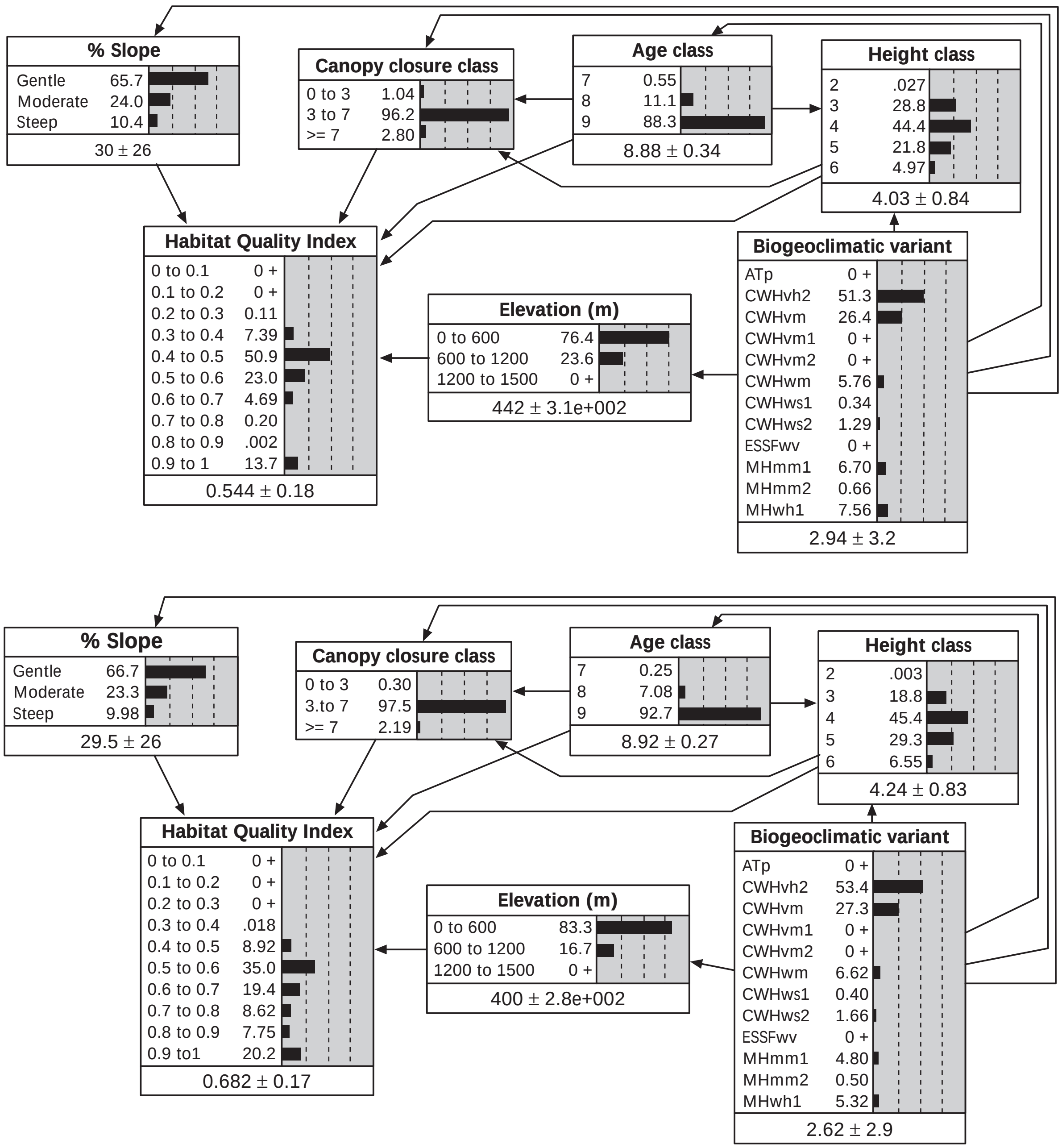

FIGURE A2.5 *Example scenarios of 500 000 ha (top) and 300 000 ha (bottom) for a nesting capacity of 3500 pairs (North Coast model). The horizontal bars in each node indicate the suggested proportion of the landscape in the indicated classes that will provide the 3500 nesting pairs. Arrows represent conditional dependencies (e.g., Height Class is partly correlated with Age Class). These are not unique solutions, but the* BBN *will not propose a solution that is not feasible. Note that for 300 000 ha to be sufficient, reliance on height-class 3 and higher-elevation areas had to diminish. The objective could not be met on less than 200 000 ha and then only if almost all of the better habitat types are retained.*

This BBN (Figure A3.1) is parameterized (via a case file) using the results of a stochastic population model developed in Excel. The BBN is used to weight the outcomes of the 89 000+ combinations of demographic and habitat parameter values that are projected in the Excel model. Using the Excel model directly to assess possible outcomes rapidly becomes intractable as the number of possible parameter values increases—the number of combinations increases geometrically with the number of parameters.

The model parameters (nodes) are:

Max. Nesting Capacity: The nesting population ceiling reached at the time selected in Years to Final K.

% Affected by Nesting Quality: The proportion of the nesting capacity subject to edge effects at time selected in Years to Final K.

Years to Final "K": Length of time to reach final Max. Nesting Capacity and % Affected by Nesting Quality.

Starting % Affected: The proportion of the nesting capacity subject to edge effects at the start of simulations.

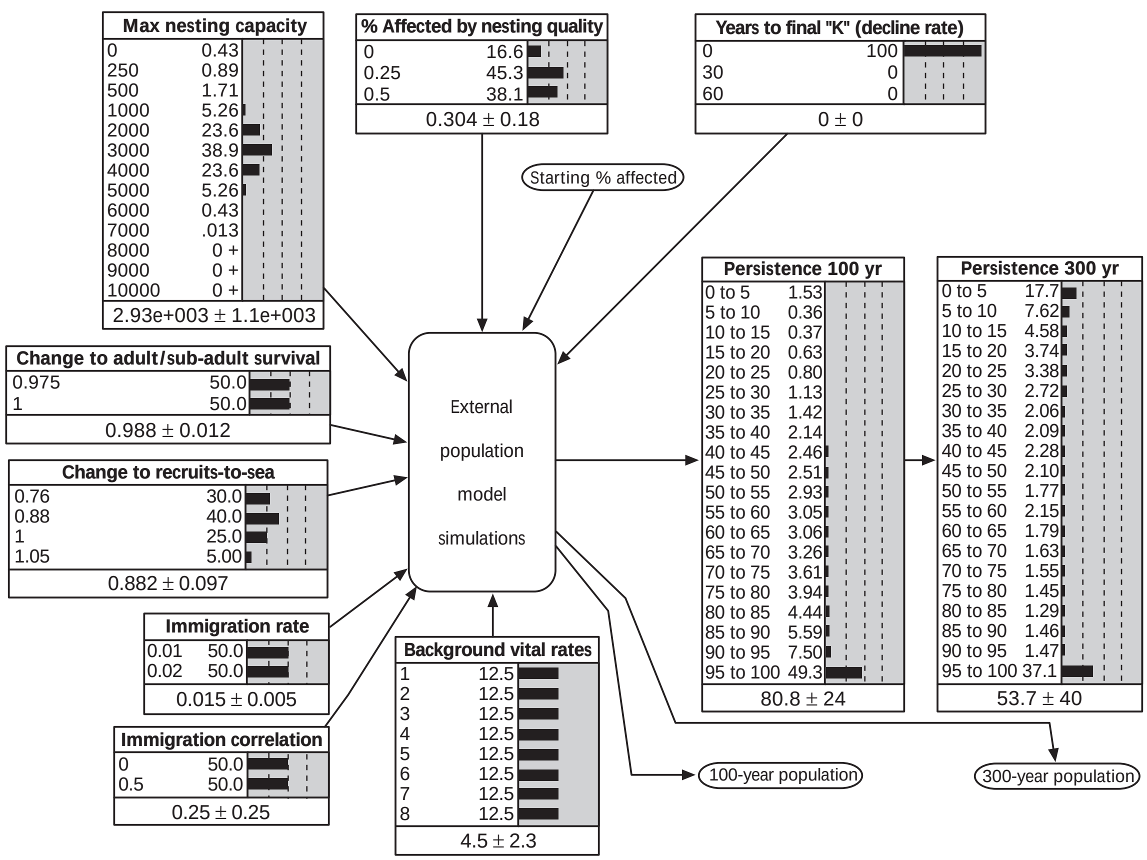

FIGURE A3.1 *Demography model BBN.*

Change to adult/sub-adult survival: Survival multiplier applied to the proportion of nesting capacity subject to edge.

Change to recruits-to-sea: Survival multiplier applied to the proportion of nesting capacity subject to edge effects.

Immigration rate: Annual input of immigrants as a proportion of the previous year sub-adult population.

Immigration correlation: Correlation of immigration rate with local population size. If this parameter is 0, there is no direct correlation with the previous year's population size, and the number of immigrants varies annually based on the sub-adult population. If 0.5, the number of immigrants is partly correlated with the previous year's population size using an auto-regression function (see later description of Excel model).

Background vital rates: Combinations of survivorship and fecundity assumptions (see later description of Excel model).

External population model simulations: The length of time to which 90% of the simulations persisted (the 90% persistence time) conditional on the states of other nodes.

Persistence 100 yrs and persistence 300 yrs: Proportion of simulations that remained at >50 adult females for at least 100 or 300 years, respectively.

100-year population and 300-year population: Median population size at 100 years and 300 years, respectively.

Structure of Excel Population Model

The Excel model is a simple birth pulse, pre-breeding season, age/stage structured population projection model (Figure A3.2). Each year in the model begins at the start of the breeding season (i.e., numbers in each stage are updated before the breeding season begins) and the time step is 1 year. Immigration links the local population to populations in other regions.

Each combination of input parameter values was simulated for 500 years, with 200 iterations to capture stochastic variation. For each scenario, the numbers of females in each age class are tracked for the length of the simulation and summary statistics are collected (means, medians, and SD for each realized population growth rate [λ], population size, length of time that populations persist, and vital rates for each age class). Also collected were separate statistics on the realized population size and λ during periods of habitat change and stability.

The primary output of the Excel model used in the BBN was the number of years to which 90% of the projected populations (iterated 200 times) persisted. We then express these as the probability of persisting to specified time periods (100 and 300 years).

Age/Stage Structure: The MAMU population was modelled as females only and assumed an equal sex ratio. Three life-stages are modelled: juveniles (~1 year old), which are previous-year recruits-to-sea that survive their first winter; sub-adults (2–4 years old); and adults. While ages of sub-adults were tracked, those of adults were not. The parameters shown in Figure A3.2 are defined as follows (see also the definitions of vital rates below, and values applied in Table A3.1):

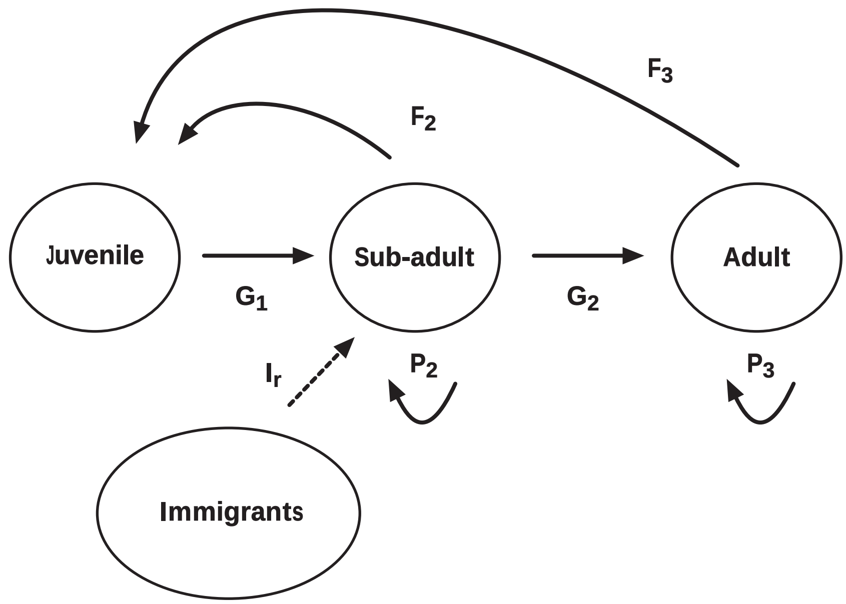

FIGURE A3.2 *Life cycle graph for Marbled Murrelets used in the Excel-based stochastic demography model. Solid circles are life stages for a local population; the dotted circle represents immigrants from other populations. See text for parameter definitions.*

G_1 Probability that a juvenile survives and grows into the sub-adult stage (calculated as the combined realized RS from sub-adults and adults that breed multiplied by realized S_j).

G_2 Probability that a sub-adult survives and grows into the adult stage. This probability is a function of realized S_s and the annual age-specific probability of maturing to an adult (see "Age at First Breeding" below).

P_2 Probability that a sub-adult survives and remains in the sub-adult stage. This probability is a function of realized S_s and 1- G_2: the annual age-specific probability of maturing to an adult.

P_3 Probability that an adult survives and remains in the adult stage. This probability is a function of realized S_a.

F_2 Realized fecundity (RS) from sub-adults that attempt to breed. Because few data exist to assess breeding success of sub-adults, we assume this is the same as adult RS.

F_3 Realized fecundity (RS) from adults that attempt to breed.

I_r Numbers of immigrants to the sub-adult stage.

Age at First Breeding: Age at first breeding was not fixed in our model. Cam et al. (2003) considered that the proportion of females that attempt to breed gradually increases from 5% of females in their second year to 80% at year 6. We simplified this to 0.05, 0.4, and 0.6 at ages 2, 3, and 4 years, respectively, and to 95% for 5+ years. After sub-adults first breed they are moved into the adult pool. Thus, we assume that the proportion of females remaining as sub-adults after 4 years of age is small (see Burger 2002; Cam et al. 2003) and consider these as breeding-age females. Long-term average proportion of sub-adults that breed each year, and the proportion of adults breeding each year are modelled with some stochastic variation (drawn from a normal distribution using the proportion breeding [from above] with an SD of 0.025).

TABLE A3.1 *State variables, parameters, and range of average values defined for the components of the Excel demographic model*

State variable type	Parameter	Symbol	Range of values [a]
Population			
Proportions breeding	Proportion of adult females breeding/year	Pa	0.95
	Proportion of sub-adult females breeding/year	Ps	0.5
Vital rates (fecundity and survivorship[b])	Long-term average at-sea fecundity (female offspring per adult breeding female)	RS	0.175–0.35
	Long-term average juvenile survival (before habitat or at-sea adjustment)	S_j	0.61–0.64
	Long-term average sub-adult survival (before habitat or at-sea adjustment)	S_s	0.76–0.82
	Long-term average adult survival (before habitat or at-sea adjustment)	S_a	0.88–0.92
	Correlation among annual variation in vital rates	VRc	0.5
Immigration	Immigration rate (per-capita proportion of females permanently immigrating into the breeding population) estimated as a proportion of N	Ir	1–2%
	Correlation of Ir with "outside" pool of females (i.e., not correlated with N)	Ic	0 or 0.5
Habitat	Edge effects on vital rates (multiplier of base rate)	E_{RS}	0.76–1.15
		E_{Ss}	0.975–1.0
		E_{Sa}	0.975–1.0

a Single values represent the long-term average value; a spread of values indicates that a range of long-term average values was applied. Realized annual values may be outside this range, depending on the amount of stochastic variation applied each year (see Table A3.4).

b This represents local survival for birds within the study area, and includes possible permanent emigration.

Immigration: Immigrants to the local population are assumed to be sub-adults. The number of immigrants is calculated in year 1 as a proportion (0.01 or 0.02) of the starting sub-adult population. If the Immigration Correlation parameter (Figure A3.1) is 0, then the number of immigrants is recalculated annually as in year 1 (i.e., using the appropriate proportion of previous-year sub-adults). If the Immigration Correlation is 0.5, then the number of immigrants is modified by correlation across years using auto-regression formulae (Halley and Kunin 1999). This correlation represents assumptions of synchrony of regional population fluctuations (immigration rates may be partially related to stochastic conditions outside the study population).

Because we are simulating across a range of initial population estimates within each management scenario, we are effectively sampling from an uncertain pool of immigrants.

Immigrants are allowed to breed in the year they immigrate into the population with the same probability as resident sub-adults.

Our small immigration rate was applied, in part, to compensate for a potential bias in survival rate estimates that also included an unknown amount of emigration (E. Cam, pers. comm.).

Annual Survivorship and Fecundity (Vital Rates): We applied eight combinations of the vital rates (local survivorship) for juveniles S_j, sub-adults S_s, and adults S_a, and recruits-to-sea (RS) (fecundity) for each stage. These scenarios represent uncertainty of future at-sea conditions (applied in the BBN in the node Background Vital Rates). These were expressed as probability distributions representing stochastic annual environmental variation. Details on how these combinations were chosen and applied are described in the Vital Rates Scenarios section.

These basic rates assume no on-shore habitat effects, but are modified in the BBN according to assumptions of density dependence (nesting capacity ceiling) and reduced survivorship due to edge effects (see Nesting Habitat below).

We assumed a constant modest correlation (correlation coefficient of 0.5) of vital rates both across age-classes, and years within an age-class (autocorrelation formulation described by Halley and Kunin 1999).

Nesting Habitat: In the Excel model, habitat was represented by a maximum nesting capacity and the proportion of that nesting capacity subject to edge effects:

1. Maximum nesting capacity. This was applied as a ceiling on the number of breeding females. If numbers of breeding-age females exceeded this ceiling, the excess was assumed not to breed but to be subject to the same survival rates as breeders. We modelled 12 levels of maximum nesting population: 250, 500, 1000, 2000… 10,000.
2. Percentage of nesting capacity subject to edge effects. We modelled three possible types of change in habitat configuration due to harvest policy: decrease in edge, no change, and increase in edge. To eliminate excessive numbers of scenarios, we limited our parameter sets of these combinations to five (Table A3.2). Effects of edge on populations were applied as multipliers of survival (recruits-to-sea, sub-adults, and adults).
3. Rate of change in nesting capacity and edge. We applied three strategies: an immediate application of the final nesting capacity (habitat held constant), an aggressive harvesting strategy (conversion of old-growth habitat to managed habitat in 30 years), and a slower rate (60 years).

The combinations of these strategies represented 180 nesting habitat scenarios.

TABLE A3.2 *Components of habitat change and ranges of values used in the habitat change scenarios*

Type of habitat change	Values		
Maximum no. of nesting females remaining after harvesting	**12 levels: 250, 500, 1000, 2000…,10 000**		
Percentage of edge in nesting habitat	Initial (%)	Final (%)	Interpretation
	25	0	Managed; mod. decrease
	0	0	Unmanaged; no change
	0	25	Unmanaged; mod. increase
	0	50	Unmanaged; high increase
	25	50	Managed; mod. increase
Rate of change in nesting habitat quality	0, 30 years; 60 years		

Vital Rate Scenarios

Central to modelling the demography of MAMU are the stochastic vital rates representing recruitment and survivorship of each age/stage, along with their associated sources of variation (including measurement error and environmental variation). There is only one British Columbia study of MAMU demography (Cam et al. 2003), and we have no way of forecasting future conditions at sea. We therefore took the approach of applying a high degree of uncertainty about future demography, represented by eight vital rate scenarios (Background Vital Rates node in the BBN).

To devise the scenarios, we first developed four sets of long-term average parameter values based on our survey of the literature and consultations with MAMU biologists. These parameter sets describe the following general demographic scenarios about the province's MAMU populations under stable habitat conditions (see also Table A3.3):

DS_1 British Columbia populations have high productivity (RS), but poor survivorship in all stages that use the ocean (S_j-S_a). To model this hypothesis, we assumed that British Columbia populations: (1) exhibit local survivorship rates similar to the midpoint values for those rates assumed by Beissinger and Nur (1997) (which are known to be low when compared with current mark-recapture data from British Columbia); and (2) lead to declining populations in the long term. We set recruits-to-sea (representing fecundity) to the highest average value that has so far been inferred from provincial data (Burger 2002).

DS_2 British Columbia populations have moderate productivity (RS) and moderate survivorship in all stages that use the ocean (S_j-S_a). To model this hypothesis, we assumed average local survivorship rates intermediate between those of DS_1 and DS_{3-4}. We set at-sea fecundity to a value that is approximately equal to the currently accepted average value for provincial data obtained from Desolation Sound (Burger 2002).

DS_3 British Columbia populations have low productivity (RS) and good survivorship in all stages that use the ocean (S_j-S_a). We assumed that local survivorship rates for adults are well within the range of those obtained from mark-recapture data from Desolation Sound (E. Cam, pers. comm.), although they are not the highest reported values in the literature. We set at-sea fecundity to a value representative of the low range of currently estimated fecundity estimates for British Columbia (Burger 2002).

DS_4 British Columbia populations have good productivity (RS) and good survivorship in all stages that use the ocean (S_j-S_a). We assumed local survivorship rates for adults as in DS_3, and RS be to the value used in DS_1.

TABLE A3.3 *Long-term means for the base vital rates applied to the four general demographic scenarios used to simulate population dynamics. Codes are: S_a=adult survival; S_s=sub-adult survival; S_j=juvenile survival; RS=recruits-to-sea survival (at-sea fecundity). Sources are given in the text.*

Demographic scenario	S_a	S_s	S_j	RS
DS_1	0.88	0.76	0.61	0.35
DS_2	0.90	0.78	0.61	0.25
DS_3	0.92	0.817	0.64	0.175
DS_4	0.92	0.817	0.64	0.35

Empirical survivorship and recruitment values for MAMU have been obtained from different sampling methods (e.g., AHY:HY ratios in fall censuses; mark recapture). Even the best current estimates are difficult to transfer directly to an explicit population model because of unknown effects of emigration and immigration and short time series (E. Cam, pers. comm.). Consequently, we used a precautionary approach to parameter determination.

Table A3.3 shows the long-term means of the parameter values from the distributions representing each demographic scenario before adjustment by habitat effects or environmental variation. The values chosen for the long-term means are neither at the lowest possible value that could be used (e.g., $S_a = 0.83$; Beissinger and Nur 1997, or the highest ($S_a = 0.96$; E. Cam et al. 2003).

The next step was parameterizing the magnitude of annual environmental variation. Few estimates exist of typical ranges of such variation in long-lived vertebrates (J. Clobert, pers. comm., for seabirds; but see Gaillard et al. 1998 for large ungulates). Field estimates often confound sampling errors with true year-to-year variation unless methods appropriately partition the contributing sources of variation (e.g., Burnham et al. 1987).

General expert opinion is that a 10% coefficient of variation (CV) for vital rates due to annual environmental fluctuations is probably low and >20–25% is probably high. We therefore modelled each demographic scenario above under two regimes of stochastic environmental variation: lower (~ 14% CV), and higher (~ 22% CV). The distributions of annual vital rates were then represented as skewed Beta distributions with shorter or longer tails to represent catastrophes (e.g., extreme events on shore or at sea). The peaks of the distributions were set at the values in Table A3.3.

We did not model catastrophes, but took the view that they are part of the survivorship distributions (Caughley 1994). As Boyce et al. (2001) put it, there was "nothing to persuade us that catastrophes are other than an arbitrary collection of population declines singled out solely on the basis of magnitude." Therefore we interpret such distributions as capturing the possibility of infrequent but severe declines in survivorship as could be caused by offshore oil spills or sudden declines in prey availability. Combining these two ranges of environmental variation with the four basic demographic scenarios yielded the eight demographic scenarios used in the analysis (Table A3.4, Figure A3.3).

Peak and range for each vital rate are shown in Tables A3.3 and A3.4.

The principal sources from which we obtained the quantitative data we used to create our demographic model parameters are listed below. Full citations for the references are provided in the "Literature Cited."

- Clayoquot Sound (Burger 2002)
- Central Coast (Schroeder et al. 1998)
- Unpublished data from several sources, expert opinion (Burger 2002)
- Breeding chronology – Desolation Sound (Lougheed 2000)
- Mark-recapture and radio telemetry – Desolation Sound (Cam et al. 2003)
- Survivorship and reproductive success – PNW (Beissinger and Nur 1997)
- Dispersal data – Desolation Sound (Cam et al. 2003)
- Dispersal in other seabirds (kittiwakes: Danchin and Cam 2002; roseate terns: Lebreton et al. 2003)

TABLE A3.4 *90% range of values for each vital rate used for the demographic scenarios including environmental variation*

Demographic scenario	S_a	S_s	S_j	RS
High environmental variation				
DS_1	0.69–0.95	0.59–0.82	0.48–0.65	0.24–0.40
DS_2	0.70–0.96	0.61–0.84	0.48–0.65	0.17–0.28
DS_3	0.71–0.98	0.64–0.88	0.50–0.69	0.12–0.19
DS_4	0.71–0.98	0.64–0.88	0.50–0.69	0.24–0.40
Low environmental variation				
DS_1	0.76–0.93	0.67–0.83	0.52–0.65	0.27–0.39
DS_2	0.77–0.95	0.67–0.83	0.52–0.65	0.19–0.28
DS_3	0.78–0.98	0.70–0.87	0.55–0.68	0.13–0.19
DS_4	0.78–0.98	0.70–0.87	0.55–0.68	0.27–0.39

Additional consultation with members of the CMMRT and other population ecologists familiar with the dynamics of long-lived vertebrates (e.g., S. Beissinger, J. Clobert) were used to supplement the primary data sources listed here.

Other sources containing parameter estimates or other data we used include:

Arcese and Sutherland 2001
Cooke 1999
Drever et al. 1998
Hooper 2001
Hull 1999
Jones and Manley 2001
Manley 1999
Manley et al. 1999
Mather and Chatwin 2001
Nelson 1997

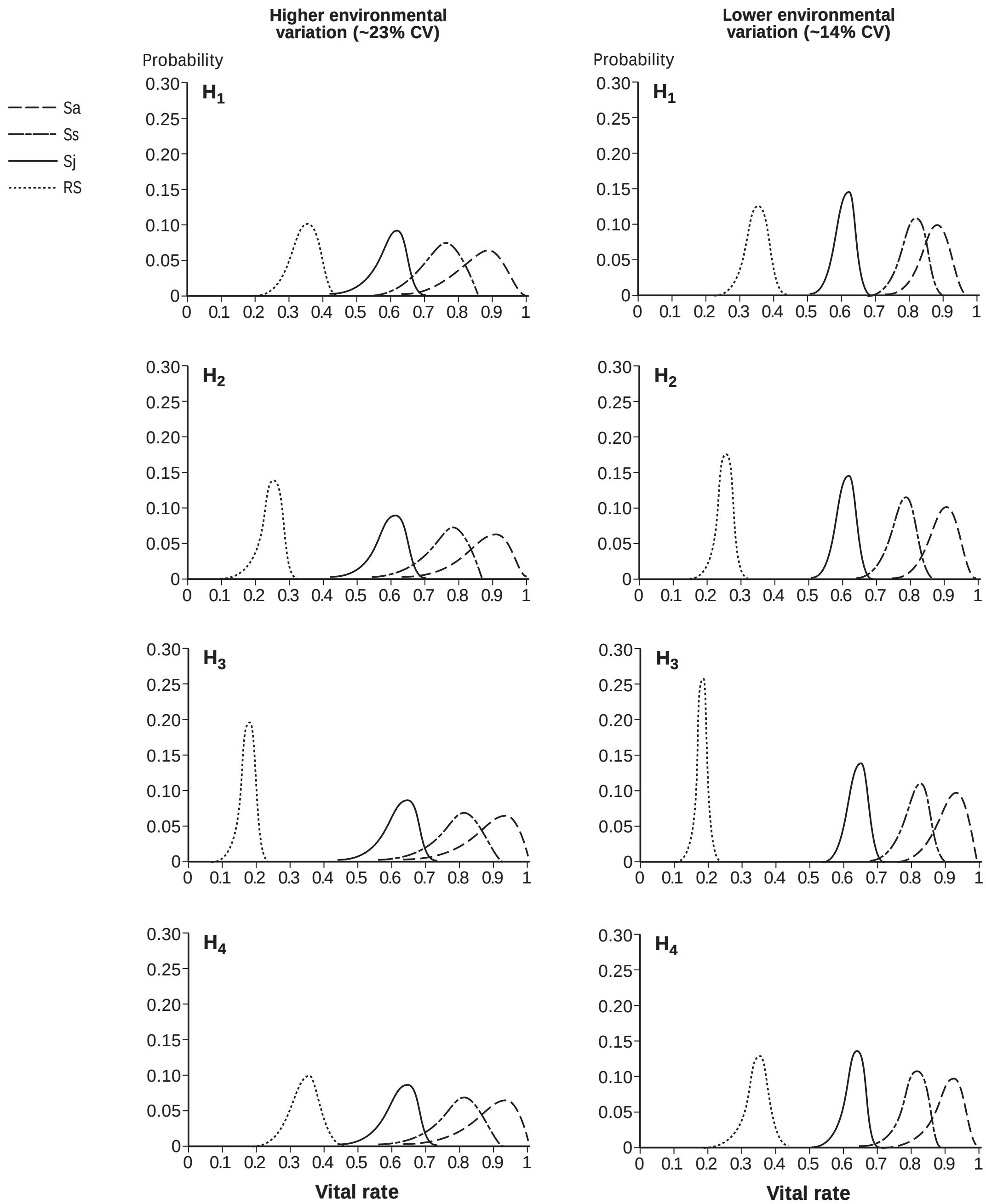

FIGURE A3.3 *Probability distributions for the vital rates used in the demography model.*

As an illustration of applying risk assessment in the context of decision-making, we used a Bayesian decision model (Figure A4.1) to examine the question: "How much area of productive forest in the operable (suitable for timber harvesting) landbase would optimally be retained as MAMU habitat, given varying assumptions of habitat quality, timber-harvesting operability, and decision emphasis of MAMU vs. timber?"

Because of uncertainty in the model, each potential management decision has a range of possible outcomes for both murrelet persistence and timber value. By explicitly incorporating that uncertainty, decision analysis helps identify the most effective trade-offs based on the evidence in the model and the management emphasis.

In our example, the total size of the hypothetical region is held constant (600 000 ha) while the proportion of MAMU habitat otherwise excluded from timber harvesting is varied from 10 to 90%.

Habitat quality of additional areas chosen from the operable landbase is assumed to be a decreasing function of the proportion preserved—that is, we assumed that higher-quality habitat will be preserved initially, but, as the proportion increases, the average habitat quality will be lower. If the entire landbase is preserved for MAMU, the overall habitat quality (combining the potentially harvestable landbase and landbase excluded from harvesting) approximates the mean densities estimated from radar studies.

For timber, we assumed that timber value decreased linearly with amount of land base, subject to uncertainty represented by scatter around that linear relationship. Thus, timber utility was the proportion of the operable landbase that remains available for harvesting.

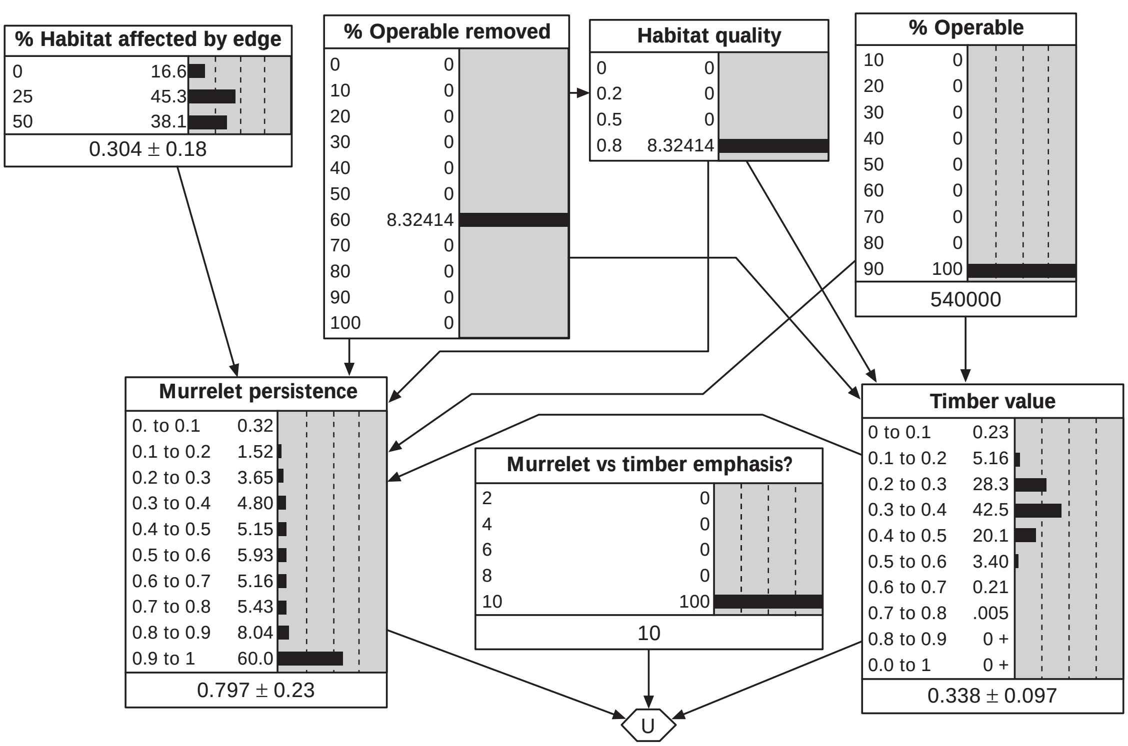

FIGURE A4.1 *Hypothetical decision analysis model.*

The decision model estimates the persistence confidence and timber value of possible decisions (% of operable landbase to preserve for MAMU and habitat quality). It then calculates the joint utility of those two values given varying priorities assigned to MAMU vs. timber, and indicates the "optimal" solution that maximizes joint utility for a given weighting of MAMU utility vs. timber utility.

Because different stakeholders are likely to weight a decision differently (because of the varying utility to them of MAMU conservation vs. timber harvest), we applied a range of MAMU emphasis. These are equivalent to considering degree of risk aversion: a high MAMU emphasis strategy is relatively risk-averse to loss of MAMU populations, and a high timber emphasis is risk-averse to lost economic value. Note that even with a high MAMU emphasis, timber utility is considered (but with less weight). As expected, the amount of landbase to reserve for MAMU increases with MAMU emphasis and percentage of potential habitat that is operable (Figure A4.2).

The model indicates optimal solution (setting aside 60% of operable landbase) when applying a 10:1 emphasis of MAMU persistence over reduced timber supply for a landscape that is 90% operable.

The variables in the decision model are:

- ***% Habitat Affected by Edge:*** The percentage of nesting habitat within 50 m of forest <40 years of age.
- ***% Operable Removed:*** Percentage of the otherwise operable forest that the model selects for retention as MAMU habitat.
- ***Habitat Quality:*** The mean Habitat Quality Index of otherwise operable habitat retained for MAMU.
- ***% Operable:*** The percentage of MAMU habitat that is also operable for timber harvesting.
- ***Murrelet Persistence:*** The resulting persistence probability distribution for a selected decision.
- ***Timber Value:*** The proportion of operable timber retained for a selected decision.
- ***Murrelet vs. Timber Emphasis:*** The relative weight put on MAMU persistence probability vs. timber value. A value of 10 m, for example, means that each percentage increase in persistence is weighted 10 × each percentage increase in timber value.

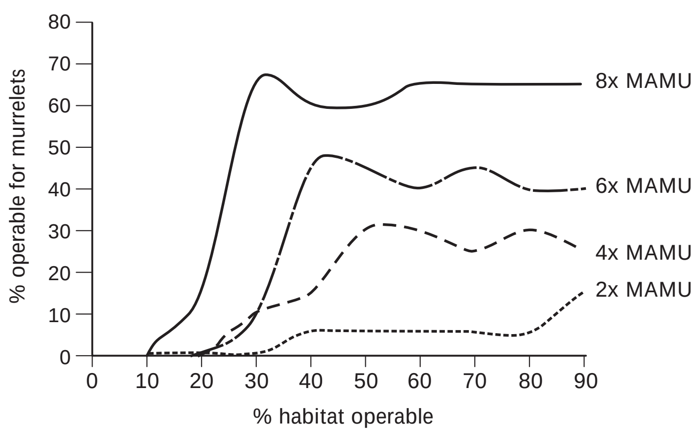

FIGURE A4.2 *Decision optimization simulations. The y-axis represents the percentage of the potential operable landbase to set aside for MAMU that maximizes the joint MAMU:timber utility function.*

After-hatching-year age class (AHY) All birds more than 1 year old.

At-sea fecundity Number of young produced per breeding female as measured when fledged young have reached the sea.

BBN Bayesian belief network. Represented graphically by boxes (nodes) and arrows (links) depicting ecological relationships that influence the outcome of interest (e.g., probability of persistence). Within the BBN, relationships between states of linked nodes are expressed in Conditional Probability Tables (CPTs) and/or probability equations.

BEC Biogeoclimatic ecosystem classification.

Belief The plausibility of a variable being a particular state or value, or an outcome (expressed as a probability) in a Bayesian belief network model.

Biogeoclimatic subzones and variants Subzones and subzone variants of the Biogeoclimatic Ecosystem Classification.

By-catch Unintended captures of non-target species in fisheries.

CMMRT Canadian Marbled Murrelet Recovery Team.

COSEWIC Committee on the Status of Endangered Wildlife in Canada, a joint federal-provincial body that recommends listing of endangered and threatened species in Canada.

CPT Conditional probability table in Bayesian belief network models. Represents the probability of a variable (node) being a particular state/value, dependent on states/values of variables feeding into it.

CV Coefficient of variation (standard deviation / mean).

CWS Canadian Wildlife Service (Environment Canada).

Demography The study of population characteristics such as survival, reproduction, and population growth rate.

Edge effects The influence of proximity to the boundary of two or more dissimilar habitats. In this analysis, murrelet habitat within 50 m of forest <40 years of age.

Expected value In Bayesian belief network nodes for quantitative variables, the expected value is the mean of the probability distribution of the state values. For our persistence results, it is the proportion of all simulations (weighted by input parameter beliefs) that persisted.

Extinction The global loss of a species.

Extirpation The loss of a species in a defined geographic area.

Fecundity The annual number of female offspring that reach independence (fledge) per female of breeding age.

Habitat-linked PVA Population Viability Analysis (PVA) in which survival and reproduction are determined by habitat composition.

Habitat Quality Index (HQI) A score from 0 to 1 representing relative habitat value.

Hatch-year age class (HY) Bird less than 1 year old (i.e., juvenile).

HY:AHY ratio Ratio of birds in hatch-year (juvenile) plumage to birds in alternate plumage recorded during at-sea surveys (see Hatch-year age class and After-hatching-year age class) and used as an index of breeding productivity.

Immature Bird that has not yet attempted breeding.

Juvenile A bird within its first year of life.

Lambda (λ) Symbol used as the measure of the annual rate of population growth. If λ equals 1, the population is stable; if λ is less than 1, the population is declining; and if λ is greater than 1, the population is increasing.

Landscape unit (LU) Usually 30 000–150 000 ha in size and covering one or more watersheds.

MAMU Marbled Murrelet (*Brachyramphus marmoratus*).

Mature bird Bird that has attempted breeding.

Nest fecundity Fecundity measured at the point of the fledgling's departure from the nest (see also Fecundity and At-sea fecundity).

Nesting capacity Maximum number of nesting pairs the forest habitat will support.

Nesting success The number of fledglings per pair of adult birds that attempt breeding.

Node Variable in a Bayesian belief network.

Persistence The ability of murrelet populations to remain above a defined population size threshold.

Population Viability Analysis (PVA) A set of analytical and modelling approaches for assessing the risk of loss (including extinction) of a population.

Recruits-to-sea (RS) Recruits-to-sea (RS) is an estimate of the number of fledglings reaching the ocean. It combines fecundity and nesting success estimates. See Burger (2002) for methods used to estimate RS.

Resilience Outcome (i.e., persistence probability) is insensitive to uncertainties in the analysis.

Risk The probability that an undesirable outcome could occur.

Robust A robust management strategy is one in which the outcome (e.g., population persistence) is insensitive to uncertainties such as seasonal fluctuations in survival.

SD Standard deviation.

SE Standard error (standard deviation of the mean).

Stochastic When a variable value is drawn randomly from a probability distribution of possible values rather than being a set value (deterministic).

Utility Expression of relative value of a decision.

Variance reduction In the context of a Bayesian belief network, the reduction in variance of the expected value of a variable of interest, given value weightings for other variables influencing it. Used as a measure of relative sensitivity of variables in the network. The higher the variance reduction, the more influence that variable has on the outcome of interest.

Vital rates Key demographic rates of survival and reproduction.