A population-viability-based risk assessment of Marbled Murrelet nesting habitat policy in British Columbia[1]

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Abstract: The Marbled Murrelet (*Brachyramphus marmoratus* Gmelin) is a small threatened seabird of the Pacific coast of North America. Through simulation modelling we varied the long-term minimum amounts and quality (nesting density) of old-forest nesting habitat to examine effects on murrelet population viability, our measure of population resilience. Applying diffusion approximations we estimated population longevity and persistence probability under uncertainties of at-sea demography and onshore edge effects affecting nesting success, time scale, spatial scale, and subpopulation structure. We cast our analysis in a Bayesian belief and decision network framework. We also applied the framework to spatially explicit land-use and murrelet inventory data for the northern mainland region of the British Columbia coast. We found a diminishing expected value of persistence probability (EVP), for a single independent population, below a nesting capacity of ≈5000 nesting pairs (≈15 000 birds), accelerating below 2000 pairs. A strategy of multiple semi-independent subpopulations provided a higher joint EVP across a wide range of total nesting capacity. There was little improvement in EVP, for any number of subpopulations, above 10 000 – 12 000 pairs (≈36 000 birds, 45%–60% of coastwide population estimate in 2001). Depending on estimates of nesting density, 12 000 pairs would require between 0.6 and 1.2 million ha of potential old-forest nesting habitat.

Résumé : L’alque marbrée (*Brachyramphus marmoratus* Gmelin) est un petit oiseau marin qui niche dans les vieilles forêts de la côte du Pacifique, en Amérique du Nord. Il est menacé de disparition. Nous avons examiné, à l’aide de modèles de simulation, les effets à long terme de la variation des quantités minimales et de la qualité (densité de nids) de l’habitat de nidification sur la viabilité des populations d’alques; notre mesure de la résilience des populations. En appliquant des approximations par diffusion, nous avons estimé la longévité des populations et leur probabilité de persistance, dans des conditions d’incertitude en ce qui a trait à des effets démographiques en mer et des effets de bordure près des rivages qui peuvent influencer le succès de nidification, la durée, l’échelle spatiale et la structure des sous-populations. Nous avons campé notre analyse dans un cadre de réseau de bayésien d’appréciation et de décision. Nous avons aussi appliqué ce cadre à des données spatialement explicites d’utilisation des terres et d’inventaire des alques dans la région continentale nord de la côte de la Colombie-Britannique. Nous avons trouvé que la valeur espérée de la probabilité de persistance (VEP) diminuait, pour une population indépendante, lorsque la capacité de nidification passait sous les ≈5000 couples nicheurs (≈15 000 oiseaux), et que la diminution s’accélérait lorsque la capacité arrivait sous les 2000 couples. Une stratégie considérant plusieurs sous-populations semi-indépendantes menait à une VEP combinée plus élevée, et ce pour un large éventail de capacités totales de nidification. Il y avait peu d’amélioration de la VEP au dessus de 10 000 – 12 000 couples (≈36 000 oiseaux, 45 % à 60 % de toute la population côtière selon des estimations de 2001), et ce peu importe le nombre de sous-populations. Dépendamment des estimations de la densité de nidification, 12 000 couples auraient besoin de 0,6 à 1,2 million d’hectares d’habitat potentiel de nidification en vieille forêt.

[Traduit par la Rédaction]

Introduction

The Marbled Murrelet (*Brachyramphus marmoratus* Gmelin) is a small sea bird (family Alcidae) of the Pacific coast of North America. Unlike most alcids that are colonial cliff nesters, this species has a unique strategy of dispersed nesting at low densities ranging as far inland as 70 km of (but usually within 30 km from) the coast. Nests occur pre-

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dominantly on large mossy limbs in the mid to upper canopy of old trees (Burger 2002).[3] During nesting, both parents forage on the ocean and commute daily to incubate or bring food to the young. Studies of the number of murrelets commuting inland (Burger 2001; Cooper et al. 2001; Burger et al. 2004), as well as the distribution of nests located using radio-tagging (Zharikov et al. 2006), suggest an approximately linear relationship of murrelet abundance with the amount of mature and old forest.

While the Marbled Murrelet is a relatively abundant and widespread species along the coast of British Columbia (Yen et al. 2004; Burger et al. 2004), it is listed as threatened under the Canadian Species at Risk Act (Government of Canada 2005), primarily because of continuing removal of old-growth forest nesting habitat (Burger 2002). This conflict with commercial forestry has been the subject of considerable controversy (e.g., Forest Practices Board 2004). A key conservation question, therefore, concerns the amount of nesting habitat necessary to sustain the species.

Risk assessment (Canadian Standards Association 1991) is the process of identifying hazards (forest harvesting in this case), estimating the probability of potential outcomes (murrelet nesting carrying capacity, population size, and distribution), and determining the consequences of alternative management decisions (concerning social objectives, population viability or resilience, legal listing). Here we consider only one of these consequences, population viability or resilience. Evaluating the acceptability of a consequence and the costs of avoiding it (risk analysis) and then selecting a course of action (a nesting-habitat policy in this case) invokes value-based judgements beyond the scope of this paper.

Using population viability assessment (PVA) modelling techniques, we considered the implications for murrelet viability of varying the amount and quality (nesting density and edge effects) of nesting habitat. We considered three generalized spatial scales representing (1) the entire British Columbia coast, (2) conservation regions proposed by the Canadian Marbled Murrelet Recovery Team (CMMRT) (2003), and (3) subregions within these conservation regions. We also applied the methods to spatially explicit land-use and murrelet inventory data for the northern mainland coast conservation region.

PVA has become an accepted approach to evaluating risk to species, and commonly employs stochastic population models to estimate population longevity (mean period of persistence), which is often converted to persistence probability over some time span of specific decision interest (Grimm and Wissell 2004; Horoshi et al. 2000). Challenges in applying PVA include appropriately structuring and parameterizing the models to avoid low precision and possible bias of estimates (Beissinger and Westphal 1998; Reed et al. 2002). Additionally, the decision as to what persistence probability, at what time scale, is deemed acceptable is subjective (Regan et al. 2002). Thus, PVA is often best used, as in this analysis, to rank hazards, assess the relative effect of policy choices, and seek policies that provide a high persistence probability despite uncertainty (Boyce et al. 2001; Dreschler et al. 2003; McCarthy et al. 2003; Horoshi et al. 2000).

We considered the estimated persistence probability to be an indicator of population resilience — the ability of a population to withstand environmental variability or recover from sustained periods of poor survival and reproduction. For Marbled Murrelets, such periods can occur as a result of temporal or cyclical fluctuations in marine conditions that affect foraging, fluctuating nesting success onshore because of forest management actions, and perhaps from rare catastrophes either at sea or onshore (Beissinger 1995; Gaston and Smith 2001; Burger 2002; Peery et al. 2004*b*). A higher nesting carrying capacity (the number of nesting pairs the forest can support) can improve viability by allowing populations to increase in size when demographic conditions are favourable, thus providing a cushion for more frequent or sustained declines due to poor survivorship or reproduction rates. A robust (resilient) nesting-habitat policy should be insensitive to the uncertainties of key assumptions in the analysis, thus indicating a high intrinsic tendency of the population to persist (Grimm and Wissell 2004).

Building and parameterizing the assessment model

We cast our analysis in a Bayesian belief network (BBN) framework (Reckhow 1999; Marcot et al. 2001; Marcot et al. 2006) because it is a flexible, transparent, and structured way of integrating biological data, expert opinion, and simulation-model results. It also allows explicit and flexible inclusion of uncertainties into analysis relationships, parameter values, and outcomes (Regan et al. 2002).

BBNs are represented by a diagram consisting of boxes and arrows (nodes and links) representing functional relationships among variables (Fig. 1). Each node assumes one or more user-defined states (categorical or numeric) and has a table that expresses the probability of each state either as prior distributions or as conditional on the probability of each state for the nodes feeding into it (the parent nodes). The probability tables can be specified directly from case files of empirical or simulated data, entered manually, or derived from a mathematical function. Belief weightings can be assigned to input parameter values (nodes with no parents) and to relationships among parameters (e.g., linear vs. nonlinear relationship of habitat quality to nesting density). Several authors (Reckhow 1999; Marcot et al. 2001; Riemen et al. 2001; Marcot et al. 2006) provide background and examples of using BBNs to solve natural resource management problems. We used the Netica® BBN software (version 2.17; Norsys Software Corporation, Vancouver, British Columbia).

The results of our murrelet population model (e.g., “persistence class” and “combined-persistence class” nodes in Fig. 1) are expressed as possible states (population persistence probability values), each with a “belief” probability

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[3] C. McShane, T. Hamer, H. Carter, G. Swartzman, V. Friesen, D. Ainley, R. Tressler, K. Nelson, A. Burger, L. Spear, T. Monagen, R. Martin, L. Henkel, K. Prindle, C. Strong, and J. Keany. 2004. Evaluation report for the 5 year status review of the Marbled Murrelet in Washington, Oregon, and California [online]. Unpublished report prepared for the US Fish and Wildlife Service, Region 1, Portland, Ore. by EDAW, Inc., Seattle, Wash. Available from http://www.earthjustice.org/backgrounder/display.html?ID = 100 [cited June 21 2005].

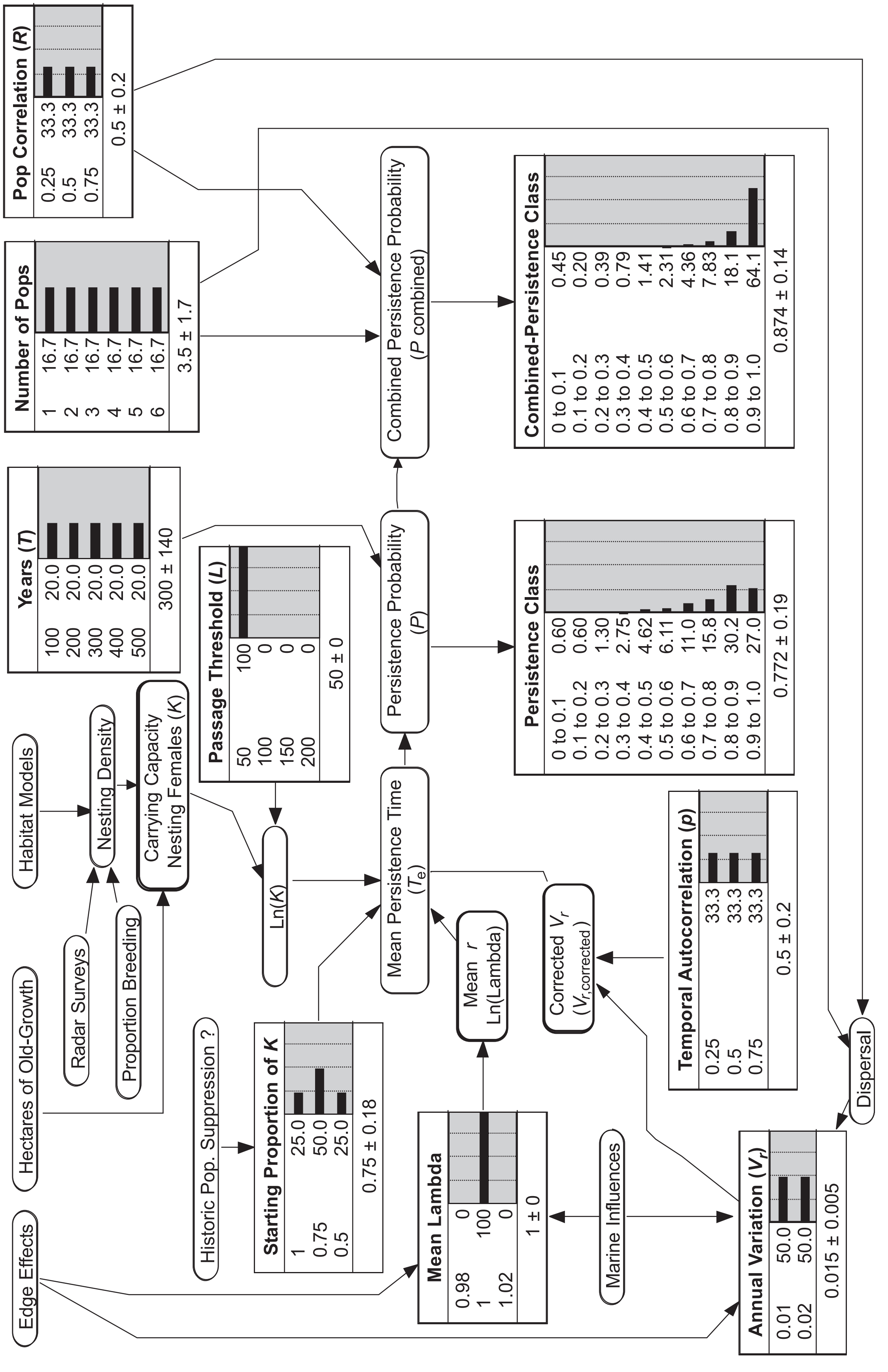

Fig. 1. Risk assessment presented as a Bayesian belief network. The results shown are with equal weighting of all state values for hectares of old growth and nesting density nodes.

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resulting from the weighting of input values and the interaction of variables through the network. With many input parameters, each with multiple values, the output (a probability distribution for each input combination) can become overwhelming and some form of summary statistic is needed. Four summary metrics produced by our BBN model were (1) the outcome with the highest belief probability, (2) the probability of exceeding a desired threshold value, (3) the expected value, and (4) the variance or standard deviation of the expected value.

We primarily present the expected value of persistence probability (EVP), which Holmes (2004) described as follows: "The expected value of extinction [persistence] multiplies the probability of extinction [persistence] given a particular set of true parameters by the probability of those parameters (specified by the posterior probability distribution)". The expected value can also be interpreted as the proportion of all population trajectories projected to remain above some minimum threshold value, subject to the weighting given to alternative input parameter values. A higher EVP indicates greater policy resilience. We conducted an analysis of the sensitivity of persistence probability to findings in other key input nodes, based on variance reduction (Marcot et al. 2006). In assessments of the sensitivity effect of varying the state value of a particular node, the state values of other nodes were weighted by their probabilities (beliefs).

Habitat and policy inputs

We considered five policy inputs: (1) the amount of old-growth nesting habitat to retain over the long term, (2) the quality of that nesting habitat in terms of average potential nesting density (independent of marine conditions), (3) the quality of that habitat in terms of logging-created forest edge potentially affecting reproductive success through nest predation, (4) the number of subpopulations, and (5) the time scale of the assessment (how far we project it into the future).

We also applied the BBN to spatial data for a ~2 million ha landscape on the northern coast of British Columbia, one of six proposed murrelet conservation regions in British Columbia (CMMRT 2003). We assumed that all the area deemed available for timber harvesting (timber harvesting land base (THLB)) as of 2002 (British Columbia Ministry of Forests and Range) would eventually be unsuitable for murrelets. Although the delineation of THLB is potentially subject to change, we use it as an approximation of potential loss of nesting habitat. The remaining forest outside the THLB that was >140 years old and ≥ 28.8 m in height was considered potential habitat (Burger et al. 2004, p. 4).

The amount of habitat ("hectares of old growth" node) was combined with the "nesting density" values to determine the ceiling on the number of nesting pairs ("carrying capacity nesting females" (*K*) node) in the population model. For the policy assessment, *K* is a deterministic product of the proposed amount of habitat and nesting density, assuming that habitat was stabilized at that level. Monte Carlo simulations (Steventon et al. 2003) showed that the trajectory of decline to the long-term policy level had only a minor influence on persistence estimates, provided the period of decline was short relative to the persistence calculation time horizon. If the decline is prolonged, then our estimates will underestimate persistence probability from the present.

For the northern mainland coast example, the amount of potential habitat was fixed on the basis of the mapped definition of the THLB, but nesting density and proportion representing breeding females were applied as probability distributions (representing uncertainty), resulting in *K* also being a probability distribution. While the abundance of murrelets commuting inland is believed to be an approximately linear function of the amount of older forest (Burger 2001), estimates of nesting density (or the probability of encountering a nesting murrelet at the stand scale) depends on how we define habitat (Burger et al. 2004) and is believed to vary with the type and location of forest retained. Thus, potential density is expected to vary with the type of forest reserved from harvest.

The range of average nesting densities we applied (0.002–0.03 pairs/ha) in our policy scenarios was informed by estimates of the number of murrelets commuting inland during the nesting season to defined catchments ("radar surveys" node) estimated using marine radar (Burger et al. 2004), and the estimated proportion of those commuting birds that represented nesting females ("proportion breeding" node). The mean density of commuting birds by region (Burger et al. 2004) ranged from 0.054 to 0.091/ha when the following definition of potential nesting habitat requirements is applied: forest age ≥ 140 years, average stand height ≥ 19.5 m, and distance to ocean ≤ 50 km. For the landscape of the northern mainland coast example we used a region-specific mean density estimate of 0.054/ha (SE = 0.008).

We applied a range of 0.25–0.45 for the proportion breeding node, implemented as a truncated normal probability distribution with a mean of 0.35 and a standard deviation of 0.05. Bradley et al. (2002), working in southern British Columbia, and Peery et al. (2004*a*), working in northern California, examined the physiological breeding status of murrelets that were also monitored for inland commuting using radiotelemetry. While substantial variation within and between years and between the sexes was reported, the data were consistent with a typical proportion of ≈35% of the incoming birds being breeding females. Since both parents attend the nest, if all the commuting birds were breeding, the proportion of breeding females would be 0.5. However, some nonbreeders (Bradley et al. 2002; Peery et al. 2004*a*) or failed breeders (Hebert et al. 2003) also commute inland, lowering the expected proportion.

An increase in nest predation has been hypothesized with the creation of high-contrast forest edges (typically defined as within 50 m of forest <40 years old) by logging (summarized in Burger 2002),[3] and with the increase in populations of corvids (crows, ravens, and jays) associated with human habitation (Marzluff et al. 2000). Peery et al. (2004*b*) deduced that nest predation, in combination with a lack of at-sea food availability, limited (at least during the 2 years of their study) a small population in California restricted to nesting in close proximity to areas of human use. Marzluff et al. (2000), in an extensive artificial-nest study in Washington State, also found that proximity to human habitation was the dominant factor explaining increased predation risk. Marzluff et al. (2000) also found, however, that landscapes with substantial mature second-growth forest had lower overall predation rates than old-growth-dominated landscapes. In southern British Columbia, Zharikov et al. (2006), using radio-tagged murrelets, found that nest survivorship was not reduced by old-forest fragmentation in a heavily logged landscape compared with a lightly logged landscape, both with little human habitation. Cam et al. (2003), working with the same radio-tagged sample that Zharikov et al. (2006) used in the heavily logged landscape, reported generally good demographic performance of murrelets. The specific demographic estimates, however, were imprecise and Cam et al. (2003) could not separate at-sea and onshore effects. The proportion of nesting habitat near high-contrast edge will vary with the rate and pattern of logging, as well as temporally (Wallin et al. 1994).

It was hypothesized that nest-predation effects, if they are real, in the BBN will possibly influence both the long-term mean population trajectory (“mean lambda” and r nodes and its variability (“annual variation” (V_r) node). At the large spatial scales we consider here, however, a relatively small proportion of the nesting habitat is likely subject to such effects at any given time. Steventon et al. (2003; Table 1) found that EVP was insensitive to hypothesized increases (and trajectory) in nest predation of the magnitude they deemed plausible (≤50% of nests exposed, ≤24% reduction in nesting success, and ≤2.5% reduction in survival of subadults and adults). High simulated variability of the population growth rate, such as we also apply here, overwhelmed the additional influence of potential edge effects. As we had no means of explicitly calculating the amount of edge for the varying policy inputs of amount of nesting habitat, and given the ambiguity around the existence and magnitude of edge impacts and the experience of Steventon et al. (2003), we included edge effects when setting conservative demographic parameter values in the population model (see the following section).

Stochastic population model

We used the diffusion approximation (DA) equations of Foley (1994) to estimate potential population longevity (mean length of time until population extinction, T_e), which is then converted to probability of persistence ($P(T)$), that is, the estimated proportion of populations persisting at various fixed time intervals (T). DA is an analytical method that considers population trajectories as a stochastic process described by a mean and variance of annual population transitions (μ_r and V_r, respectively, for the instantaneous rate of increase, r). The population is constrained by a ceiling on the maximum number of nesting pairs (K, a reflecting boundary determined by forest-management policy), and a lower threshold (quasi-extinction threshold, or passage threshold, L) that acts as an absorbing boundary. If the population trajectory crosses this lower threshold, it is deemed effectively “extinct”. We set the passage threshold (L) at 50 nesting females, in part to avoid the issue of individual demographic variability (which cannot be readily included in DA) and other effects that make DA a potentially less accurate method of estimating persistence time for very small populations (Holmes 2004). Under these assumptions, we used the following equations:

$$\text{when } \mu_r = 0, \qquad T_e = (2n_0/V_r)(k - n_0/2)$$

$$\text{when } \mu_r \neq 0, \qquad T_e = 1/(2s\mu_r)[e^{2sk}(1 - e^{-2sn_0}) - 2sn_0]$$

where $k = \ln(K - L)$, n_0 is the natural logarithm of the starting population size, and $s = \mu_r/V_r$.

We also applied Foley’s (1994) correction to V_r, which accounts for first-order temporal autocorrelation of r: $V_{r,\text{corrected}} = V_r(1 + p)/(1 - p)$, where p is the autocorrelation coefficient. T_e is then converted to persistence probability at time T, $P(T)$, by the negative exponential relationship (Grimm and Wissell 2004)

$$P(T) = 1 - (e^{-T/T_e})$$

To avoid creating artificial variability in the results, BBN nodes representing the equations described above were either deterministic or discretized with a large number of states (Marcot et al. 2006). This ensured that the variability of persistence estimates for policy combinations represented uncertainty of the input variables and not equation-solving error.

There are no suitable long-term population data sets of sufficient duration for murrelets to directly estimate μ_r, V_r, and p. Even if we had good estimates of recent or historical population trajectories, there is no assurance that the same values would continue into the future. Thus, we took the approach of applying a range of hypothetical, yet plausible, future demographic scenarios.

Marbled Murrelets are long-lived birds with a low reproduction rate (Burger 2002). Annual fluctuations in adult survival are probably modest, whereas periods of low reproduction due to variation in food resources and nest predation are more likely (Cam et al. 2003; Speckman et al. 2003; Peery et al. 2004*b*). If the intrinsic, long-term μ_r value is >0, or V_r and autocorrelations of r decrease, the influence of nesting habitat on persistence decreases logarithmically (Foley 1994; Horoshi et al. 2000). The population will be less prone to sustained periods of negative growth, will tend to hover near carrying capacity, and will have a high persistence probability. An assumption of a long-term (100–500 years in this analysis) μ_r value <0 ensures eventual extinction regardless of onshore nesting carrying capacity. Increased carrying capacity can extend the time required for extinction to occur, but only assuming that the population starts near K. If, in fact, at-sea conditions are resulting in a long-term μ_r value <0, then the solution has to be found in the marine environment. Since our objective was to analyze the potential effect of onshore nesting habitat capacity on persistence, we assumed a conservative long-term μ_r value of 0 because of marine effects. We represent uncertainty of marine conditions by varying V_r and p.

Based on the above logic, we applied $\mu_r = 0$ and a moderate range of V_r (0.01 and 0.02). The lower V_r value approximates what Steventon et al. (2003; Table 2 and Appendix 3) observed in multiple 100 year Monte Carlo simulations based on their review of murrelet demography. With this value, the median annual change in population size is about 7% and the 75th percentile annual change is about 12%. The higher V_r value represents a more pessimistic view of fluctuations in future at-sea conditions, the tendency for short-term studies to underestimate long-term variability (Reed et al. 2003), and possibly greater fluctuations in nesting suc-

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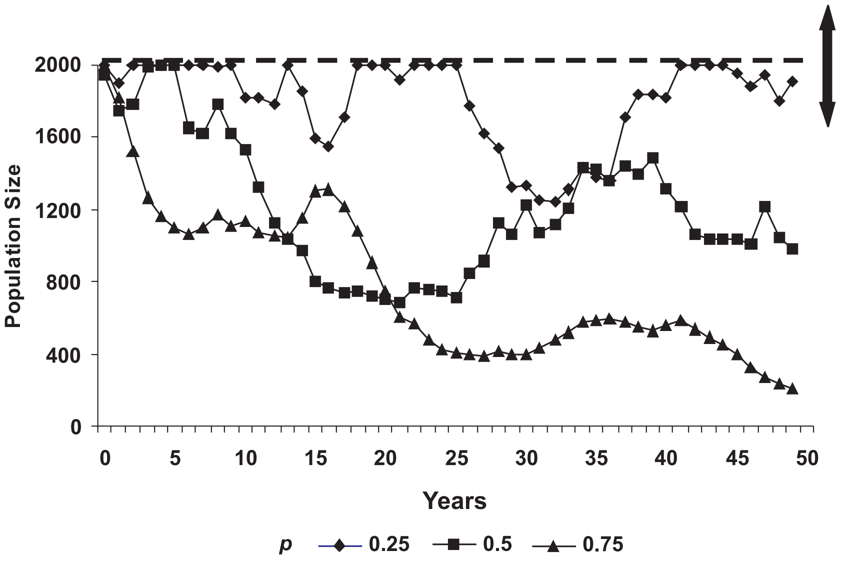
Fig. 2. Sample 50 year population trajectories of the number of breeding females represented by demographic scenarios with a V_r value of 0.01 and temporal autocorrelation (p) values of 0.25, 0.50, 0.75 applied in the diffusion approximations. Nesting K (heavy broken line) is shown at 2000 pairs and is moved up or down (arrow) to represent various nesting-habitat policies and uncertainty of estimated nesting capacity.



cess, owing to onshore edge effects. With that value, the median annual change in population size is about 10% and the 75th percentile is about 17%.

We also applied a range of temporal autocorrelation of r (p values of 0.25, 0.5, and 0.75) bracketing the value (0.5) used by Steventon et al. (2003). Higher V_r and (or) autocorrelation (p) values represent greater population volatility with more frequent and sustained periods of population decline resulting from at-sea effects and nest predation (Fig. 2). Higher autocorrelation values reduce year-to-year volatility but create longer cycles of decline and increase (Halley and Kunin 1999). Based on theory developed by Kuno (1981), Boyce et al. (2002) suggested that V_r be reduced by a factor of 1/(number of populations) to approximate random dispersal among multiple populations. Conceptually, compensatory dispersal among populations is greater with lower correlation among populations; when one population is doing well there would be more dispersal to another population suffering lower r values, thus reducing V_r. For simplicity, however, we conservatively decided to hold V_r unadjusted for the number of populations, assuming that the range we applied already incorporates those effects.

Persistence probability decreases with time span (Grimm and Wissell 2004). Rather than choose a single arbitrary analysis time scale (T), we applied uniform weighting to 100, 200, 300, 400, and 500 year time scales. Thus, the choice of appropriate time scale became a source of uncertainty in our analysis.

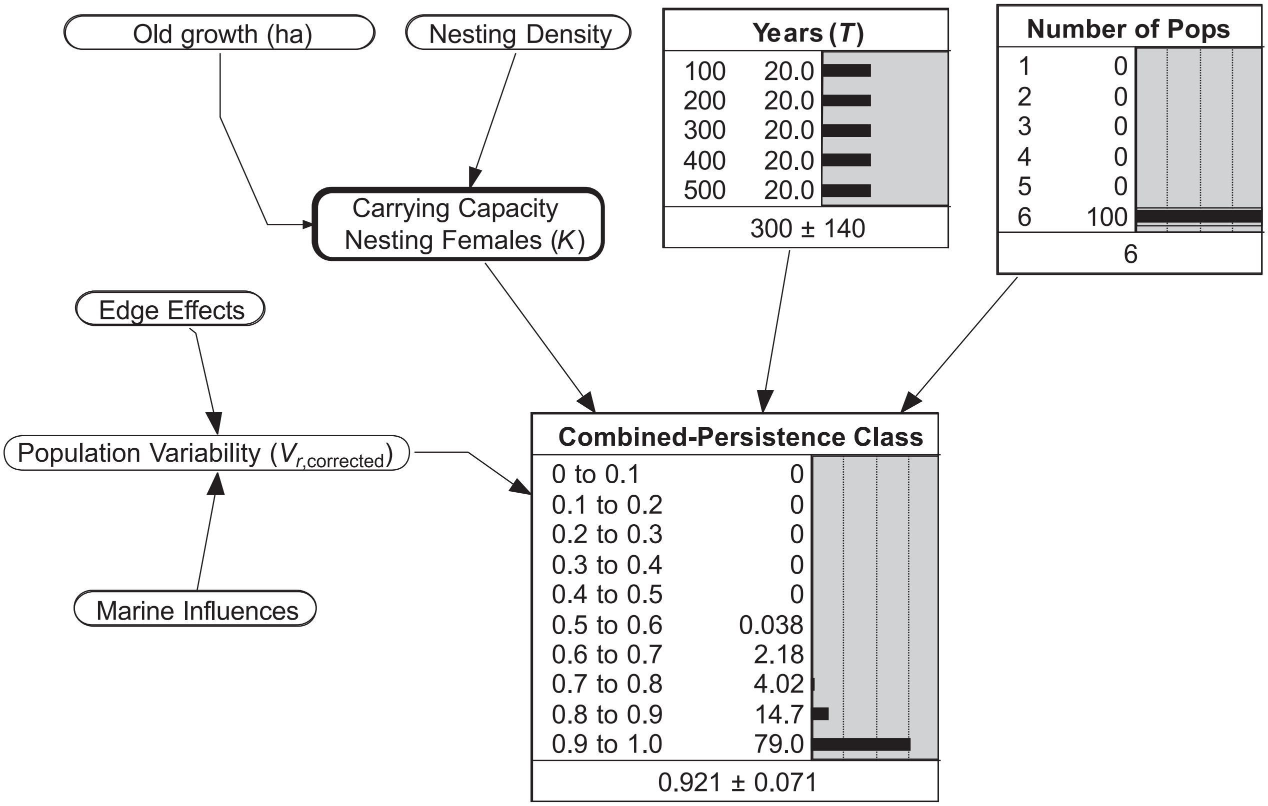
It has been argued that the relative simplicity of DA in terms of the low number of parameters required is both its strength and a weakness. Monte Carlo simulation experiments suggest DA to be generally robust, particularly if used for relative comparisons (Foley 1994; Holmes 2004; Sabo et al. 2004; but see Wilcox and Possingham 2002). The problem of parameterizing alternative, more complex Monte Carlo simulation models with individual or stage-based survivorship and reproduction rates can be severe (Clark 2003) and application less transparent because of unexplained parameter interactions (Sabo et al. 2004). DA generally works best for species, such as the Marbled Murrelet, for which density dependence can be approximated as a ceiling and assumed to function without highly eruptive or other complex dynamics (Halley and Kunin 1999; Sabo et al. 2004; Wilcox and Possingham 2002).

Defining populations

There was difficulty in unambiguously defining Marbled Murrelet populations for analysis. Murrelets are generally continuously distributed along the mainland British Columbia coast, Vancouver Island, and the Queen Charlotte Islands during the breeding season (Yen et al. 2004; Burger et al. 2004). Population genetics indicate a high level of historical interchange among areas sampled in Alaska and southern British Columbia (Congdon et al. 2000),[3] with little genetic differentiation across that range. While seasonal and dispersal movements are poorly known, there are records of substantial seasonal movements (e.g., Beauchamp et al. 1999), as well as remarkable daily commuting distances from foraging areas to nests (Whitworth et al. 2000; Hull et al. 2001). This evidence suggests high mobility and good potential for long-distance dispersal, but how this might be affected by further population reduction or fragmentation is not known.

Although it seems unrealistic to assume that murrelets along the entire British Columbia coast function as one panmictic population, it is equally unrealistic to regard the murrelet conservation regions as totally independent populations. Within each conservation region there may also be semi-independent subpopulations. We explored the effect of assuming independence among and within regions using the

Fig. 3. Simplified version of the analysis BBN used to assess policy options. Nodes that had little influence, remained static, or represented intermediary calculations were "absorbed". Results shown are for a policy requiring 400 000 ha of habitat in each of six subpopulations, with a mean nesting density of 0.01 pairs/ha.



"bet-hedging" approach of Boyce et al. (2002). This approach views individual regions or subregions as otherwise independent populations linked through correlated environmental variation and dispersal. Greater correlation of environmental variation among regions decreases the combined-persistence probability. It increases the chance of all populations suffering the same fate simultaneously through coincident periods of poor survival or productivity at sea, and through a reduction in compensating dispersal among populations (Boyce et al. 2002). The formula for the combined-persistence probability (the probability of at least one population persisting) of i populations at time T is

$$P(T)_{\text{combined}} = 1 - \{E(T)_{\text{all}} + [E(T)_{\text{min.}} - E(T)_{\text{all}}]R^2\}$$

where $E(T)_{\text{all}}$ is the product of all the subpopulation extinction probabilities ($\Pi E(T)_i$), $E(T)_{\text{min.}}$ is the lowest individual-population extinction probability, and R^2 is the coefficient of determination of r among populations. We do not have empirical estimates of R, so we applied values of 0.25, 0.5, and 0.75. For the northern mainland coast example we divided the region into three subregions: Douglas Channel (a), southern outer coast (b), and northern outer coast (c).

Model simplification

In most applied modelling exercises it is desirable to keep the model as simple as possible without losing key details (Marcot et al. 2006). The BBN approach using the Netica® software allowed easy simplification of our model through the process of "node absorption". Unnecessary nodes and links were removed while the inferential relationship among the remaining nodes were maintained (i.e., the same results would be obtained as with the original network). Figure 3, a simplified version of the BBN shown in Fig. 1, was used in the policy analysis. We absorbed most nodes that had little influence on the results, represented intermediate calculations, or were held static in the analyses. Preliminary sensitivity analyses showed that EVP (our measure of resilience) was most sensitive to time scale, demographic parameters V_r and p (combined in $V_{r,\text{corrected}}$), nesting K, and the number and correlation (R) of subpopulations.

Policy assessment

The sensitivity of persistence probability to fluctuations in survival and reproduction ($V_{r,\text{corrected}}$), time scale (T), and number of subpopulations diminished nonlinearly with increasing nesting K, most dramatically for multiple subpopulations (Fig. 4). This illustrates how the onshore component of risk to murrelets interacts with the at-sea component. Higher onshore nesting capacity and multiple populations can, within limits, offset risk associated with uncertainty of demography due to marine conditions and onshore nest predation.

EVP increased nonlinearly with both amount of habitat and nesting density (Fig. 5). For example, achieving an EVP of 0.75 for a single independent population required 75 000 ha (assuming a nesting density of 0.02 pairs/ha, one-

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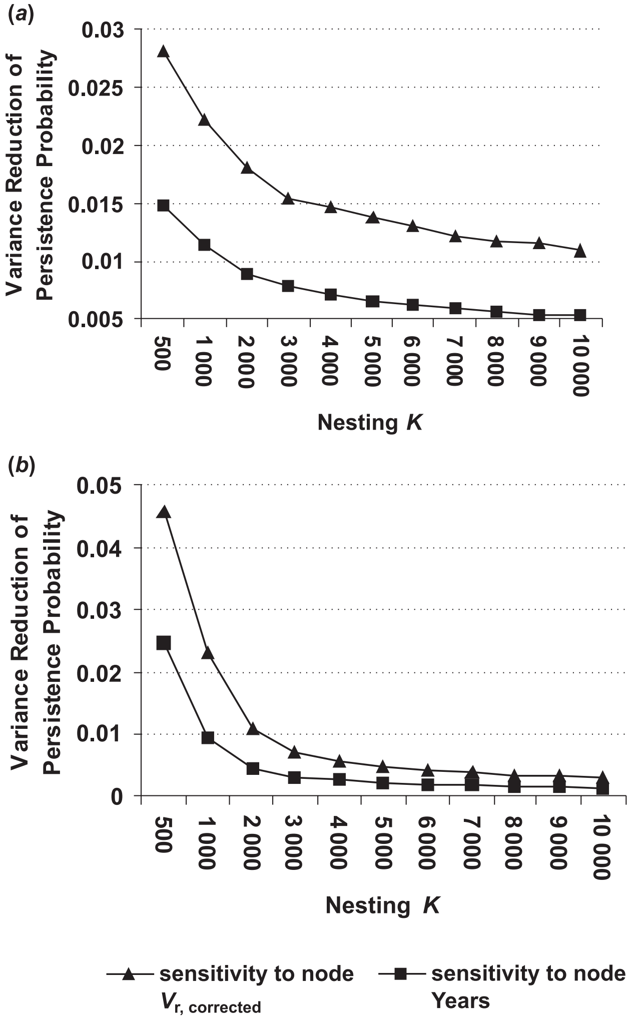
Fig. 4. Sensitivity of persistence probability as a function of nesting K, choice of demographic scenario ($V_{r,\text{corrected}}$ node), and choice of time frame ("years" node) for a single independent population (*a*) and assuming that nesting K is divided among five interacting populations (*b*). Persistence probability was more sensitive to $V_{r,\text{corrected}}$ than years and declined more rapidly with nesting K for the multiple-populations scenario. Variance reduction = $\Sigma_f (P(f)[E(Q|f) - E(Q)] \wedge 2)$, where $P(f)$ is the belief weighting of a finding, $E(Q|f)$ is the EVP conditional on that finding, and $E(Q)$ is the expected value of persistence with the prior probability distribution for all values of (f). State values of other nodes are weighted by their respective probabilities.



third of the "CMMRT-ALL" mean coastwide density of commuting birds from Burger et al. (2004; Table 2)), whereas an EVP of 0.80 required 225 000 ha, a threefold increase. If nesting density averaged only 0.01 pairs/ha, then EVPs of 0.75 and 0.80 required 175 000 and 475 000 ha, respectively. There was little improvement in EVP for combinations of habitat area and nesting density that resulted in a K value greater than 5000 nesting pairs (≈15 000 birds in total).

A strategy of multiple semi-independent subpopulations (e.g., stratifying the coast into multiple conservation regions) greatly reduced risk at the coastwide scale (Fig. 6). Improvement diminished above approximately K = 11 000 nesting pairs (≈33 000 birds in total) divided among three or more semi-independent subpopulations. Additional subpopulations, however, will help maintain resilience in the future should unexpected catastrophes (temporary or permanent loss of a subpopulation) occur, and allow for the possibility of reduced variance of r (parameter V_r in the model) through dispersal among more populations, which has a strong influence on persistence estimates. Similarly, distributing nesting habitat within a region to potentially create semi-independent subpopulations may reduce risk. For the northern mainland coast example, the three subregions had individual EVPs of 0.783, 0.801, and 0.785, while the combined EVP was 0.901. With the same amount of habitat modelled as one population, the EVP was 0.830. With the appropriate geographic information system (GIS) data, this type of spatially explicit approach could be expanded to include other regions, allowing examination of trade-offs among and within regions.

The answer as to whether a policy is "resilient" or the population no longer "at risk" is not absolute, but depends on the weighting of parameter values (uncertainty) and on the amount of risk and cost a decision-maker can tolerate (Regan et al. 2002). An advantage of using DA in a BBN framework was the ability to rapidly (including interactively with decision-makers) modify parameter-value weightings (beliefs) to explore sensitivity, or to apply probability distributions for assumptions that represented views of multiple decision-makers (such as the choice of assessment time scale, T).

Which conservation strategy is most efficient will depend on the relative cost of increasing the amount of habitat versus increasing its quality in each conservation region. Similarly, the trade-off between investing in research or using adaptive management and monitoring to reduce uncertainty of habitat models can be compared with simply saving more habitat or better habitat. If those relative costs can be reasonably estimated, the most efficient use of conservation resources could be explicitly examined using decision-optimization techniques (Haight et al. 2002). Such analyses can prevent waste of limited conservation resources.

In an earlier assessment of British Columbia murrelets, Steventon et al. (2003) used a more complex stage-based Monte Carlo simulation approach. They suggested strongly diminished risk for individual independent populations as K increased to 2000 (based on the EVP for T = 100 years), or 12 000 divided among six populations (the number of proposed conservation regions). There was little improvement in EVP for a single population above K = 5500. More generally, Reed et al. (2003) estimated population sizes required for an EVP of 0.99 over 40 generations (which would be ~400 years for murrelets), based on population-trajectory data for 102 species varying in life-history attributes. The median value they calculated was 7000 breeding-age individuals (sexes combined) and the most extreme value they reported for birds was 25 000. This extreme value would equate to a nesting K value of ≈12 000 pairs, which is similar to our coastwide estimate, above which further improvement of EVP was unlikely.

Based on our analysis, plus those of Steventon et al. (2003) and Reed et al. (2003), a coastwide nesting K value of ≥12 000 (≈36 000 birds) distributed among three to six re-

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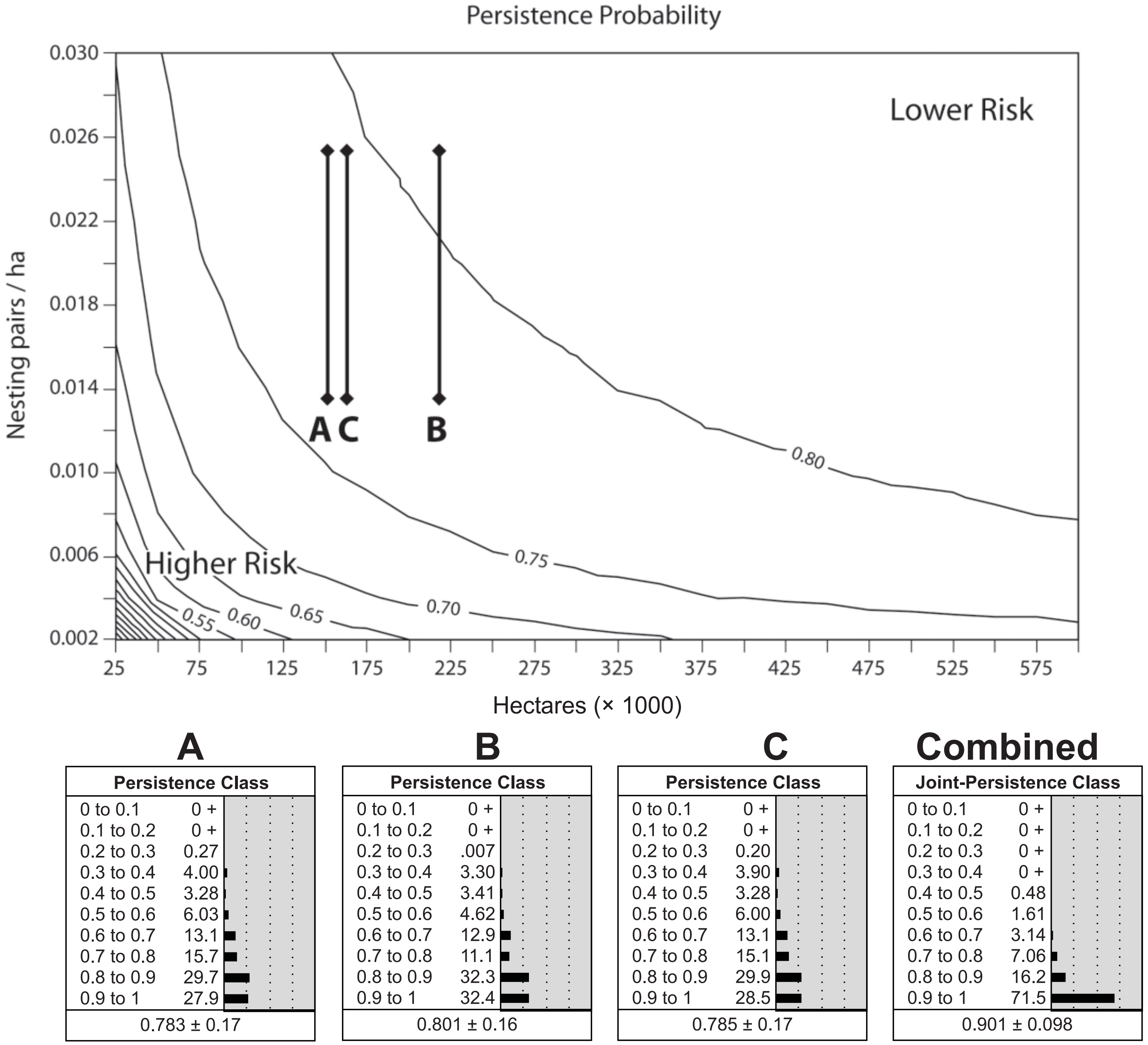
Fig. 5. Expected value of persistence as a function of amount of habitat and nesting density; risk decreases from the lower left to the upper right, each contour representing an improvement of 0.05 in EVP. The intervals between contours represent combinations of hectares and nesting density with similar persistence probability. The three vertical lines (A, B, and C) represent the ranges of potential nesting density for the three northern mainland coast subregions; the boxes below show the associated persistence probability distributions.



A

Persistence Class	
0 to 0.1	0 +
0.1 to 0.2	0 +
0.2 to 0.3	0.27
0.3 to 0.4	4.00
0.4 to 0.5	3.28
0.5 to 0.6	6.03
0.6 to 0.7	13.1
0.7 to 0.8	15.7
0.8 to 0.9	29.7
0.9 to 1	27.9
0.783 ± 0.17	

B

Persistence Class	
0 to 0.1	0 +
0.1 to 0.2	0 +
0.2 to 0.3	.007
0.3 to 0.4	3.30
0.4 to 0.5	3.41
0.5 to 0.6	4.62
0.6 to 0.7	12.9
0.7 to 0.8	11.1
0.8 to 0.9	32.3
0.9 to 1	32.4
0.801 ± 0.16	

C

Persistence Class	
0 to 0.1	0 +
0.1 to 0.2	0 +
0.2 to 0.3	0.20
0.3 to 0.4	3.90
0.4 to 0.5	3.28
0.5 to 0.6	6.00
0.6 to 0.7	13.1
0.7 to 0.8	15.1
0.8 to 0.9	29.9
0.9 to 1	28.5
0.785 ± 0.17	

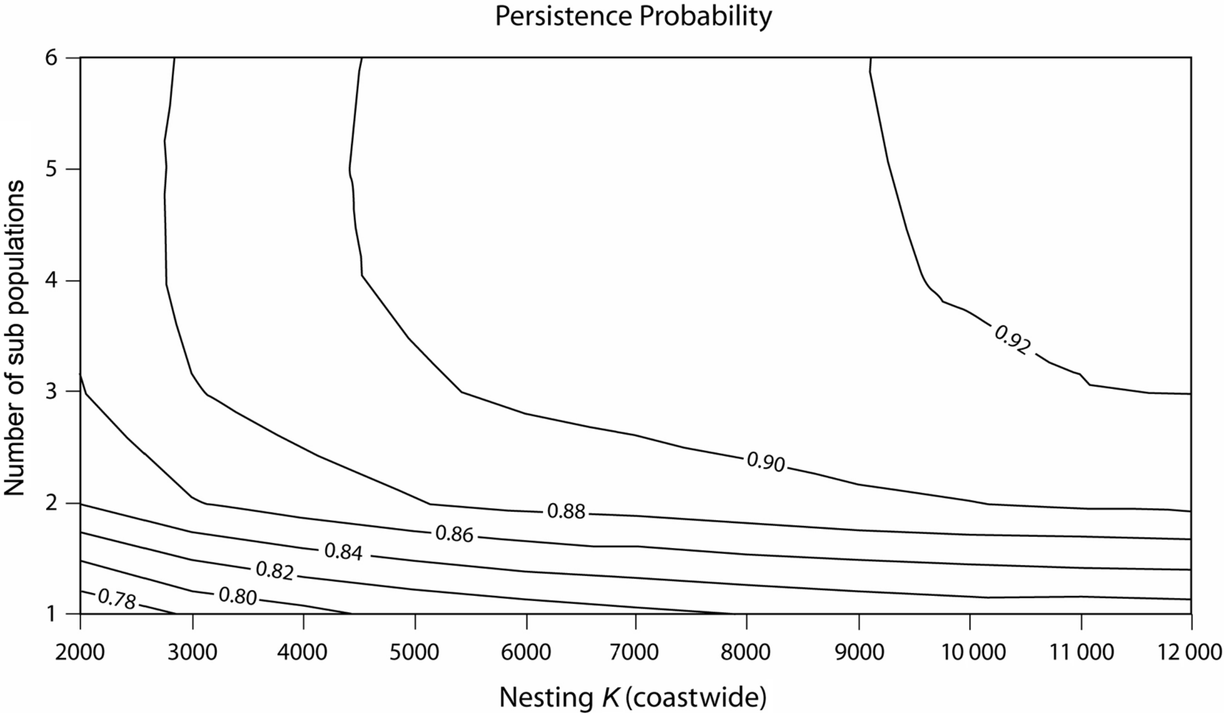
Combined

Joint-Persistence Class	
0 to 0.1	0 +
0.1 to 0.2	0 +
0.2 to 0.3	0 +
0.3 to 0.4	0 +
0.4 to 0.5	0.48
0.5 to 0.6	1.61
0.6 to 0.7	3.14
0.7 to 0.8	7.06
0.8 to 0.9	16.2
0.9 to 1	71.5
0.901 ± 0.098	

gions (1000–4000 nesting pairs per region) appears robust in terms of population viability across spatial scales, temporal scales, parameter uncertainty, and modelling approach. This equates to 45%–60% of coastwide population estimates in 2001 (Burger 2002). The area of old forest needed to meet that threshold will depend on habitat-quality assumptions (nesting density) and risk tolerance. Assuming 0.02 nesting pairs/ha, based on one-third (estimated proportion representing nesting females) of recent inland murrelet density estimates (Burger et al. 2004, CMMRT-ALL mean pooled estimate in Table 2), 600 000 ha would be required, or 1.2 million ha assuming that retained habitat averages 0.01 pairs/ha (half the recent density estimate). That level of habitat protection would achieve high resilience coastwide while accepting some decrease in resilience at the individual region or subregion scale. Abundance, however, would be substantially reduced from historical levels and unknown ecological interactions with other species possibly diminished.

It has been estimated recently that between 36% and 52% of coastwide murrelet nesting habitat is protected (Burger et al. 2004). Land-use planning in three of the conservation re-

Fig. 6. Coastwide expected values of persistence probability (EVP) as a function of coastwide nesting *K* and number of subpopulations. Each contour represents an improvement of 0.02 in EVP. The intervals between contours represent combinations of nesting *K* and number of populations with similar EVPs.



gions (northern mainland coast, central mainland coast, and Queen Charlotte Islands) is likely to result in additional protected habitat. Some regions have considerable forested area that is not presently economic to harvest, and in the regions of greatest historical habitat loss, most of the reduction may have already occurred (Wells et al. 2003; Holt 2004; British Columbia Ministry of Forests Timber Supply Reviews [online], available from http://www.for.gov.bc.ca/hts/tsr.htm). This suggests that finding sufficient additional nesting habitat consistent with high viability or resilience of the breeding population of Marbled Murrelets is still achievable.

Population viability is only one measure of sustainability for murrelets, and murrelets are but one species involved in the complex question of sustainability of coastal forest ecosystems. Selecting nesting-habitat objectives appears to be more a question of how abundant we desire murrelets to be in the broader ecosystem-management context, and less a question of species viability.

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