Appendix C

Population Viability Analysis

A population viability analysis approaches was used to evaluate the potential future (50-year) effects of proposed management alternatives (A through H) on marbled murrelets in Washington. A stochastic, two-population model was developed that linked murrelet demographic rates to forest conditions on DNR-managed and non-DNR-managed lands. The model was used to evaluate each proposed alternative's relative potential to lead to *risk* or *enhancement* of murrelet populations.

Note on Data Used to Parameterize the Population Viability Model

The marbled murrelet meta-population model and population viability analysis presented in this appendix was parameterized using at-sea survey data from Zones 1 and 2 (Washington) over the period 2001 through 2015. However, more recent at-sea survey data are now available for 2017 through 2018 (McIver and others 2019). (At the initiation of the contract between DNR and Peery/Jones, the 2001 through 2015 data were the most recently available data.) This note briefly describes why more recent data was not included in the model.

1. **Re-parameterizing the model was not possible in time for the final environmental impact statement (FEIS) for the marbled murrelet long-term conservation strategy**. The at-sea survey data feeds into a number of components of the model, including (a) initial population size in "year 0" of the simulation, (b) variance in survival and fecundity rates used in the projections (the coefficient of variation, or CV, of simulated populations should be similar to process CV in recent at-sea survey estimates), and (c) the carrying capacity scaling used within the model to help simulated declines match observed recent declines. Changing the input data would require adjusting all of these components, each of which requires time-consuming analyses. There was not adequate time to engage in these analyses and make subsequent adjustments to the model.

2. **2001 through 2015 survey data are more robust because they are complete and contain no missing survey years.** The at-sea survey data in Zones 1 and 2 over the period 2001 through 2015 are complete, but contain missing data for these zones in years 2016 through 2018 (McIver and others 2019). Specifically, Zone 1 is missing data from 2017, and Zone 2 is missing data from 2016 and 2018. This missing data increases the uncertainty in the actual count of murrelets in the state of Washington from 2016 through 2018. In population viability analyses, it is important to minimize the uncertainty in the components that feed into the population model. Using data from 2001 through 2015 makes that possible.

3. **Continued observed/estimated declines in the Washington murrelet population (McIver and others 2019) fall within the range predicted by the population viability model.** In effect, the first three years of forward projection presented in this appendix should represent the projected female murrelet population in Washington from 2016 through 2018. Estimates for these years (assuming 1/2 the population is female, and under the *Risk* parameterization where mean adult survival = 0.87), compared to the empirical data, are as follows:

    a. 2016: mean = 6695 (95% range = 5713-7590) (McIver = 7494)

    b. 2017: mean = 6335 (95% range = 5144-7450 (McIver = 7095)

    c. 2018: mean = 6024 (95% range = 4731-7312) (McIver = 5984)

   As one can see, the empirical data reported by McIver and others (2019) fall within the 95 percent predicted range of the population viability model for all three years. This leads to the conclusion that (a) the model is performing well and (b) does not need to be re-parameterized with more recent data.

4. **Re-parameterizing the model would be unlikely to produce different qualitative results.** The power in population viability analyses is the ability to distinguish *among* plausible management scenarios. If the parameterization of the model was fiddled with to incorporate 2016 through 2018 at-sea survey data (refer to point #2) and the corresponding, slight decrease in the rate of population decline in Washington, the result may be a change in the absolute number of projected murrelets in any given year of the scenario; however, it would be unlikely to produce changes in the *relative comparisons among scenarios.* That is, Alternative F would likely still produce the highest murrelet numbers after 50 years, and Alternative B the lowest, and so on.

Literature Cited

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Using population viability analyses to assess the potential effects of Washington DNR forest management alternatives on marbled murrelets

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EXECUTIVE SUMMARY

The marbled murrelet (*Brachyramphus marmoratus*) was listed as threatened in Washington, Oregon, and California under the Endangered Species Act in 1992 due to commercial logging of nesting habitat, oil spills, and gill net entanglement. In 2012, the Washington Department of Natural Resources (DNR) initiated the development of a statewide, long-term conservation strategy for marbled murrelets to replace the 1997 Habitat Conservation Plan implemented after initial listing. We used population viability analysis (PVA) approaches to evaluate the potential future (50-year) effects of proposed management alternatives (A – H) on marbled murrelets in Washington. To do so, we developed a stochastic, two-population model linking murrelet demographic rates to forest conditions on DNR and non-DNR lands, and used this model to evaluate each proposed alternative's relative potential to both lead to *Risk* and *Enhance* murrelet populations. Proposed alternatives F and G generally resulted in the greatest number of murrelets and lowest quasi-extinction probabilities, whereas alternative B always resulted in the lowest murrelet population size and highest quasi-extinction probabilities, in both the *Risk* and the *Enhancement* scenarios and at the two spatial scales considered (DNR lands versus state of Washington). Thus, alternative B posed the greatest risk to murrelet populations and alternatives F and G provided the greatest capacity to enhance murrelet populations. For example, at the state scale alternative F was projected to lead to 60 and 280 more murrelets than alternative B under the *Risk* and *Enhancement* scenarios, respectively. All alternatives except B were projected to lead to larger murrelet population sizes at year 50 than alternative A (the "no action" alternative), regardless of the spatial scale or scenario (one exception was alternative D in the *Risk* analysis, which resulted in slightly lower murrelet population sizes than alternative A). The same pattern

was generally observed for quasi-extinction probabilities. In a separate sensitivity analysis, we found that, acre-for-acre, murrelet population growth was most sensitive to changes in higher-quality nesting habitat (Pstage 0.89 and 0.62), and while still sensitive, less so to changes in the raw acreage of nesting habitat or nesting habitat configuration (i.e., edge conditions). While we believe our model is sufficiently robust and well-parameterized to help assess how the proposed management alternatives may impact murrelet populations, our results must be considered in light of uncertainly about the effects of future changes in climate and stressors in the marine environment. Future efforts would benefit from using spatially-explicit models that provide (i) geographically-targeted (local) estimates of risk, (ii) prioritize stands for conservation and management, and (iii) generate more realistic insights into how changes in the spatial arrangement of nesting habitat may influence regional murrelet population viability. However, spatially-explicit population models are relatively complex in structure and would benefit from additional research designed to fill key information gaps in our understanding of murrelet ecology and environmental factors influencing murrelet populations.

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INTRODUCTION

The U.S. Endangered Species Act of 1973 (hereafter "ESA") prohibits the "take" of species listed as threatened or endangered (U.S. Congress 1973). In 1982 the ESA was amended to provide flexibility to non-federal land owners with endangered species on their property by granting an "incidental take permit" if they developed a Habitat Conservation Plan (HCP). Under Section 10 of the ESA, HCPs represent planning documents intended to ensure that anticipated take of a listed species will be minimized and mitigated to the maximum extent practicable by conserving the habitat upon which the species depend. Since issuance of an incidental take permit is a federal action, consultation under Section 7 of the ESA must also occur. Through the consultation process the U.S. Fish and Wildlife Service (FWS) determines if the proposed action is likely to lead to "jeopardy" which, according to the regulations implementing the ESA, is when an action "…reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild by reducing the reproduction, numbers, or distribution of that species" (50 CFR §402.02). Although not a statutory requirement, another component of HCP development is addressing whether proposed management alternatives contribute to the recovery of the species as a whole, which is considered to be "an integral product of an HCP…" (USFWS 1996).

HCP negotiations and Section 7 consultations typically consider a wide range of information pertinent to the threatened or endangered species including, but not limited to, current habitat distribution and population trends as well as projections of future habitat and population status. Modeling approaches such as Population Viability Analyses (PVA) are frequently used as part of Section 7 consultations and HCP negotiations to evaluate the potential effects of proposed activities on threatened and endangered species (Harding et al. 2001, Morris

et al. 2002). While the ability of PVA approaches to evaluate absolute levels of risk has been questioned, they remain well-suited to compare the relative effects of alternative management strategies on species of concern (Beissinger and Westphal 1998). However, addressing how well different management alternatives both lead to risk and support recovery raises conceptual and practical challenges, even when projections are limited to relative comparisons. Many, if not most, endangered species are declining in numbers and face extirpation due to the cumulative effects of multiple environmental stressors over broad geographic areas that extend beyond the effects of local habitat management within the HCP planning area. In these cases, understanding an alternative's capacity to support recovery may require additional, optimistic assumptions about, for example, improvements to other stressors that impact vital rates. Thus, simultaneously addressing these two questions—namely risk of extirpation/extinction and potential for recovery— as part of Section 7 consultations for endangered species, may require two distinct, yet parallel, modeling efforts. Further, modeling results must often be coupled with consideration of other factors such as geographic distribution for a complete jeopardy analysis.

The marbled murrelet (*Brachyramphus marmoratus*) is a small seabird endemic to the west coast of North America that generally nests in coastal old-growth forests and forages in marine nearshore environments (Meyer et al. 2002). The murrelet was listed as a federally threatened species in Washington, Oregon, and California under the ESA in 1992 primarily because of the loss of older, complex-structured forests to timber harvest, and edge effects from ongoing forest fragmentation (USFWS 1997). However, a host of other factors unrelated to forest management likely impact murrelet populations including marine foraging conditions, disease, oil spills, and by-catch from gill net fishing (Peery et al. 2004, Raphael 2006). Nevertheless, the relative importance of each of these factors in driving recent population

declines is not well understood (Falxa and Raphael 2016).

The Washington Department of Natural Resources (DNR) manages forests on "state trust lands" as fiduciary trusts to provide revenue to specific trust beneficiaries, such as schools, universities and other public institutions. In accordance with Section 10 of the ESA, the DNR developed a Habitat Conservation Plan in the late 1990's (WDNR 1997) which was an ecosystem-based forest management plan intended to help the DNR develop and protect habitat for at-risk species, including several federally threatened species (e.g., marbled murrelet and northern spotted owl *Strix occidentalis caurina*), while carrying out forest management and other activities on the state trust lands it manages. In 2012, the DNR formally began a process to amend the 1997 HCP to include a long-term conservation strategy for the marbled murrelet that incorporated a more recent body of scientific information on murrelet biology and habitat needs. The revision of the DNR's HCP seeks to simultaneously address the question of risk and contribution to recovery, a question complicated by the fact that by our analytical framework, habitat on DNR lands contains only about 15% of the estimated carrying capacity for murrelets in Washington (and less in the tri-state area) and multiple, poorly understood environmental stressors likely impact murrelet populations regionally.

To provide insight as to whether forest management alternatives proposed as DNR's long-term conservation strategy may lead to risk or support significant contributions to recovery of murrelet populations in Washington, we used two parallel modeling frameworks—a "*Risk*" and an "*Enhancement*" analysis—that differed in assumptions about future impacts of environmental factors on murrelets beyond habitat change on DNR lands. In the *Risk* analysis, we assumed that current population declines were, in part, a function of recent loss of nesting habitat, and that the current population exceeded the nesting carrying capacity and was expected

to decline further because of density-dependent effects. However, we also assumed that undetermined, chronic environmental stressors have contributed to population declines by reducing vital rates (reproduction and survival) such that the population was expected to continue to decline even after the population reached carrying capacity, albeit at a slower rate. While there is uncertainty in the environmental and anthropogenic factors responsible for recent population declines, parameterizing the model such that projected populations declined at approximately the same rate as recent estimates provided some biological realism to the model. This analysis was thus intended to provide a relative comparison of future state-level risk among management alternatives and to provide a general assessment of how risk can be modulated by forest management alternatives on DNR lands, particularly in light of recent population declines (Miller et al. 2012).

While the first analysis provides perspective on risk, estimating differences in risk among alternatives superimposed on expected future, substantial (ca. 5% annual) population declines does not necessarily provide a basis for assessing the extent to which the alternatives may support murrelet recovery. Put simply, we had an *a priori* expectation that potential increases in nesting habitat on DNR-managed lands are unlikely, by themselves, to provide a substantial contribution to the recovery of the considerably larger state-wide population experiencing significant declines likely owing to a host of factors in addition to the nesting habitat on state lands. From the perspective of evaluating a forest management plan, the question of recovery might be cast as: "if other stressors are ameliorated, how do the alternatives differ in their ability of DNR managed-lands to increase local breeding populations?" Therefore, in the *Enhancement* analysis, we developed an alternative parameterization of the model where we assumed that (i) the availability of nesting habitat was the primary cause of recent population declines and the

most important factor limiting future population growth, and (ii) that other environmental stressors would not appreciably limit potential future recovery. Thus, as with the *Risk* analysis, murrelets were expected to decline initially at approximately the same rate as estimated with at-sea monitoring, but at some point in the future, the population would reach equilibrium with nesting carrying capacity and that the intrinsic population growth rates were sufficient for the population to increase in response to potential increases in nesting habitat. This second approach, then, provided a more direct means to "credit and debit" the DNR by evaluating potential population response to expected increases and decreases in nesting habitat on DNR lands using population metrics, under the important assumption that other chronic stressors in the environment will not impede recovery.

We implemented this dual modeling approach using a stochastic meta-population model that provided a framework for projecting expected changes in the abundance of murrelets in the state of Washington under various forest management alternatives currently under consideration by DNR and FWS. The model links changes in murrelet population dynamics to expected changes in the quantity, quality, and configuration of nesting habitat on DNR lands over time (that varied among management alternatives) through ecological processes that were reasonably well-supported by the literature and that were agreed upon by DNR and FWS (WDNR 2016). It included two subpopulations linked demographically by dispersal, where the subpopulations represented murrelets nesting on DNR and non-DNR lands. In our model, the dispersal process was spatially implicit; we did not explicitly consider the complex, landscape-scale distribution of murrelet nesting habitat on different landownerships in the state of Washington because many of these processes are not well understood and fully addressing these complexities was deemed beyond the scope of the Conservation Strategy negotiations by the involved resource agencies.

The metapopulation model made a number of additional simplifying assumptions as the secretive behavior and marine habitats of marbled murrelets challenges field studies needed to parameterize the model described below. Thus, and as is the case with all PVA exercises, projections of risk should not be considered as absolute estimates, and only be interpreted as a way to compare the relative consequences of different scenarios (Beissinger and Westphal 1998). However, our objective was to develop a population model where differences in projected risk among management alternatives were sufficiently robust to violations of assumptions and uncertainty that the involved agencies could identify which alternative best met joint objectives. More broadly, we sought to understand how using parallel *Risk* and *Enhancement* analyses could facilitate management decisions and endangered species conservation while meeting legal obligations of the Endangered Species Act and DNR's policy goal of making a "significant contribution" to murrelet conservation. *In doing so, we recognize it is beyond our purview to provide recommendations as to whether individual alternatives impact murrelets such that "...survival and recovery in the wild is appreciably reduced" or whether they benefit murrelet populations to the point that they "contribute to the recovery of the species as a whole".* While we do highlight when, and under what circumstances, an individual alternative might increase/decrease risk or may increase the likelihood of recovery via population gains, we make no judgments as to whether modeled impacts on populations are sufficient to meet specific FWS regulatory criteria related to jeopardy or population recovery. While this distinction is subtle, we believe it is an important one.

METHODS

Model Structure and Parameterization

Matrix Model Structure. We developed a female-based, stochastic meta-population model that employed a one-year time step in accordance with the annual breeding cycle of marbled murrelets (Nelson 1997). Each of the two subpopulations (DNR and non-DNR lands) contained five stages classes: juveniles, 1-year old subadults, 2-year old subadults, adult ($\geq$3-year olds) nonbreeders that did not breed because of insufficient nesting habitat, and adult breeders ($\geq$3-year olds; Figure 1). The five stage classes were indexed $x = 1, 2,\ldots, 5$ in the order presented above, and DNR and non-DNR lands were indexed as $L = 1$ and 2, respectively. Note that, at times, the $\geq$1-year-old stage classes (non-juveniles) are collectively referred to as after-hatch-year (AHY) individuals for convenience. Model parameters are defined in Table 1, and the rationale for assumptions behind the selected model structure and parameter values are described throughout the next several sections.

The life-cycle diagram can be expressed mathematically as a matrix model that determines the number of individuals in each stage class at time $t + 1$ based on the number of individuals in each stage class in year t (Caswell 2001, Morris and Doak 2002). The murrelet meta-population model $\mathbf{A}_t$ consisted of four submatrices that defined local demographic and dispersal processes (Hunter and Caswell 2005):

$$\mathbf{A}_t = \begin{bmatrix} \mathbf{A}_{1,t} & \mathbf{M}_{2,t} \\ \mathbf{M}_{1,t} & \mathbf{A}_{2,t} \end{bmatrix}$$

The two submatrices on the main diagonal ($\mathbf{A}_{L,t}$) governed local demographic processes on DNR

and non-DNR lands, denoted $\mathbf{A_{1,t}}$ and $\mathbf{A_{2,t}}$, respectively. The two submatrices in the off-diagonal

determined murrelet dispersal between the two landownerships where the submatrix governing

dispersal from DNR lands to non-DNR lands was $\mathbf{M_{1,t}}$ and the submatrix governing dispersal

from non-DNR to DNR lands was $\mathbf{M_{2,t}}$ (the dispersal matrices are described in more detail

below). The demography submatrices were structured as follows:

$$
\mathbf{A_{L,t}} =
\begin{bmatrix}
0 & 0 & s_{3,L,t}g_{3,L,t}bf_{L,t} & s_{4,L,t}g_{4,L,t}bf_{L,t} & s_{5,L,t}(1-g_{5,L,t})bf_{L,t} \\
s_{1,L,t} & 0 & 0 & 0 & 0 \\
0 & s_{2,L,t} & 0 & 0 & 0 \\
0 & 0 & s_{3,L,t}(1-g_{3,L,t})(1-d_{L,t}) & s_{4,L,t}(1-g_{4,L,t})(1-d_{L,t}) & s_{5,L,t}g_{5,L,t} \\
0 & 0 & s_{3,L,t}g_{3,L,t}(1-d_{L,t}) & s_{4,L,t}g_{4,L,t}(1-d_{L,t}) & s_{5,L,t}(1-g_{5,L,t})
\end{bmatrix}
$$

In these matrices, $s_{x,L,t}$ represented the annual survival rates, $g_{x,L,t}$ represented the probability of

transitioning (transition rate) from stage class x (conditional on survival and population fidelity),

$d_{L,t}$ was the annual dispersal rate, b was the breeding probability, and $f_{L,t}$ was nest success. Note

that $g_{1,L,t}$ and $g_{2,L,t}$ were always equal to 1 and are therefore not presented in either the life cycle

diagram or the matrix model.

Parameterizing Survival Rates ($s_{x,L,t}$*)*. The model was parameterized with an annual survival rate

of 0.87 and 0.90 in the *Risk* and *Enhancement* analyses, respectively, for after-hatch-year

females ($s_{2,L,t}$ to $s_{5,L,t}$) based on a mark-recapture study of 331 individual marbled murrelets in

central California (Peery et al. 2006b) (Table 1). A pooled survival rate was used for these four

stages classes because it was not possible to distinguish beyond juvenile versus after-hatch-year

at the time of the mark-recapture study. We assumed the annual juvenile survival (s_1 and s_6) was

70% of after-hatch-year survival based on differences in survival rates between these stage

classes in other alcid species (insufficient juveniles were captured to estimate juvenile survival directly; Peery et al., 2006a).

Parameterizing Breeding Probabilities (b,$f_{L,t}$*).* We treated the parameter *b* as the expected proportion of individuals in the breeding stages (i.e., that were "in possession" of a nest site) that actually nested in each year. We assumed that some fraction of breeders did not nest each year because, in seabirds, some individuals typically forgo nesting due to, for example, poor foraging conditions (Peery et al. 2004). The proportion of breeders has been estimated using radio-telemetry in the state of Washington, but estimates are likely biased low as a result of transmitter effects (Peery et al., 2006b, M. G. Raphael *pers. comm.*). A similar study in central California (Peery et al. 2004) used assays of plasma calcium (an indicator of eggshell deposition) and vitellogenin (an egg yolk precursor) to identify radio-marked individuals that did not nest but were physiologically in breeding condition at the beginning of the breeding season (indicating they likely would have nested in the absence of radio-tagging). Peery et al. (2004) found that 77% of sampled murrelets either initiated nesting or were physiologically in breeding condition. However, some individuals that were not detected nesting and were not in breeding condition may have nested and failed prior to radio-tagging. Thus, we used *b* = 0.90 as a reasonable estimate for the proportion of breeders in the state of Washington. Note that we assumed *b* was constant across years and equal 0.90 in both landownerships. However, we incorporated the effects of environmental variability on *b* implicitly by treating expected fecundity ($m_{L,t}$: the product of the proportion of breeders, *b,* and nest success, $f_{L,t}$, divided by two; see below) as a random beta-distributed variable in the population projection model as described above.

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Modeling Transition Probabilities ($g_{x,L,t}$*).* Transition rates ($g_{x,L,t}$) provided the primary

mechanism linking the demographic model to potential changes in the availability of nesting

habitat resulting from forest management activities. Transition rates for the 2-year subadult and

nonbreeding stages into the breeding stage class ($g_{3,L,t}$ and $g_{4,L,t}$, respectively) were calculated

based on the number of individuals seeking nests sites relative to the number of available nests in

year $t + 1$ in landownership L. For example, if the number of murrelets seeking nest sites (i.e., 2-

year old subadults plus nonbreeders) was less than the number of available nest sites, then

$g_{3,L,t}$ and $g_{4,L,t}$ = 1, such that all murrelets found nest sites. If the number of murrelets seeking

nest sites exceeded the number of available nest sites, then $g_{3,L,t}$ and $g_{4,L,t}$ < 1 such that not all 2-

year old subadults and nonbreeders in the population become breeders in year $t + 1$. Thus, if the

number of nest sites in a given landownership ($K_{L,t}$) declined, for example as a result of timber

harvesting, transition rates into the breeding class would also decline and fewer individuals

would reproduce (effectively reducing the expected population growth rate). Conversely, if the

number of nest sites increased (for example, as a result of forest growth and maturation),

transition rates into the breeding class would tend to increase and more individuals would

reproduce (effectively increasing the expected population growth rate). Mathematically,

transition probabilities for landownership L in year t and were calculated as follows:

$$g_{3,L,t} = g_{4,L,t} = \frac{K_{L,t+1} - s_{5,L,t}n_{5,L,t}(1 - g_{5,L,t})}{s_{3,L,t}, n_{3,L,t} + s_{4,L,t}n_{4,L,t}}$$

The numerator in this equation represented the number of available nest sites (carrying capacity

minus the number of surviving breeders from the previous year), whereas the denominator

represented the number of potential new breeders seeking nest sites (surviving 2-year subadults

and nonbreeders from year t).

Reductions in the number of nests sites ($K_{L,t}$) could also impact population growth by causing some breeders in possession of a nest site in year t to transition to the nonbreeder stage in year $t + 1$ ($g_{5,L,t}$):

$$g_{5,L,t} = 1 - \frac{K_{L,t+1}}{K_{L,t}}$$

For example, if half of existing nest sites were lost in year t, half of the surviving breeders in year t would transition to the nonbreeder stage in year $t + 1$. As described above, nonbreeders could transition back to the breeding stage if nests became available (e.g., through forest growth), but the model assumed that breeders that lost their nest sites as a result of habitat loss became nonbreeders for at least one year.

Parameterizing Dispersal Rates ($d_{L,t}$*) and Modeling Dispersal Processes.* Modeled murrelet populations in the two landownerships were linked demographically by the dispersal of individuals, where the annual dispersal rate from DNR to non-DNR lands, and from non-DNR to DNR lands, was defined as $d_{1,t}$ and $d_{2,t}$, respectively. The submatrix representing dispersal from land ownership L was structured as follows:

$$\mathbf{M}_{L,t} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{3,L,t}g_{3,L,t}d_{L,t} & s_{4,L,t}g_{4,L,t}d_{L,t} & 0 \end{bmatrix}$$

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For example, if $L = 1$, then the matrix $\mathbf{M}_{1,t}$ would represent dispersal from DNR to non-DNR lands in year t. The model assumed that dispersal movements were made by 2-year subadults and nonbreeders as these individuals transitioned to breeding stages in either landownership; juveniles and 1-year subadults remained in their natal population until they were old enough to breed. Individuals in breeding stages were assumed to remain in their respective populations such that "breeding dispersal" was effectively zero, a reasonable assumption based on anecdotal observations of the re-use of the same nesting site by murrelets in consecutive years (R. T. Golightly *pers. comm.*) as well as generally strong breeding fidelity in alcids (Gaston and Jones 1998). Dispersal rates between DNR and non-DNR lands are unknown, but approximately 85% of existing carrying capacity for murrelets in Washington occurs on non-DNR lands and 15% occurs on DNR lands. Thus, if we assume natal dispersal is random with respect to landownership, d_1 would be 0.85 and d_2 would be 0.15. However, a cap to the number of dispersers, and thus the dispersal rates was imposed by the number of available nest sites in the receiving population. Thus, if the number of dispersers calculated based on the dispersal rate exceeded the number of available nest sites in the receiving population, the "realized" dispersal rate was adjusted as follows for murrelets dispersing from DNR lands:

$$d_{1,t} = \frac{K_{2,t+1} - (s_{3,2,t}n_{3,2,t} + s_{4,2,t}g_{4,2,t}n_{4,2,t} + s_{5,2,t}[1 - g_{5,2,t}]n_{5,2,t})}{s_{3,1,t}(1 - g_{3,1,t})n_{3,1,t} + s_{4,1,t}(1 - g_{4,1,t})n_{4,1,t} + s_{5,1,t}g_{5,1,t}n_{5,1,t}}$$

Here, the numerator represents the number of available nest sites on non-DNR lands in year $t + 1$ after "local" recruitment by resident 2-year subadults and nonbreeders, whereas the denominator represents the number of available recruits from DNR lands in year $t + 1$. The analogous adjustment for dispersal rates from non-DNR lands was made as follows:

$$d_{2,t} = \frac{K_{1,t+1} - (s_{3,1,t}n_{3,1,t} + s_{4,1,t}g_{4,1,t}n_{4,1,t} + s_{5,1,t}[1 - g_{5,1,t}]n_{5,1,t})}{s_{3,2,t}(1 - g_{3,2,t})n_{3,2,t} + s_{4,2,t}(1 - g_{4,2,t})n_{4,2,t} + s_{5,2,t}g_{5,2,t}n_{5,2,t}}$$

As with local recruitment into the breeding stage, the model assumed that dispersing individuals selected nesting habitat in the destination population independent of habitat quality and edge conditions.

Initial Population Sizes ($n_{x,L,0}$*).* We set the population size in year $t = 0$ of model projections equal to one-half of the mean annual population size (our model was female-based and we assumed a 50% sex ratio) for the state of Washington estimated with at-sea monitoring from 2011 to 2015 ($n = 3,616$ individuals; Falxa et al. 2016). While more recent surveys for murrelets have been completed in Washington, 2015 was the last year that a state-wide census was completed. The total number individuals (i.e., females) was allocated to DNR and non-DNR lands in proportion to the estimated carrying capacity of nesting habitat that exists on each of the two land ownerships (0.15 and 0.85, respectively), which yielded a total 542 individuals in the DNR subpopulation and 3,074 individuals in the non-DNR subpopulation. Within each subpopulation, we allocated individuals to the stage classes in accordance with the expected stable age distribution associated with a deterministic version of the matrix model structure that was parameterized as described above. Initially, nonbreeding and breeding stages ($n_{4,L,0}$ and $n_{5,L,0}$, respectively) were pooled (both classes treated as "adults") when determining the stage distribution in year $t = 0$. Adults were then allocated to the nonbreeding and breeding stages in year $t = 0$ as described below such that the number of adults exceeded the carrying capacity to a degree that provided reasonable correspondence between modeled population trajectories and

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observed trends in the Washington population.

Evaluating "*Risk*" and "*Enhancement*"

We parameterized the matrix model in both the *Risk* and *Enhancement* analyses using the values described above and listed in Table 1. We assumed that 40% of individuals of breeding age (≥ 3 years old) were in the nonbreeding stages in year $t = 0$ for each subpopulation and thus that the number of adult-aged individuals exceeded nesting carrying capacity for both analyses (see below). As described above, we made this assumption to reflect nesting habitat loss in the state of Washington that may have resulted in a nonbreeding component of the population. Moreover, associated density dependent effects on population growth allowed projected populations to decline in the initial years of the modeling period in reasonable accordance with recent observed declines (see below). The after-hatch-year annual survival rate was set to 0.87 and 0.90 in the *Risk* and *Enhancement* analyses, respectively. Higher survival rates in the *Enhancement* than *Risk* analysis allowed projected populations in this scenario to increase in response to potential gains in nesting habitat. For the portion of the *Enhancement* analysis focusing on DNR lands only, we assumed no dispersal between subpopulations to highlight "debits" and "credits" of forest management alternatives for losses and gains in nesting habitat, respectively, using population metrics.

Together, these assumptions yielded deterministic projections of population growth under constant habitat conditions that were reasonably consistent with the recent estimates of population trends (5% annual decline) in the initial years of the population projection. As the breeding-age component of modeled populations approached nesting carrying capacity, the rate of population growth increased in both the *Risk* and *Enhancement* analyses. The expected

population growth rate stabilized around year 15 under the *Risk* analysis, but stabilized below 1 (a population growth rate of 1 is indicative of a stable population), and the simulated populations were thus expected, on average to decline (by approximately 1.5% annually) over the projection period. By contrast, population growth stabilized above 1 under the *Enhancement* analysis, and thus we expected small population increases (approximately 1% annually) over the modeling period.

Modeling the Impact of Nesting Habitat Change on Marbled Murrelet Populations

As described above, we modeled the potential effects of forest management alternatives on marbled murrelet population dynamics by linking the maximum number of breeders (carrying capacity, $K_{L,t}$) and nest success rates ($f_{L,t}$) to forest conditions (i.e., nesting habitat) present in the two landownerships in each year t. We assumed that availability of nesting habitat limits murrelet breeding opportunities and that forest fragmentation reduces nest success via edge effects. Specific measures of nesting habitat considered were nesting habitat (1) area, (2) quality, and (3) configurations (WDNR 2015). These three measures were initially quantified at the forest stand scale using DNR's spatially-explicit forest inventory database which contains information on mapped stands of known acreage such as characteristics of age, origin (natural vs. planted), and composition (Douglas-fir vs. shade-tolerant). Stand-level characteristics were ultimately aggregated to develop estimates of the maximum number of breeders and expected nest success in each landownership. The analytical methods, rationale, and assumptions used to derive estimates of carrying capacity and nest success are described below in conceptual terms. For a more detailed, mathematical explanation, we direct the reader to Appendix A.

Effects of Forest Conditions on Carrying Capacity ($K_{L,t}$*).* The model imposed a limit to the

number of breeders ($K_{L,t}$) in each landownership based on the total amount, quality, and

configuration of nesting habitat in each year *t*. Nesting carrying capacity ($K_{L,t}$) was assumed to

be positively related to the amount of nesting habitat present on landownership *L* in year *t* in a

one-to-one manner; for example, a forest stand 100 ha in size would be expected to contain twice

as many breeding murrelets as a stand 50 ha in size, all other factors being equal (i.e., nesting

habitat quality and configuration). In Washington, a positive association has been observed

between radar counts of murrelets flying inland and the amount of late-seral stage forest at the

watershed scale, and the slope of this relationship is approximately one (Raphael et al. 2002).

Nesting density was assumed to be related to stand-level "habitat quality" based on generalized

probabilities of murrelet use that were associated with stages of successional development in

DNR-managed forest in southwest Washington (Raphael et al. 2008). Based on DNR's forest

inventory, stands were assigned to one of six nesting habitat quality categories ("Pstage"), non-

habitat (Pstage = 0) and five classes of habitat with Pstage values 0.25, 0.36, 0.47, 0.62, 0.89. In

the previous version of the report, the Pstage value at sites occupied by murrelets was reassigned

to an additional Pstage class, Pstage = 1; in the current version of the report we did not

redistribute the Pstage value at occupied sites to 1 but instead used the underlying Pstage value

(0.25, 0.36, 0.47, 0.62, or 0.89). This revised approach more precisely reflects estimated habitat

quality and permits increases in carrying capacity to occur at occupied sites through forest

maturation as forest stands transition into higher Pstage classes. Classification was based on

stand age, origin (natural vs. planted), and species composition, where (i) older stands were

assumed to have greater nesting densities than younger stands, (ii) naturally-regenerated stands

(unlike planted) were assumed to be capable of developing as habitat within the analysis period,

and (iii) stands dominated by western hemlock (*Tsuga heterophylla*) were assumed to develop into suitable habitat and thus greater nesting densities at an earlier age than stands dominated by Douglas-fir (*Pseudotsuga menziesii*). Together these three variables were assumed to represent the development of key murrelet nesting habitat characteristics such as large trees with large limbs and complex canopy structure. In our population model, the Pstage value represented the stand's maximum nesting density where, for example, ~3.5 acres of Pstage 0.25 provide the same nesting opportunities as one acre of Pstage 0.89.

Maximum nesting density was also influenced by edge effects, where availability of nest sites (and thus nesting density), was assumed to be lower in portions of stands adjacent to edges with non-habitat. Wind-throw as well as hotter, drier microclimate at the edge of young stands created by timber harvest can lead to the mortality of platform-bearing trees as well as epiphyte mortality that reduces platform abundance in surviving trees (Chen et al. 1992; van Rooyen et al. 2011). Edge effects were assumed to occur when a stand of suitable habitat (Pstage > 0) occurred adjacent to a stand dominated by trees < 80' (approximated as <40 years old) and were categorized based on the condition of adjacent young forests as "hard" (<40' tall approximated as <20 years old) or "soft" (40'-80' tall). Empirical values of tree density and suitable platform abundance from van Rooyen et al. (2011) formed the basis for adjustments to nesting density (Pstage) for the two edge types, 0.25 adjacent to hard edges and 0.60 at soft edges. Habitat in small, often linear fragments that were entirely edge, called *Strings* was assumed to have no value. Edge effects on larger habitat patches with areas over 100 meters from edge are assumed to be greatest near edges and decline with distance, generalized to "outer" and "inner" edges within 50 meters and between 50 and 100 meters from edge (Chen et al. 1992). Full effects were assumed to occur in outer edges, half-effects were assumed for inner edges, and "interior" habitat

>100 m from edge was assumed to be unaffected. Thus as informed by DNR's spatially-explicit

forest inventory, nesting density was estimated for each factorial combination of Pstage (five

classes), edge distance (three classes: outer, inner, interior), and edge type (hard and soft). This

process resulted in 20 combinations of five Pstage classes by edge-distance (outer, inner) and

edge-type (hard, soft) plus five Pstage classes in interior habitat providing 25 different nesting

density adjustments applied to current and alternative-specific projected future habitat maps. For

example, nesting density was assumed to be 14.2 times greater in Pstage = 0.89, interior forest

than in Pstage = 0.25 subject to the hard, outer edge effect of 0.25 (14.2 = 0.89 / (0.25*0.25).

Pstage and edge adjustments for non-DNR lands followed the assumptions of Raphael et al.

(2008) and were held constant over the modeling period.

Original nesting carrying capacity estimates (see Appendix A) based on the number of

adult female murrelets based on at-sea surveys failed to yield population trajectories consistent

with recent ~5% annual declines in the state (Falxa et al. 2016). Using deterministic simulations,

we found that when we set nesting carrying capacity such that 40% of adult murrelets were non-

breeders (i.e. the population was above carrying capacity), initial simulated population declines

better approximated recent observed ~5% annual declines. Therefore we set initial nesting

carrying capacity ($K_{L,0}$) to equal the number of adult breeders on each landownership L ($n_{5,L,0}$),

which was 60% of the number of female adult murrelets in year 0 based on a stable age

distribution (Table 1). In each subsequent year ($t \geq 1$), carrying capacity $K_{L,t \geq 1}$ changed based on

projected losses (from harvesting) or gains (through forest growth) in nesting habitat in each

Pstage by edge-type and distance combination and the nesting density relationships described

above. Moreover, because a single nesting carrying capacity was considered for each

landownership that reflected aggregate habitat conditions, we assumed that recruiting murrelets

choose nests sites randomly with respect to edge type and Pstage (i.e., they recruit into habitat in proportion to the abundance of potential nest sites it is assumed to provide).

Effects of Forest Conditions on Nest Success ($f_{L,t}$*).* The model also linked population growth rates to nesting habitat conditions by treating nest success rates (number of female offspring produced per nesting female) in landownership L and year t ($f_{L,t}$) as a function of the distribution of interior, inner edge, and outer edge forest in the landownership. Nest success was assumed to be greatest where edge effects were absent and to be reduced where nesting habitat occurred adjacent to a hard edge, with inner edges assumed to promote higher nest success than outer edges. Soft edges were assumed to have no influence in nest success (Raphael et al. 2002, Malt and Lank 2009). Estimates of nest success rates in soft- or non-edge influenced forest (0.550) and outer edge (0.380) were drawn from the upper and lower bounds assumed for this parameter in demographic analyses conducted by McShane et al. (2004). An intermediate value of 0.465 was assumed for nest success in inner edge near hard edges. In sum, greater relative amounts of edge habitat under a given management alternative were expected lead to a greater fraction of the population nesting near edges, lower mean nest success, and lower population growth rates.

Forest Management Alternatives

We considered eight forest management alternatives (A-H), each involving different approaches to timber harvesting and habitat conservation on DNR-managed land in western Washington (WDNR and USFWS 2018). Each alternative was built around *long-term forest cover* (LTFC), areas of existing conservation commitments made under the HCP (e.g., high-quality spotted owl habitat, riparian management zones), DNR's Policy for Sustainable Forests and state law. The

alternatives then variously add LTFC to further conserve and restore murrelet habitat. The abundance, configuration, and location of this murrelet-specific LTFC differs among alternatives, reflecting a range of conservation approaches. All alternatives provide for new habitat growth through the life of the HCP. Common among alternatives, initial ($t = 0$) forest conditions were set to current conditions on DNR-managed lands (DNR database and landscape models of potential murrelet nesting habitat) and other landownerships in Washington (Raphael et al. 2016). Projections of future habitat conditions over the 50-year modeling period were conducted by DNR using the Forest Vegetation Simulator (FVS), where differences in harvest and conservation among the management alternatives led to different expected trajectories in the amount, quality and configuration of murrelet nesting habitat on the landscape, and thus differences in carrying capacity and nest success among the alternatives (Figure 2). The eight alternatives are more thoroughly defined elsewhere (dnr.wa.gov/mmltcs), but they, and a baseline scenario (i.e., static forest conditions) are briefly summarized below:

1. **Alternative A** is the "no-action" alternative, approximating continued DNR operations as authorized under the 1997 HCP. This alternative includes approximately 600,000 acres of LTFC, with murrelet-specific conservation including: all occupied sites as delineated by HCP-directed surveys, with a 100-meter buffer; all reclassified habitat in OESF; all reclassified habitat in the Straits, South Coast and Columbia planning units that has not been identified as "released" for harvest under the interim strategy; in the North Puget and South Puget planning units, all suitable habitat that has not been identified as "released" for harvest subject to the 2007 concurrence letters, all newly identified habitat, and all potential habitat that has a Pstage value >0 in decade 0.

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2. **Alternative B** focuses on protecting the known locations of marbled murrelet occupied sites on DNR-managed land. Under this alternative, LTFC totals approximately 576,000 acres, and includes occupied sites delineated by the 2008 Science Team recommendations (Raphael et al. 2008). This approach results in approximately 16,000 acres more than the HCP delineations used by Alternative A, as well as occupied sites identified by DNR staff in the North and South Puget planning units. This is the only alternative that does not provide buffers on occupied sites.

3. **Alternative C** is designed to protect occupied sites and current habitat as well as grow new habitat over the life of the HCP. LTFC totals approximately 617,000 acres. This alternative contains both marbled murrelet "emphasis areas" and "special habitat areas." Seven emphasis areas from 4,100 to 15,600 acres are identified in strategic landscapes for the purpose of protecting and reducing fragmentation around occupied sites, and developing future marbled murrelet habitat. Twenty special habitat areas, 40 to 8,000 acres, are generally smaller than emphasis areas and are designed to increase murrelet productivity by reducing edge and fragmentation around more isolated occupied sites that are not within an emphasis area. Outside of emphasis or special habitat area boundaries, this alternative will also buffer all other existing occupied sites and will maintain all higher quality habitat (Pstage value 0.47 and greater).

4. **Alternative D** concentrates conservation into thirty-two special habitat areas, 40 to 14,400 acres. LTFC totals approximately 618,000 acres. All acreage within special habitat areas is designated as LTFC. Special habitat areas are designed to increase the productivity of existing occupied sites by increasing habitat abundance and reducing edge effects. They include: strategically located occupied sites with 100-meter buffers;

adjacent Pstage habitat (both existing and expected to develop through 2067); adjacent, non-habitat areas intended to provide security to existing and future habitat (security forests). The boundaries of the special habitat areas were identified based on existing landscape conditions (management history, watershed boundaries, natural breaks or openings). Because of its focus on reducing fragmentation around existing, occupied sites, Alternative D would allow more acres of potential habitat (habitat that has or will develop a Pstage value) to be harvested throughout the analysis area than Alternative C. However, the overall amount of LTFC is similar under Alternatives C and D.

5. **Alternative E** combines the conservation approaches of Alternatives C and D, for a total of approximately 621,000 acres of long-term forest cover. This alternative includes the following murrelet-specific conservation: occupied sites, with 100 meter buffers; all habitat with a Pstage value of 0.47 and greater throughout the analysis area; emphasis areas as designated under Alternative C; special habitat areas as designated under Alternative D (where emphasis areas and special habitat areas overlap, emphasis area will be the designation).

6. **Alternative F** proposes to apply the conservation recommendations presented in the 2008 Science Team report (Raphael et al. 2008), which evaluated conservation opportunities in the four coastal HCP planning units and recommended the establishment of 45 marbled murrelet management areas of up to 15,500 acres. It also applied the principles of Raphael et al. (2008) to establish 20 similar areas of up to 47,400 acres in the North and South Puget planning units. In total approximately 743,000 acres of LTFC is designated under this alternative. All occupied sites would be protected with a 100-meter buffer. Additionally, all Old Forest in the OESF would receive a 100-meter buffer.

Existing, mapped low quality northern spotted owl habitat in designated owl conservation areas (nesting/roosting/foraging, dispersal and OESF) is included as LTFC (Alternatives A through E only include high quality owl habitat as LTFC).

7. **Alternative G** is a new alternative, added between the DEIS and RDEIS. This alternative was developed based on comments received on the DEIS from federal and state agencies, environmental groups, and various individuals. Alternative G includes approximately 642,000 acres of LTFC. This alternative includes, emphasis areas, special habitat areas, and marbled murrelet management areas and applies 100 meter buffers to all occupied sites. Alternative G includes the following murrelet specific conservation lands: all habitat with a Pstage value of 0.47 and greater throughout the analysis area; in the OESF, all habitat with a Pstage greater than zero in decade zero; Emphasis Areas as designated under Alternative C; special habitat areas as designated under Alternative D (where emphasis areas and special habitat areas overlap, an emphasis area will be the designation); areas where the Pstage model did not identify potential existing habitat or applied a lower Pstage value than thought appropriate based on expert opinion (WDFW Polygons); the marbled murrelet management area in the Elochoman block, as drawn for Alternative F, managed as an Emphasis Area; and the following marbled murrelet management areas in the North Puget Planning Unit: Spada Lake/Morningstar, Whatcom, Middle Fork Hazel/Wheeler Ridge, Marmot Ridge.

8. **Alternative H** is DNR's preferred alternative. Alternative H is based on direction from the Board of Natural Resources to minimize impacts, offset impacts and address uncertainty, and reduce disproportionate financial impacts to trust beneficiaries. Alternative H minimizes impacts by conserving all existing occupied sites, capturing

existing habitat within special habitat areas, and metering harvest of habitat outside conservation areas in strategic locations. Metering delays harvest of a portion of habitat until the second decade of the modelling period. Metering is designed to maintain nesting carrying capacity on DNR-managed lands such that capacity always equals or exceeds baseline conditions. Alternative H offsets impacts and addresses uncertainty by applying 100-meter buffers on all occupied sites, locating special habitat areas in strategic locations, and increasing the amount of interior forest habitat in LTFC. This alternative reduces disproportionate financial impacts identified in the DEIS in Pacific and Wahkiakum counties under Alternatives C through F by placing less conservation on State Forest lands in these counties. Alternative H includes approximately 604,000 acres of LTFC.

9. **Baseline** represents a static habitat scenario, where the raw amount of murrelet nesting habitat that presently exists on DNR lands excluding habitat located in "strings" (162,592 acres) remains constant over the 50-year modeling period. Carrying capacity ($K_{1,t} = 217$) and nest success ($f_{1,t} = 0.5343$) also remain fixed. Although it is biologically unrealistic, the baseline scenario offers a useful benchmark by which to compare scenarios with changing habitat conditions.

In addition to the eight proposed alternatives, the DNR and USFWS proposed an additional analysis which would show how the modeled murrelet population on DNR lands might respond to Alternative H *without* the delayed harvest implementation (**Alternative H – 'no meter'**) under both *Risk* and *Enhancement* scenarios. This additional exploratory scenario sought to gauge how a more rapid rate of habitat decline (but less prolonged decline) might influence

projected murrelet populations.

For the eight primary alternatives and one exploratory alternative, forest conditions on non-DNR lands were assumed to be stationary over the modeling period. While we recognize that habitat conditions on non-DNR lands are not static, we lacked sufficient information for non-DNR lands to project habitat changes over time. Because our modeling objective was to evaluate how changes in habitat conditions on DNR lands may influence murrelet populations over time, it was appropriate to evaluate the range of alternatives in the context of the current conditions on non-DNR lands. Although this assumption is clearly unrealistic, some habitat will be lost to harvest and natural disturbances, and habitat will develop on federal lands reserved from harvest under the Northwest Forest Plan (Raphael et al. 2016), it was adopted because it simplified presentation and interpretation of population responses to changes on DNR-managed land which contain about 15% of murrelet nesting carrying capacity in Washington according to our analytical model.

Model Projections, Stochasticity, and Estimating Risk

Model Projections. We projected the model forward in time as follows:

$$\mathbf{n}_{t+1} = \mathbf{A}_t \cdot \mathbf{n}_t$$

where $\mathbf{n}_t$ was a 10 by 1 vector of murrelet abundance in the five stage classes $x = 1,2,\ldots,5$ and two landownerships $L = 1, 2$ in year t, and $\mathbf{A}_t$ was the matrix of vital rates (described above). The vector of population sizes $\mathbf{n}_1$ was:

$$\mathbf{n_1} = \begin{bmatrix} 83 \\ 52 \\ 46 \\ 145 \\ 217 \\ 472 \\ 293 \\ 260 \\ 819 \\ 1229 \end{bmatrix}$$

where the first five elements represent the number of juveniles, 1-year subadults, 2-year

subadults, and adults (nonbreeders and breeders) on DNR lands assuming a stable age

distribution. The second five elements would be the number of individuals in each of these stage

classes on non-DNR lands under the same sets of assumptions. The number of adults in the

nonbreeding and breeding classes (the fourth and fifth elements for each landownership) were

allocated based on deterministic carrying capacity simulations (see above).

Incorporating Environmental Stochasticity. The model incorporated the effects of stochasticity

by allowing survival and reproductive rates to vary randomly from year to year. After-hatch-year

survival rates in year *t* were selected randomly from a beta distribution. Selecting survival rates

from a beta distribution ensured that survival rates fell between 0 and 1. As discussed above, we

set the mean value for annual survival for after-hatch-year murrelets to 0.87 and 0.90 in the *Risk*

and *Enhancement* analyses, respectively, based on mark-recapture studies in California (Peery et

al. 2006b). Annual variability in survival has not been estimated rigorously for marbled

murrelets, but setting the variance in annual survival $[var(s)]$ to 0.004 resulted in few years with

survival < 0.75, and thus provided a reasonable degree of biological realism. Frequent survival

rates below 0.75 seemed implausible given the modest annual variability in population size

estimated from at-sea surveys (Falxa et al. 2016). Juvenile survival in year *t* was set to 70% of

after-hatch-year survival such that these two rates are assumed to co-vary perfectly. Stochasticity

in reproduction was modeled by first calculating expected fecundity (the number of female

juveniles per female adult denoted $m_{1,t}$ and $m_{2,t}$ for DNR and non-DNR lands, respectively)

which is simply the product of the expected proportion of females that breeders (b) and nest

success ($f_{L,t}$) divided by 2 (because approximately half of fledging juveniles are female).

Fecundity was then randomly selected in year t from a beta distribution with an expected value

of $m_{L,t}$ and a variance $[var(m)]$. An attempt was made to use the variance in reproductive data

from central California, but simply using a value of 0.016 for $[var(m)]$ yielded more realistic

projections. Fecundity on DNR and non-DNR lands was assumed to be perfectly correlated and

vary with the same magnitude. Survival and fecundity were assumed to co-vary independently

among years since these vital rates appear to be driven by different environmental processes

(Peery et al. 2006b, Becker et al. 2007). The variances of $[var(s)] = 0.004$ for survival and

$[var(m)] = 0.016$ for reproduction resulted in a mean coefficient of variation (CV) in simulated

populations over the first 15 years (CV = 0.201) that aligned with expectations based on the

process variance observed in murrelet at sea counts in WA from 2001 to 2015 (CV = 0.203),

when we used demographic values and nesting carrying capacity that led to approximately 5%

annual declines ($s_{\geq 2,L,t} = 0.87$ and $d_{L,t} = 0$).

Quantifying Population Risk. For each of the management alternatives (see below), we projected

10,000 simulated populations forward in time for $t = 50$ years (where $t = 0$ represented present

conditions). To assess patterns of risk, we estimated (i) the mean change in population size

between $t = 0$ and 50 and (ii) the "quasi-extinction probability", defined as the proportion of

simulated populations where $\sum_{i=1}^{x} n_{x,L,50}$ was lower than subjectively defined quasi-extinction

thresholds. Quasi-extinction thresholds were set to one half, one quarter, one eighth, and one

sixteenth of the starting population size (i.e., $\sum_{i=1}^{x} n_{x,L,0}$).

Sensitivity Analysis

While the scenario-based analysis of murrelet population viability allowed us to compare

potential effects of proposed forest management alternatives, the relative influence of changes in

individual habitat classes (e.g., inner edge vs. interior forest) on murrelets was confounded

because the alternatives included simultaneous changes in many or all habitat classes each year

throughout the 50-year modeling period. We developed a sensitivity analysis to explore the

relative influence of each the nine habitat classes (the three edge types and five Pstage

categories) on murrelet populations by simulating a change in one habitat class while controlling

for effects of other classes. Specifically, we simulated an immediate loss of 10,000 acres of

murrelet habitat in year $t = 0$ within either (*i*) one edge class (e.g., inner edge), where Pstage

classes were reduced in proportion to their availability within the focal edge class, or (*ii*) one

Pstage class, where edge classes were reduced in proportion to their availability within the focal

Pstage class. We created one additional scenario ("acreage") in which the simulated 10,000-acre

loss in habitat occurred proportionally across all 15 edge-Pstage combinations as a basis for

comparing the relative influence of habitat amount (raw acreage) vs. habitat quality (e.g., edge

conditions, Pstage) on murrelet populations.

Using 10,000 acres (~5.9% of total raw acreage) ensured that proportional losses to

certain habitat classes did not exceeded their availability on the landscape. For each of the 10

scenarios in the sensitivity analysis we simulated the 10,000-acre loss of habitat in year 0, ran the

population model for 50 years under the *Enhancement* parameterization, and repeated 10,000

simulations using SAS 9.3. We then compared the average percent population change on DNR lands after 50 years for all scenarios and compared these changes to a baseline scenario in which no habitat loss occurred. Results of the sensitivity analysis should be interpreted as the relative (as opposed to absolute) influence of different habitat classes (raw acreage, edge, Pstage) on murrelet population growth in the region.

RESULTS

Forest Management Scenarios

Four of the eight management alternatives (C, E, F, and G) were projected to result in a net gain in total acres of nesting habitat on DNR lands at the end of the 50-year modeling (Figure 2a), while the remaining four management alternatives (A, B, D, and H) were projected to result in less total acres of nesting habitat (Figure 2a). All eight management alternatives were projected to result in higher nesting carrying capacity and expected nest success on DNR lands at the end of the 50-year modeling period (Figure 2b-c). Nevertheless, some alternatives differed from one another considerably with respect to all three metrics (Figure 2a-c). The most optimistic scenario for change in raw murrelet habitat was alternative F, in which net habitat increased by 30% over the 50-year modeling period. In contrast, the most pessimistic scenario for change in raw habitat was alternative B, which ended with a net 13% loss in habitat after 50 years. In terms of raw habitat change, the remaining alternatives fell between B and F (Figure 2a). Similarly, differences in nesting carrying capacity (K) among the eight alternatives were bounded on the upper end by alternative F and on the lower end by alternative B. Carrying capacity increased by 149% under alternative F, while alternative B ended with a net 36% increase in nesting carrying

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capacity despite a net loss in nesting habitat. Carrying capacities for the remaining alternatives always fell between B and F (Figure 2b). Mean nest success, which contributed to estimates of annual fecundity, generally increased in all scenarios over the first 30 years of the simulation then gradually decreased for the final 20 years (Figure 2c). In contrast to the eight management alternatives, the baseline scenario did not vary temporally but was structured such that the amount of raw habitat, nesting carrying capacity, and mean nest success remained constant over the 50-year modeling period.

Changes to raw habitat, nesting carrying capacity, and nest success for the exploratory variant of alternative H (H – 'no meter') can be found in Figure 2d-f. Alternative H – 'no meter' tracked alternative H closely except over the first two decades for raw habitat and carrying capacity, because alternative H – 'no meter' was not designed to implement the delayed harvesting strategy as in alternative H (Figure 2d-e). Nest success for alternatives H and H – 'no meter' was identical (Figure 2f).

Population Viability Analysis

Risk analysis, DNR population. In the *Risk* analysis, we observed considerable variation in the probability of the murrelet population on DNR lands reaching quasi-extinction thresholds across the eight management alternatives and baseline scenario (Figure 3). The probability of murrelet populations on DNR lands reaching 1/2 their initial size after 50 years ranged from 0.7805 (alternative F) to 0.9387 (alternative B). Likewise, alternative F defined the lower boundary and alternative B defined the upper boundary of quasi-extinction probabilities for smaller thresholds: at 1/4 of initial N, quasi-extinction probability ranged from 0.3494 (alternative F) to 0.6618 (alternative B); at 1/8 of initial N, quasi-extinction probability ranged from 0.0670 (alternative F)

to 0.2434 (alternative B); and at 1/16 of initial N, quasi-extinction probability ranged from 0.0043 (alternative F) to 0.0387 (alternative B). A complete list of quasi-extinction probabilities for all alternatives is provided in Table 2.

Mean female population size on DNR lands declined from 542 individuals to 200.9 (most optimistic) and 124.8 (most pessimistic) under alternatives F and B representing a 62.9% and 77.0% decline in population size, respectively, after 50 years. Mean female population size for the remaining alternatives (as well as the baseline scenario) fell between that of alternatives F and B after 50 years (Figure 4). A complete list of mean female population sizes at 10-year intervals across the 50-year modeling period is provided in Table 3.

Risk analysis, Washington population. In the *Risk* analysis, quasi-extinction probabilities for the Washington murrelet population were much more tightly clustered among the management alternatives (Figure 5). Projections of risk were presumably relatively uniform because modeled management actions were limited to DNR lands, which contained a relatively small portion (~15%) of carrying capacity for murrelets nesting in the state. The probability of the Washington murrelet population reaching 1/2 of its initial size after 50 years ranged from 0.7804 (alternative F) to 0.8150 (alternative B). For the remaining quasi-extinction thresholds, alternative F generally formed the lower bound and alternative B formed the upper bound. At 1/4 of initial N, quasi-extinction probability ranged from 0.2993 (alternative F) to 0.3406 (alternative B); at 1/8 of initial N, quasi-extinction probability ranged from 0.0476 (alternative F) to 0.0534 (alternative B). At 1/16 of initial N, quasi-extinction probability ranged from 0.0024 (alternative E) to 0.0038 (alternative B), although the difference between these probability estimates represents only 14 of 10,000 simulations. A complete list of quasi-extinction probabilities for all alternatives is

provided in Table 2.

Mean female population size on all lands in Washington declined from 3,616 to 1,125 (most optimistic) and 1,065.5 (most pessimistic) under alternatives F and B representing a 68.9% and 70.5% decline in population size, respectively, after 50 years. Mean female population size among the remaining alternatives (as well as the baseline scenario) fell between that of alternatives F and B after 50 years (Figure 6). A complete list of mean female population sizes at 10-year intervals across the 50-year modeling period is provided in Table 3.

Enhancement analysis, DNR population. In the *Enhancement* analysis, quasi-extinction probabilities were lower on DNR lands than in the *Risk* analysis (Figure 7). The probability of murrelet populations on DNR lands reaching 1/2 their initial size after 50 years (in the absence of dispersal among land ownerships) ranged from 0.0470 (alternative F) to 0.1863 (alternative B). At 1/4 of initial N, quasi-extinction probabilities among alternatives ranged from 0.0027 (alternative G) to 0.0122 (alternative B); at 1/8 and 1/16 of initial N, quasi-extinction probability was nearly equal to zero across all alternatives (i.e. three or fewer of 10,000 simulations reached quasi-extinction thresholds for all alternatives). A full table of quasi-extinction probabilities for all alternatives is found in Table 2.

With the exception of the baseline scenario, in which female population size continued to decline over the 50-year modeling period, all management alternatives resulted in a murrelet population trajectory characterized by an initial decline for the first 10-20 years followed by a gradual and sustained increase through the end of the modeling period (Figure 8). Female population size on DNR lands increased from 542 individuals to 650.1 (most optimistic) and declined to 388.4 (most pessimistic) under alternatives F and B representing a 20% increase and

28.3% decline in population size, respectively, after 50 years. Mean female population size among the remaining alternatives fell between that of alternatives F and B after 50 years (Figure 8). A complete list of mean female population sizes at 10-year intervals across the 50-year modeling period is provided in Table 3.

Enhancement analysis, Washington population. Quasi-extinction probabilities among alternatives for the Washington murrelet population were considerably lower in the *Enhancement* than the *Risk* analysis (Figure 9). The probability of the Washington murrelet population reaching 1/2 of its initial size after 50 years ranged from 0.0488 (alternative F) to 0.0737 (alternative B). Quasi-extinction probability was nearly equal to zero for all other thresholds among all alternatives (i.e. fewer than 25 of 10,000 simulations reached quasi-extinction thresholds for all alternatives). A complete list of quasi-extinction probabilities for all alternatives is provided in Table 2.

In contrast to the *Risk* analysis, in which the Washington murrelet population followed a relatively steep and steady decline throughout the 50-year modeling period, female population size in the *Enhancement* analysis declined for 20-30 years but then remained approximately stable for the remainder of the modeling period across all alternatives (Figure 10). Female population size in the state of Washington declined from 3,616 individuals to 2,734.2 (most optimistic) and 2,454.2 (most pessimistic) individuals under alternatives F and B representing a 24.4% and 32.1% decline in population size, respectively, after 50 years. Mean female population size among the remaining alternatives fell between that of alternatives F and B after 50 years (Figure 10). A complete list of mean female population sizes at 10-year intervals across the 50-year modeling period is provided in Table 3.

Exploratory analyses with variant of alternative H. We evaluated the exploratory variant of alternative H under the *Risk* and *Enhancement* scenarios for DNR lands only. In the *Risk* analysis, quasi-extinction probabilities were always higher for alternative H – 'no meter' compared with alternative H (Figure 3, Table 2). The probability of the murrelet population on DNR lands reaching 1/2 its initial population size after 50 years was 0.8864 for alternative H – 'no meter' and 0.8467 for alternative H. At 1/4 of initial N, the quasi-extinction probability was again higher for alternative H – 'no meter' (0.5326) compared to alternative H (0.4282) and the same pattern continued at 1/8 and 1/16 of initial N (Figure 3, Table 2). Female population size declined from 542 individuals to 153.0 and 176.5 individuals under alternatives H – 'no meter' and H, respectively, after 50 years (Figure 4). A complete list of quasi-extinction probabilities is provided in Table 2, and mean female population sizes at 10-year intervals is provided in Table 3.

Similar to the *Risk* analysis, quasi-extinction probabilities in the *Enhancement* analysis were higher for alternative H – 'no meter' than for alternative H. At 1/2 of initial N, quasi-extinction probability was 0.1057 for alternative H – 'no meter' followed by alternative H (0.0870). This pattern persisted at 1/4 of initial N but the differences among scenarios was smaller; quasi-extinction probability was 0.0056 for alternative H – 'no meter' and 0.0043 for alternative H. At 1/8 and 1/16 of initial N, quasi-extinction probability was nearly zero for both alternatives (Figure 7, Table 2). Mean female population size declined from 542 individuals to 476.3 and 487.6 individuals under alternatives H – 'no meter' and H, respectively, after 50 years (Figure 8, Table 3). A complete list of quasi-extinction probabilities is provided in Table 2, and mean female population sizes at 10-year intervals is provided in Table 3.

Sensitivity Analysis

Murrelet population growth was most sensitive to changes in the highest Pstage (habitat quality) classes 0.89 and 0.62; reducing the prevalence of these habitat classes on the landscape by 10,000 acres resulted in population estimates that were 18.7% and 13.4% lower than the baseline (static habitat) scenario after 50 years, respectively. Removing 10,000 acres of murrelet habitat across the 18 Pstage-edge class combinations in proportion to their availability ('acreage') resulted in a population estimate 10.4% lower than the baseline, which had a slightly weaker effect on murrelet population growth than removing 10,000 acres of interior forest (11.6% lower than baseline). Removing inner edge and outer edge resulted in final populations 9.1% and 8.1%, lower than the baseline scenario, respectively. Removing 10,000 acres of Pstages 0.47, 0.36, and 0.25 resulted in final populations 10.2%, 8.0%, and 5.9% lower than the baseline scenario, respectively (Figure 11).

DISCUSSION

Implications for Population Risk and Enhancement

We developed a stochastic, demographic meta-population model to compare the relative differences among alternative forest management strategies for DNR lands on the viability of marbled murrelet populations in the state of Washington. Moreover, we carried out parallel *Risk* and *Enhancement* analyses to help assess the relative manner in which proposed management actions were projected to increase population risk or the likelihood of population recovery given that it was not possible to assess both of these HCP considerations with a single analysis. Two

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alternatives (B and D) were projected to reduce murrelet population size compared to alternative A ("no-action"; i.e., continued management under the 1997 HCP guidelines) on DNR lands if murrelet populations continue to decline as a result of environmental factors unrelated to changes in nesting habitat quality and quantity (i.e., under the *Risk* analysis), but only alternative B reduced murrelet population size compared to alternative A when all lands were considered (Table 3). Conversely, our findings suggest that all other alternatives (C, E-H) are expected to lead to larger murrelet populations than alternative A should the population continue to decline as a results of these factors. Alternative B appeared to provide less capacity for murrelet populations to increase in size than alternative A, whereas alternatives C through H led to larger murrelet populations than alternative A, under the assumption that environmental stressors likely impacting murrelets are ameliorated (i.e., in the *Enhancement* analysis). The same patterns were generally observed for quasi-extinction probabilities.

Differences in ending population size among the proposed alternatives were greater when inference was limited to the "DNR population" as opposed to the entire state of Washington, particularly when differences were considered on a percentage basis. Compared to the "no-action" alternative (A), ~1.3 times as many murrelets were expected to occur on DNR lands under alternative F after 50 years according to both *Risk* and *Enhancement* analyses (i.e., a 30% difference). While percentage differences in ending population sizes among alternatives were greater for the DNR "population" than they were for the entire Washington population, differences in the number of individuals among alternatives were more similar at the two spatial scales. For example, the difference in mean ending population size between alternative F and "no-action" (alternative A) alternatives was 48.3 for DNR lands and 36.3 individuals for the state of Washington in the *Risk* analysis. Thus, differences in abundance among the alternatives at the

state level were largely the result of changes in abundance on DNR lands, which were included in state level projections of population sizes.

Comparison of Individual Alternatives

For both *Risk* and *Enhancement* analyses, alternative B consistently resulted in the lowest projected murrelet numbers after the 50-year simulation period, and generally had the highest quasi-extinction probabilities. Alternative B was the only proposed alternative that resulted in lower murrelet numbers than the "no-action" alternative (alternative A) in all analyses; both *Risk* and *Enhancement* analyses at the scale of DNR lands and the state of Washington. This finding was, to a certain extent, consistent with the fact that alternative B would include the least (576,000 acres) LTFC among all alternatives. By comparison, the "no-action" alternative (A) would involve the protection of 600,000 acres of LTFC. Compared to the "no-action" alternative (see above for details), alternative B focused only on protecting the known locations of marbled murrelet occupied sites on forested state trust lands, and was the only alternative that did not provide buffers on occupied sites. Similar to alternative B although to a lesser extent, alternative D sometimes also yielded lower projected murrelet numbers than alternative A after 50 years for both DNR lands and the state of Washington under the *Risk* analysis, but yielded slightly higher numbers than alternative A under the *Enhancement* analysis (Table 3).

In contrast, alternative F consistently resulted in the highest projected murrelet numbers after the 50-year simulation period for both *Risk* and *Enhancement* analyses. At the state level, alternative F was projected to lead to an average of 59.5 and 280 more female murrelets than alternative B under the *Risk* and *Enhancement* scenarios, respectively. Alternative F also generally had the lowest quasi-extinction probabilities. Under alternative F, 101,000 more acres

(743,000 acres total) of LTFC than any other alternative (alternative G being the second most conservative, involving the protection of 642,000 acres).

In sum, alternative B posed the greatest risk to murrelet populations and alternative F (often closely followed by alternative G) provided the greatest capacity to enhance murrelet populations. Importantly, our population simulations suggested that alternatives F and B were generally the "best" and "worst", respectively, with respect to murrelet population viability for DNR lands and the state of Washington in both the *Risk* and *Enhancement* analyses. This result is useful from a forest management perspective, because whether or not unrelated chronic environmental stressors are alleviated (i.e., the major difference in model assumptions between *Risk* and *Enhancement* analyses), alternative F is predicted to have the most positive effect on murrelet populations over the next 50 years because it provides the greatest amount of habitat and carrying capacity with the least edge effects.

Alternative H with delayed harvest suggested that harvesting over two decades as opposed to one decade (Figure 2d) ultimately translates to greater murrelet numbers and lower quasi-extinction probabilities (Tables 2 and 3). The delayed pace of harvest appears to balance with forest growth and development such that although harvesting under H results in a decline of overall habitat in the first 20 years of the simulation (Figure 2d), nesting carrying capacity remains steady and begins to increase over the same period (Figure 2e). This steady and increasing carrying capacity in the initial years of alternative H alleviates the downward pressure that projected murrelet populations experience when harvest is more rapid, resulting in greater capacity for population growth and therefore greater murrelet numbers.

Sensitivity of Marbled Murrelet Populations to Habitat Change

The sensitivity analysis suggested that murrelet populations were most sensitive to changes in the amount of higher-quality nesting habitat (Pstages 0.89 and 0.62), which exerted a stronger influence on modeled trajectories than changes in either the raw amount of nesting habitat or edge conditions (habitat configuration). Murrelet nests are typically located in large, decadent platform-bearing trees which, because of their age and economic value are relatively uncommon across the landscape and likely represent a limiting factor with respect to murrelet population densities (Burger 2001, Raphael et al. 2002). Because the highest Pstage classes represent forest stands with greater densities of platform-bearing trees suitable for nesting and presumably higher levels of murrelet use, it is therefore unsurprising that murrelet population growth appeared to be more sensitive to loss of the highest-quality habitat which, acre-for-acre, has a disproportionate influence on the population density of breeding-age murrelets. While change in habitat configuration (edge) was linked to nest success as well as nesting density in our analytical model, it nevertheless had a relatively modest influence on murrelet population growth presumably because the proportion of interior forest is considerably higher for the highest Pstages than the other categories on DNR-managed land (WDNR and USFWS 2018).

Caveats and Future Directions

Our model was parameterized with published demographic information collected for marbled murrelets from intensive field studies and structured based on a reasonable understanding and interpretation of murrelet ecology and nesting habitat needs. Moreover, the reproductive component of the model was informed by detailed assessments forest conditions in the state of Washington, and particularly on DNR lands. However, changes in climate and other

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environmental factors, particularly in the marine environment, that were not considered explicitly here likely also impact murrelet population dynamics and will continue to do so in the future. For example, unanticipated increases in marine stressors could further diminish murrelet populations regardless of projected increases to the amount and quality of nesting habitat. Nevertheless, the scope of this analysis was to estimate the potential and relative effect of habitat management alternatives using parameters largely under the control of land management agencies. Future areas of research could involve the development of a population model that more explicitly links risk to, for example, potential future changes in climate, oil spills, fisheries interactions, and predators.

As is always the case in PVA analyses, our model required a number of simplifying assumptions. We assumed that murrelets recruiting into the breeding population (e.g., 2-year subadults) selected nesting habitat independent of quality. Rather, individuals recruited into habitat types "proportionally" such that if, for example, three murrelets recruited into the breeding population, ~2 would do so into Pstage = 0.47 habitat and ~1 would recruit into Pstage = 0.25 habitat, even if additional nests were available in Pstage = 0.47 habitat. Second, we assumed that breeders remained in the same landownership unless they were displaced by habitat loss, and thus assumed that only nonbreeding individuals recruiting into the breeding population dispersed among landownerships. In other words, natal dispersal was permitted but, in the absence of habitat loss, breeding dispersal was not. Third, we assumed that displaced breeders (by habitat loss) could become nonbreeders for at least one year (for analytical tractability) and that displaced breeders could become breeders again if nesting habitat was available the year after they became nonbreeders. All of these aspects of murrelet breeding ecology are not well understood, and violations of associated assumptions could influence inferences regarding risk to

the population.

Population viability analyses range from simple count-based approaches to more complicated spatially-explicit demographic meta-population approaches (Morris and Doak 2002). Here, we used a two-population model (DNR vs non-DNR lands) as a simplification of the complex spatial arrangement of murrelet nesting habitat in Washington given time and budgetary constraints, this simplification being agreed upon by DNR and FWS. However, the spatial arrangement of murrelet nesting habitat likely plays an important role in murrelet movement and dispersal processes throughout the state. Future efforts using spatially-explicit models could provide geographically-targeted (local) estimates of risk, prioritize stands for conservation and management, and generate more realistic insights into how changes in the spatial arrangement of nesting habitat may influence regional murrelet population viability. However, uncertainty about the landscape ecology of murrelet habitat selection and use as well as dispersal processes could obscure inference from such an effort. Finally, we note that results from PVA analyses such as ours typically constitute one of many sources of information (e.g., habitat mapping, expert opinion, etc.) that can inform species conservation and land management decisions and we recommend that they be treated as such.

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TABLES AND FIGURES

Table 1. Parameter values used is in the marbled murrelet meta-population model.

Parameter	Analysis	DNR	non-DNR	Reference/Justification
Initial (female) population size ($n_{x,L,0}$)	Both	$\sum\limits_{i=1}^{x} n_{x,1,0} = 542$	$\sum\limits_{i=1}^{x} n_{x,2,0} = 3{,}074$	Falxa *et al.* (2016); Lance and Pearson (2016)
Initial (female) adult non-breeders ($n_{4,L,0}$)	Both	$n_{4,1,0} = 145$	$n_{4,2,0} = 819$	40% of adult females begin as non-breeders because the population is above carrying capacity
Initial (female) adult breeders ($n_{5,L,0}$)	Both	$n_{5,1,0} = 217$	$n_{5,2,0} = 1{,}229$	
Mean 1-year old survival rate ($s_{1,L,t}$)	Both	$s_{1,1,t} = s_{2,1,t} \cdot 0.7$	$s_{1,2,t} = s_{2,2,t} \cdot 0.7$	Peery *et al.* (2006a, b)
Mean >1-year old survival rates ($s_{\geq 2,L,t}$)	*Risk*	$s_{2,1,t}, .., s_{5,1,t}$ $= 0.87$	$s_{2,2,t}, .., s_{5,2,t}$ $= 0.87$	Peery *et al.* (2006a, b)
	Enhancement	$s_{2,1,t}, .., s_{5,1,t}$ $= 0.90$	$s_{2,2,t}, .., s_{5,2,t}$ $= 0.90$	Peery *et al.* (2006a, b)
Variance in survival rates	Both	$var(s) = 0.004$	$var(s) = 0.004$	Yields coefficient of variation (CV) in simulated populations similar to process CV in population estimates from at-sea surveys
Maximum dispersal rate ($d_{L,t}$)	*Risk, Enhancement* (WA population	$d_{1,t} = 0.85$	$d_{2,t} = 0.15$	Equal to proportion of murrelet habitat on DNR and non-DNR lands, lower if

	only)			number of dispersers exceeds availability of nest sites in other landownership
	Enhancement (DNR population only)	$d_{1,t} = 0$	$d_{2,t} = 0$	Assumes DNR and non-DNR populations are demographically independent
Proportion of breeders (possess a nest site) that breed per year (b)	Both	$b = 0.90$	$b = 0.90$	Peery *et al.* (2004)
Mean nest success rate ($f_{L,0}$)	Both	$f_{1,0} = 0.5347$ $f_{1,\geq 1}$ varies by management alternative	$f_{2,0} = 0.5418$ $f_{2,\geq 1}$ remains constant	See Appendix A
Fecundity rate ($m_{L,t}$)	Both	$m_{1,t} = \dfrac{b \cdot f_{1,t}}{2}$	$m_{2,t} = \dfrac{b \cdot f_{2,t}}{2}$	
Variance in fecundity rate	Both	$var(m) = 0.016$	$var(m) = 0.016$	Yields coefficient of variation (CV) in simulated populations similar to process CV in population estimates from at-sea surveys
Carrying capacity (number of nests) ($K_{L,t}$), scaled	Both	$K_{1,0} = 217$ $K_{1,\geq 1}$ varies by management alternative	$K_{2,0} = 1,229$ $K_{2,\geq 1}$ remains constant	See Appendix A

Table 2. Quasi-extinction probabilities for proposed forest management alternatives (A – H) under the *Risk* and *Enhancement* analyses. Note that a quasi-extinction probability of 0.0001 represents 1 out of 10,000 simulations.

| | *Risk - DNR lands* | | | | | *Risk - Washington* | | | |
| | Fraction of Initial Population Size | | | | | Fraction of Initial Population Size | | | |
Alternative	1/16	1/8	1/4	1/2	Alternative	1/16	1/8	1/4	1/2
A	0.0220	0.1581	0.5292	0.8879	A	0.0029	0.0506	0.3214	0.8039
B	0.0387	0.2434	0.6618	0.9387	B	0.0038	0.0534	0.3406	0.8150
C	0.0131	0.1230	0.4644	0.8458	C	0.0026	0.0493	0.3158	0.7950
D	0.0253	0.1652	0.5449	0.8869	D	0.0036	0.0526	0.3274	0.7985
E	0.0099	0.1059	0.4423	0.8330	E	0.0024	0.0507	0.3215	0.7880
F	0.0043	0.0670	0.3494	0.7805	F	0.0029	0.0476	0.2993	0.7804
G	0.0055	0.0725	0.3709	0.7914	G	0.0034	0.0496	0.3132	0.7827
H	0.0061	0.0895	0.4282	0.8467	H	0.0033	0.0528	0.3187	0.7916
H (no meter)	0.0217	0.1653	0.5326	0.8864	-	-	-	-	-
Baseline	0.0086	0.1022	0.4637	0.8970	Baseline	0.0032	0.0529	0.3237	0.8034

| | *Enhancement - DNR lands* | | | | | *Enhancement - Washington* | | | |
| | Fraction of Initial Population Size | | | | | Fraction of Initial Population Size | | | |
Alternative	1/16	1/8	1/4	1/2	Alternative	1/16	1/8	1/4	1/2
A	0	0.0001	0.0059	0.0981	A	0	0	0.0017	0.0664
B	0	0.0003	0.0122	0.1863	B	0	0	0.0016	0.0737
C	0	0.0003	0.0053	0.0682	C	0	0.0001	0.0024	0.0600
D	0	0.0003	0.0058	0.1030	D	0	0.0002	0.0022	0.0627
E	0	0	0.0040	0.0732	E	0	0.0001	0.0020	0.0574
F	0	0	0.0035	0.0470	F	0	0	0.0019	0.0488
G	0	0	0.0027	0.0545	G	0	0	0.0014	0.0584
H	0	0.0001	0.0043	0.0870	H	0	0	0.0026	0.0583
H (no meter)	0	0.0001	0.0056	0.1057	-	-	-	-	-
Baseline	0	0.0001	0.0055	0.1616	Baseline	0	0.0001	0.0029	0.0676

Table 3. Projected mean population sizes (average of 10,000 simulations) at each 10-year interval for proposed forest management alternatives (A – H) in the *Risk* and *Enhancement* analyses.
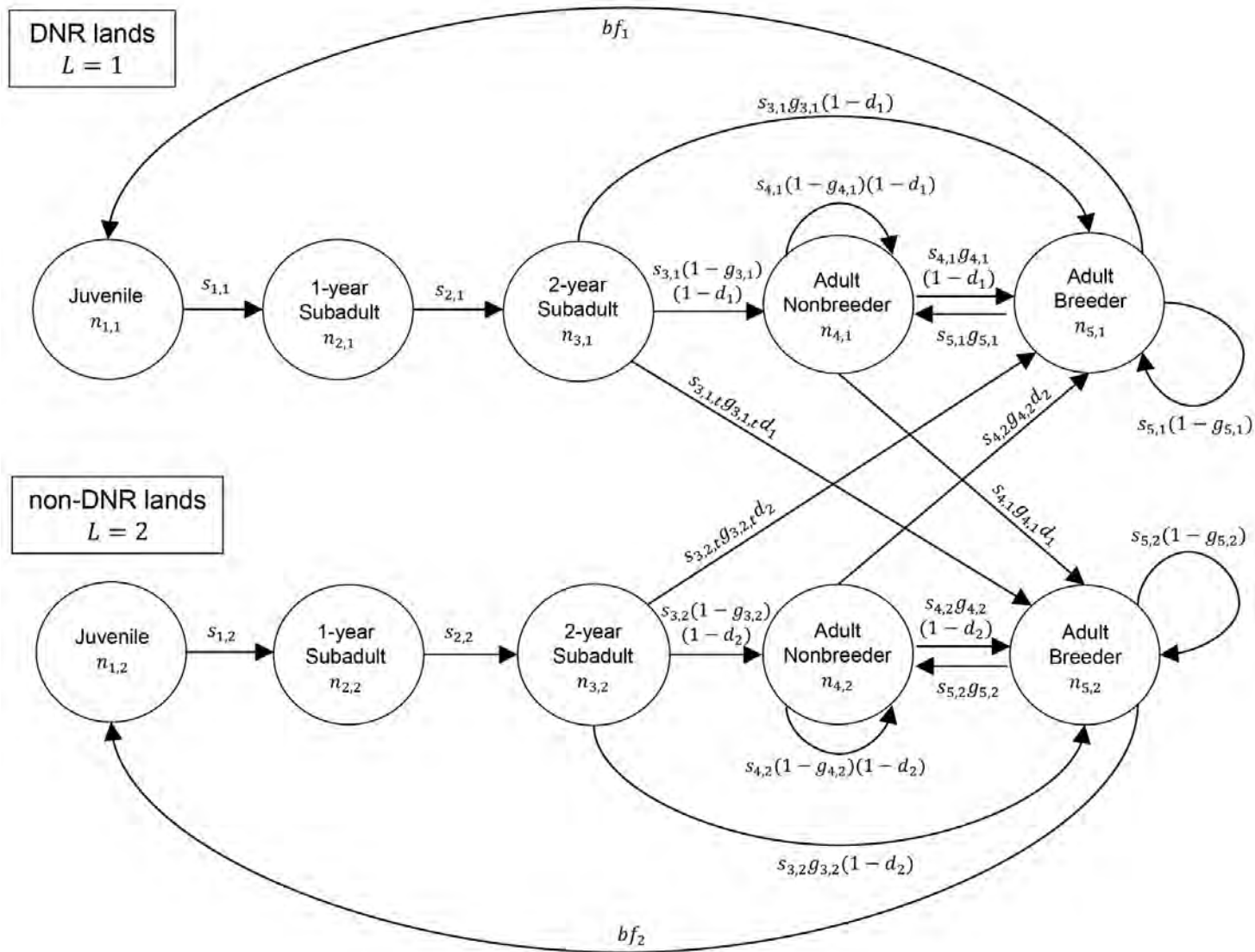
	Risk - DNR lands Year of Simulation							*Risk - Washington* Year of Simulation					
Alternative	0	10	20	30	40	50	Alternative	0	10	20	30	40	50
A	542	306.4	240.5	208.1	179.2	152.6	A	3616	2320.3	1837.3	1533.0	1291.5	1088.7
B	542	277.6	194.8	168.5	145.6	124.8	B	3616	2294.2	1806.2	1500.2	1260.3	1065.5
C	542	326.9	272.4	233.5	201.7	172.5	C	3616	2338.3	1873.4	1549.7	1311.9	1110.1
D	542	302.2	237.1	205.7	176.7	152.1	D	3616	2310.5	1837.3	1530.7	1287.3	1096.5
E	542	336.7	280.0	242.0	207.7	177.9	E	3616	2345.8	1869.6	1557.7	1312.0	1114.0
F	542	371.9	318.8	274.8	235.3	200.9	F	3616	2362.3	1892.0	1576.7	1327.5	1125.0
G	542	366.4	310.1	266.6	228.5	196.0	G	3616	2355.3	1875.9	1562.2	1316.9	1119.5
H	542	350.0	279.0	238.1	205.2	176.5	H	3616	2345.0	1862.5	1551.1	1310.5	1114.1
H (no meter)	542	305.6	239.7	206.3	178.3	153.0	-	-	-	-	-	-	-
Baseline	542	348.6	275.9	227.1	188.2	157.5	Baseline	3616	2340.0	1863.2	1545.2	1291.0	1088.8

	Enhancement - DNR lands Year of Simulation							*Enhancement - Washington* Year of Simulation					
Alternative	0	10	20	30	40	50	Alternative	0	10	20	30	40	50
A	542	407.4	374.1	394.1	432.9	478.5	A	3616	2868.3	2616.6	2522.4	2514.4	2531.8
B	542	379.2	315.2	324.1	352.4	388.4	B	3616	2842.8	2558.0	2472.4	2452.8	2454.2
C	542	427.7	413.6	442.4	485.2	534.8	C	3616	2885.0	2647.5	2582.6	2578.5	2599.8
D	542	403.9	370.7	393.7	434.2	482.2	D	3616	2863.2	2613.3	2540.2	2530.6	2541.0
E	542	430.8	419.7	449.0	495.2	544.2	E	3616	2886.9	2658.6	2585.1	2576.5	2598.4
F	542	458.0	470.2	516.1	575.3	650.1	F	3616	2918.2	2715.3	2661.2	2681.0	2734.2
G	542	451.4	457.4	495.1	547.3	608.0	G	3616	2913.7	2701.3	2635.2	2632.8	2671.3
H	542	431.8	397.5	407.3	444.4	487.6	H	3616	2893.2	2649.2	2557.9	2537.3	2557.7
H (no meter)	542	405.5	371.0	391.1	430.6	476.3	-	-	-	-	-	-	-
Baseline	542	431.1	392.3	374.1	365.4	357.5	Baseline	3616	2890.0	2640.1	2526.3	2466.8	2427.8

Figure 1. Life-cycle diagram for the demographic meta-population model used to evaluate the potential effects of Washington DNR's

management alternatives on marbled murrelets. $n_{x,L}$ represents the number of female murrelets; $s_{x,L}$ represents the survival probability; $g_{x,L}$ represents the transition probability; d_L represents the dispersal probability; b represents the breeding probability; f_L represents nest success rate; the subscript $x = 1,2,\ldots,5$ represents stage classes juvenile, 1-year subadult, 2-year subadult, adult nonbreeder, and adult breeder, respectively; the subscript $L = 1, 2$ represents DNR and non-DNR lands, respectively. Note that time t was not included in the diagram for simplicity.
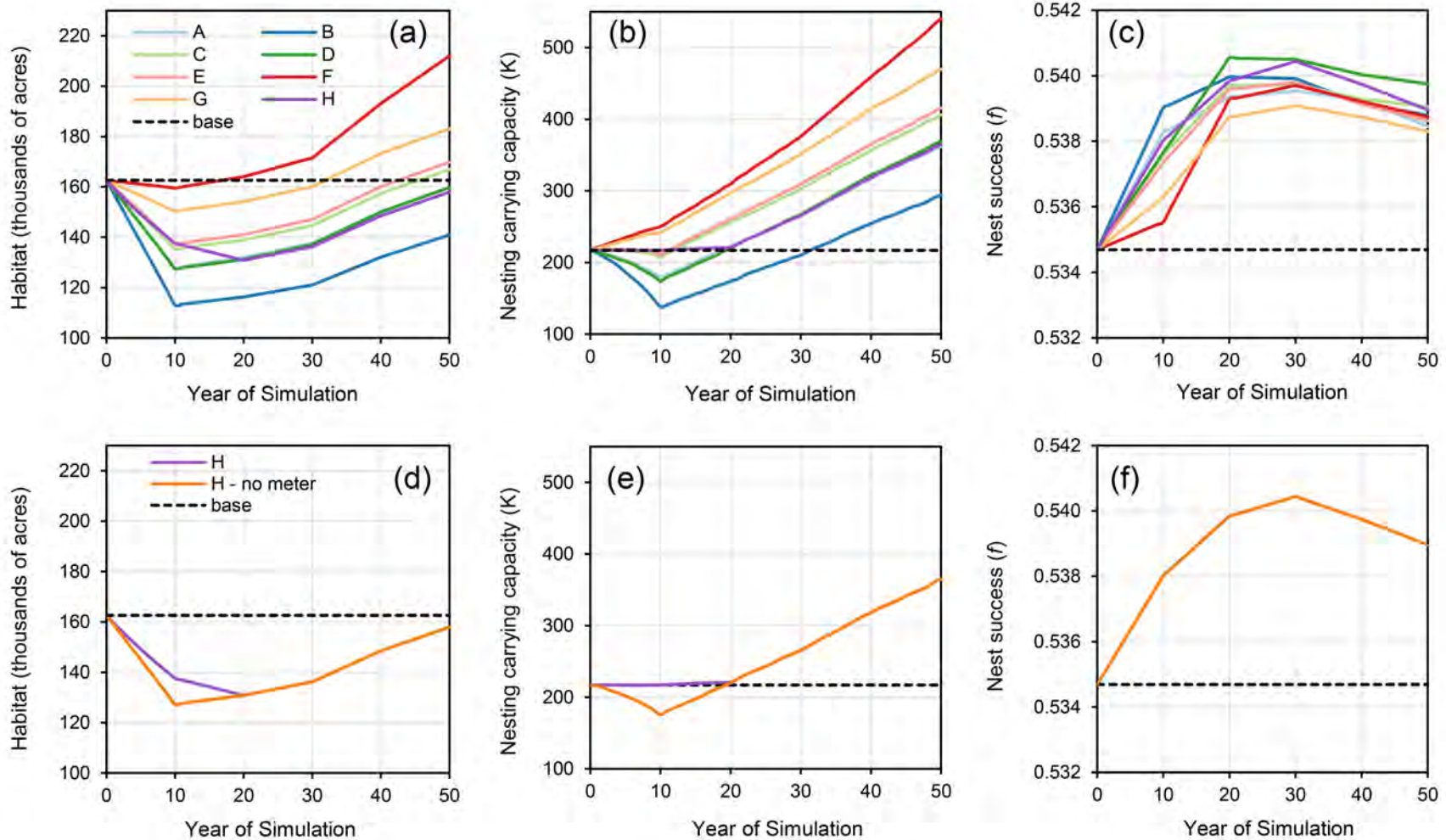
Figure 2. Forest management alternatives proposed by the Washington DNR and the U.S. Fish and Wildlife Service. The raw amount

of nesting habitat, carrying capacity, and nest success on DNR-managed lands for each of the primary alternatives (A – H) over the

modeling period are presented in panels a – c, respectively. Habitat "strings" are not included in these estimates. The same measures

for the exploratory alternative (H – 'M') is shown in panels d – f, and includes alternative H for the purposes of comparison.

Note: The lines showing nest success for alternatives H and H-M are on top of one another.
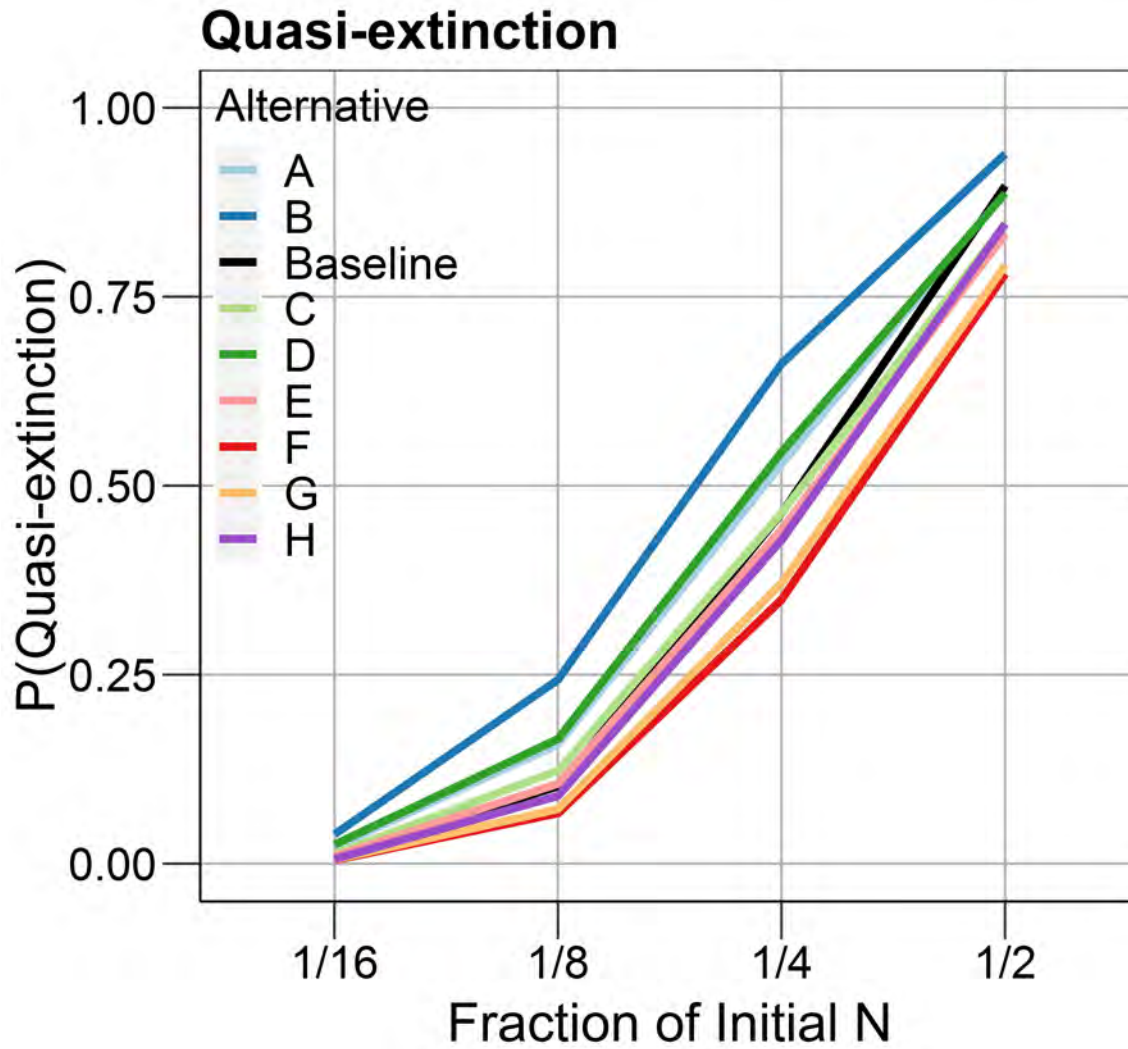
Figure 3. *Risk* analysis – DNR lands. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the proposed management alternatives.
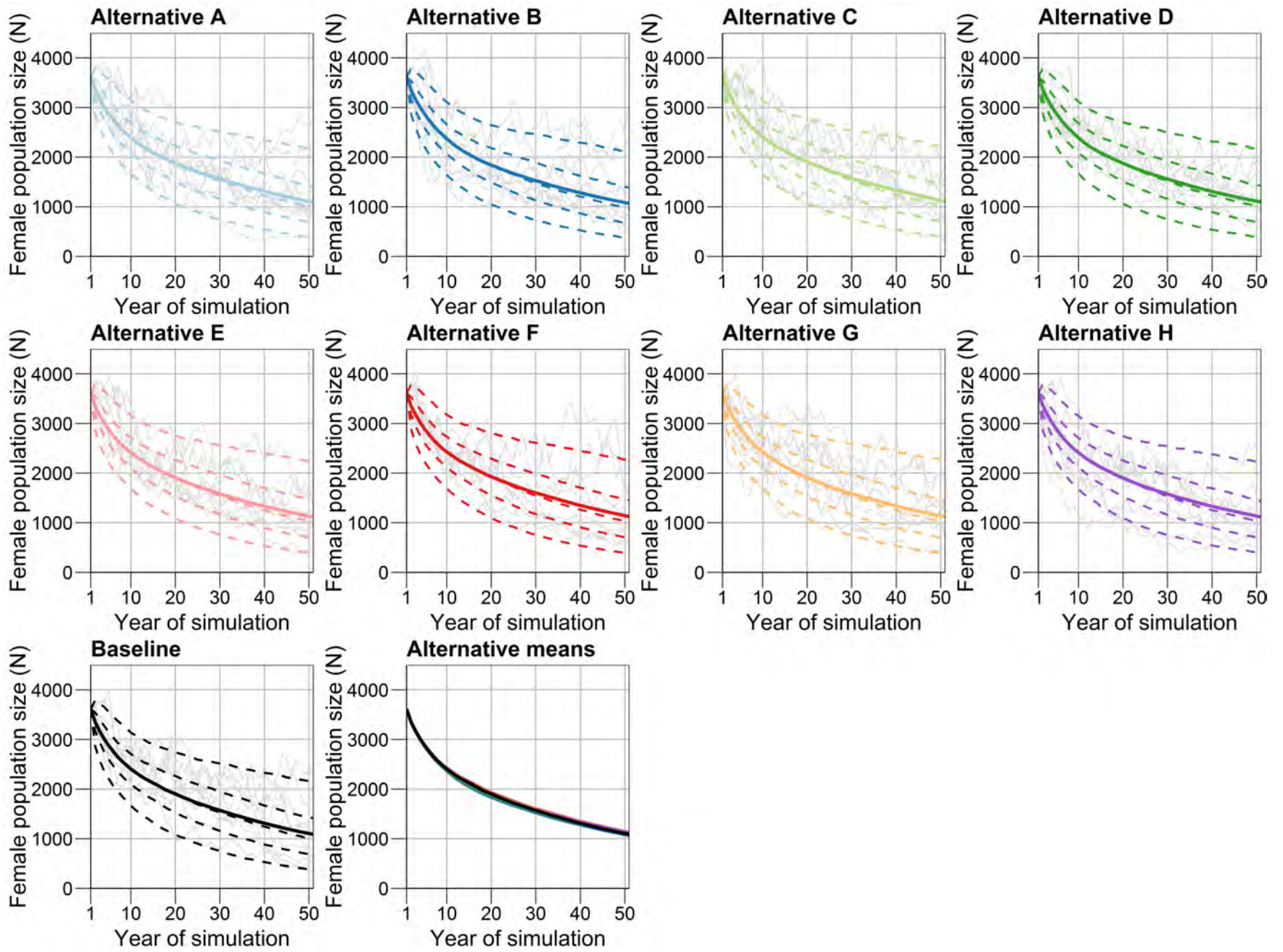
56
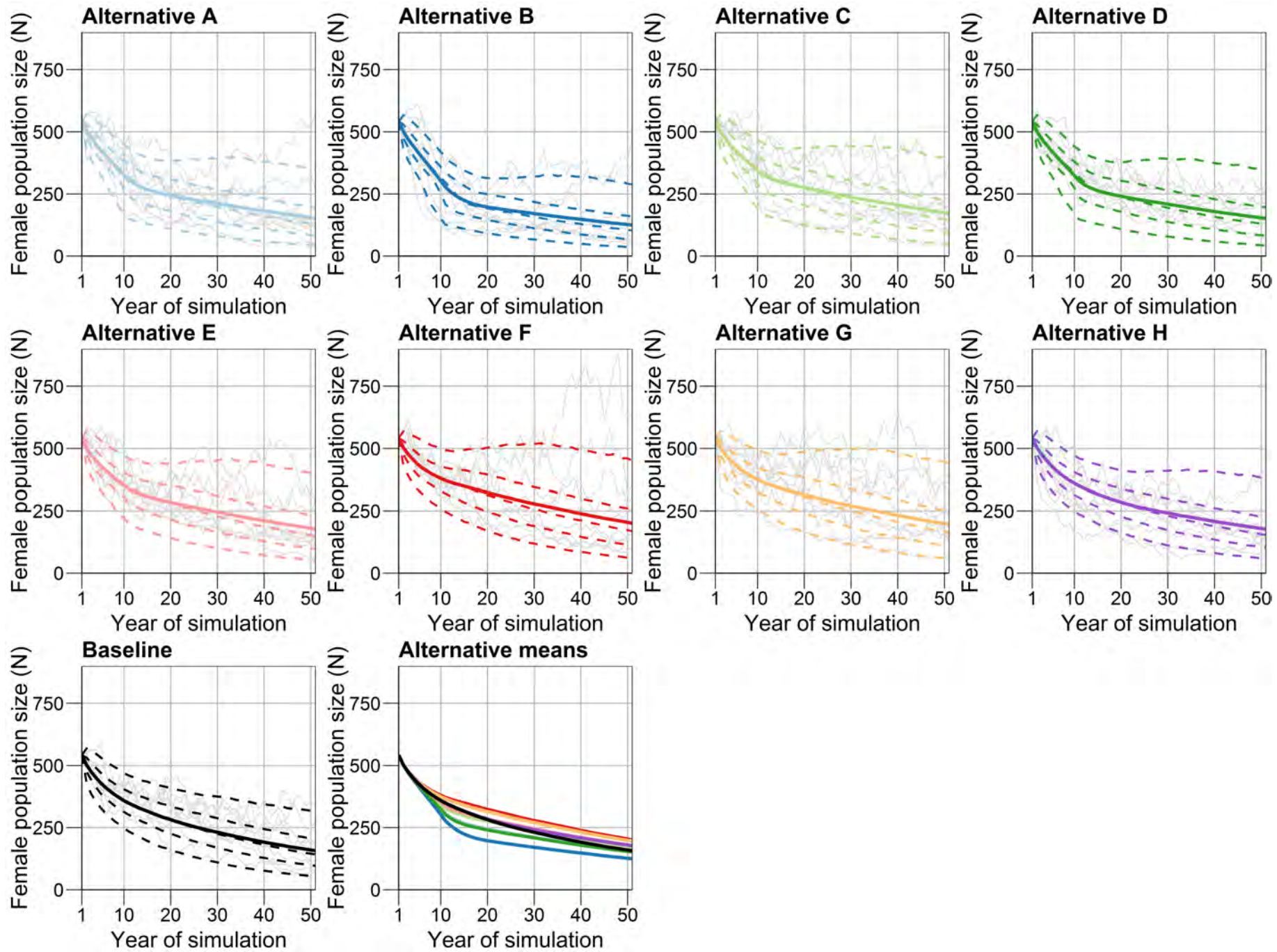
Figure 4. *Risk* analysis – DNR lands. Projected murrelet population sizes as a function of proposed management alternatives. In each

panel the solid colored line represents the mean annual population size averaged over 10,000 simulations, the dashed colored lines

represent the 5%, 25%, 50% (median), 75%, and 95% quantiles, and the grey lines represent a random subsample (n = 10) of

individual simulation outcomes. The bottom-right panel ("Alternative means") plots the mean from each alternative on a single graph
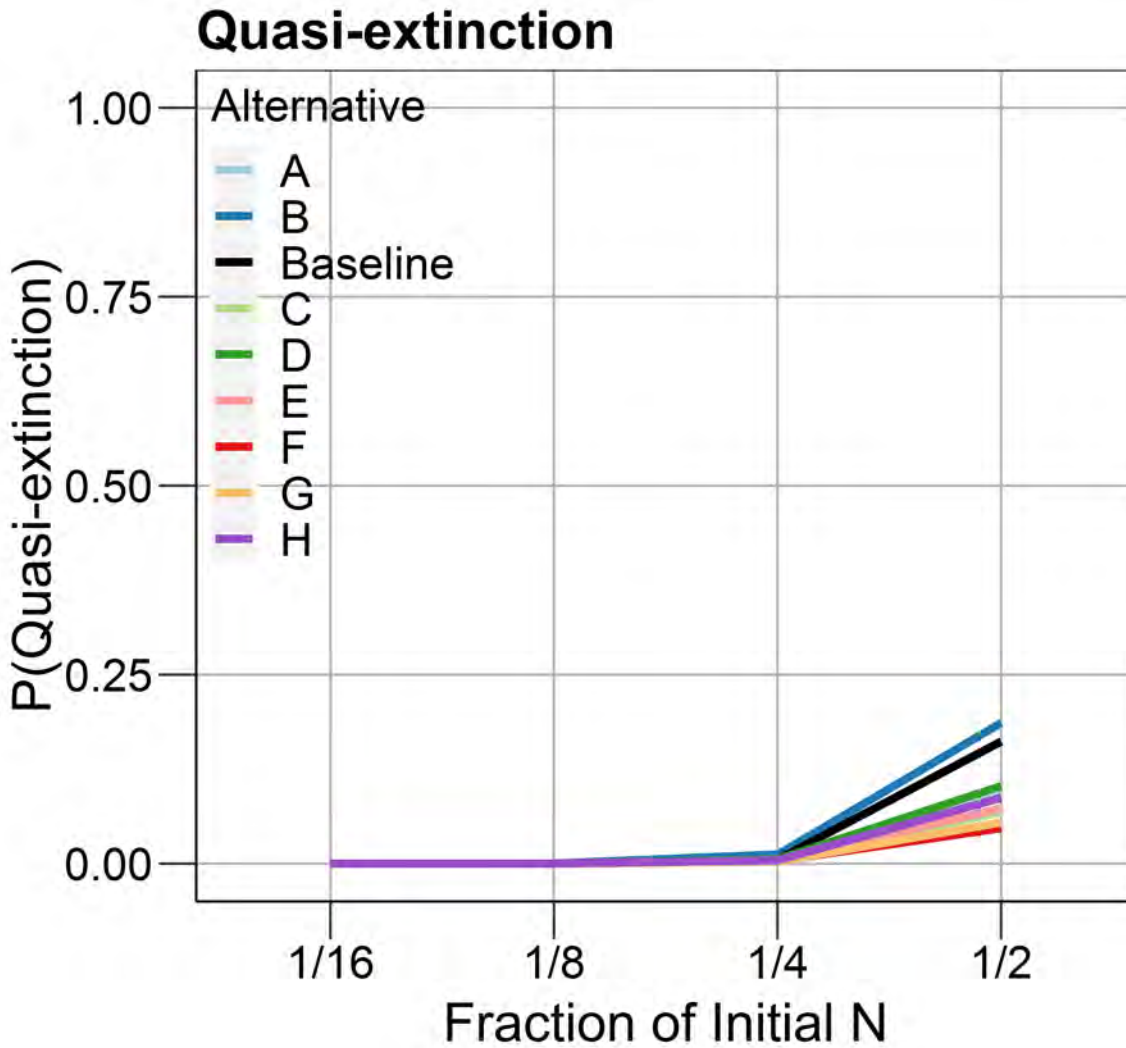
for the purposes of comparison.
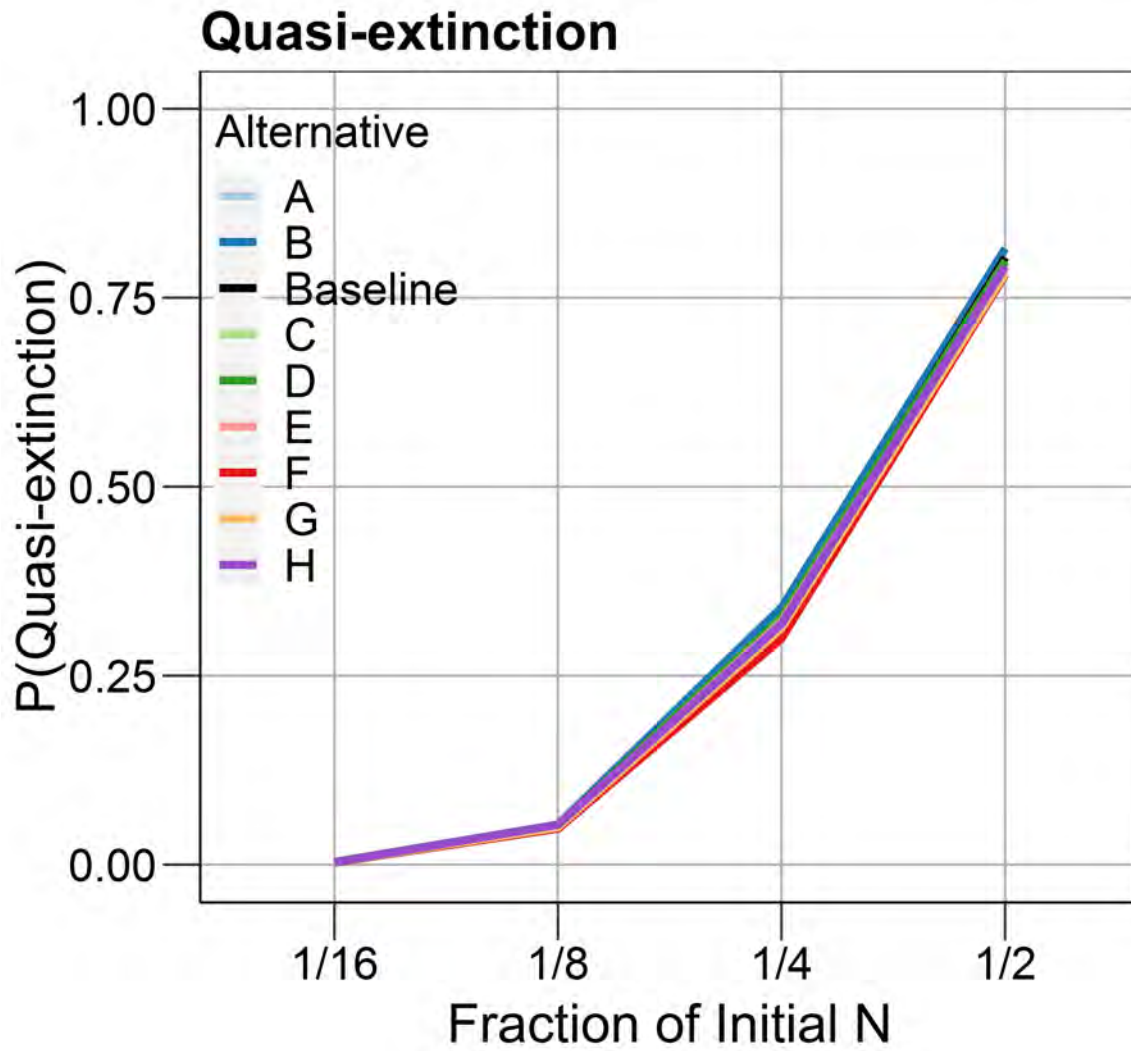
Figure 5. *Risk* analysis – Washington. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the proposed management alternatives.
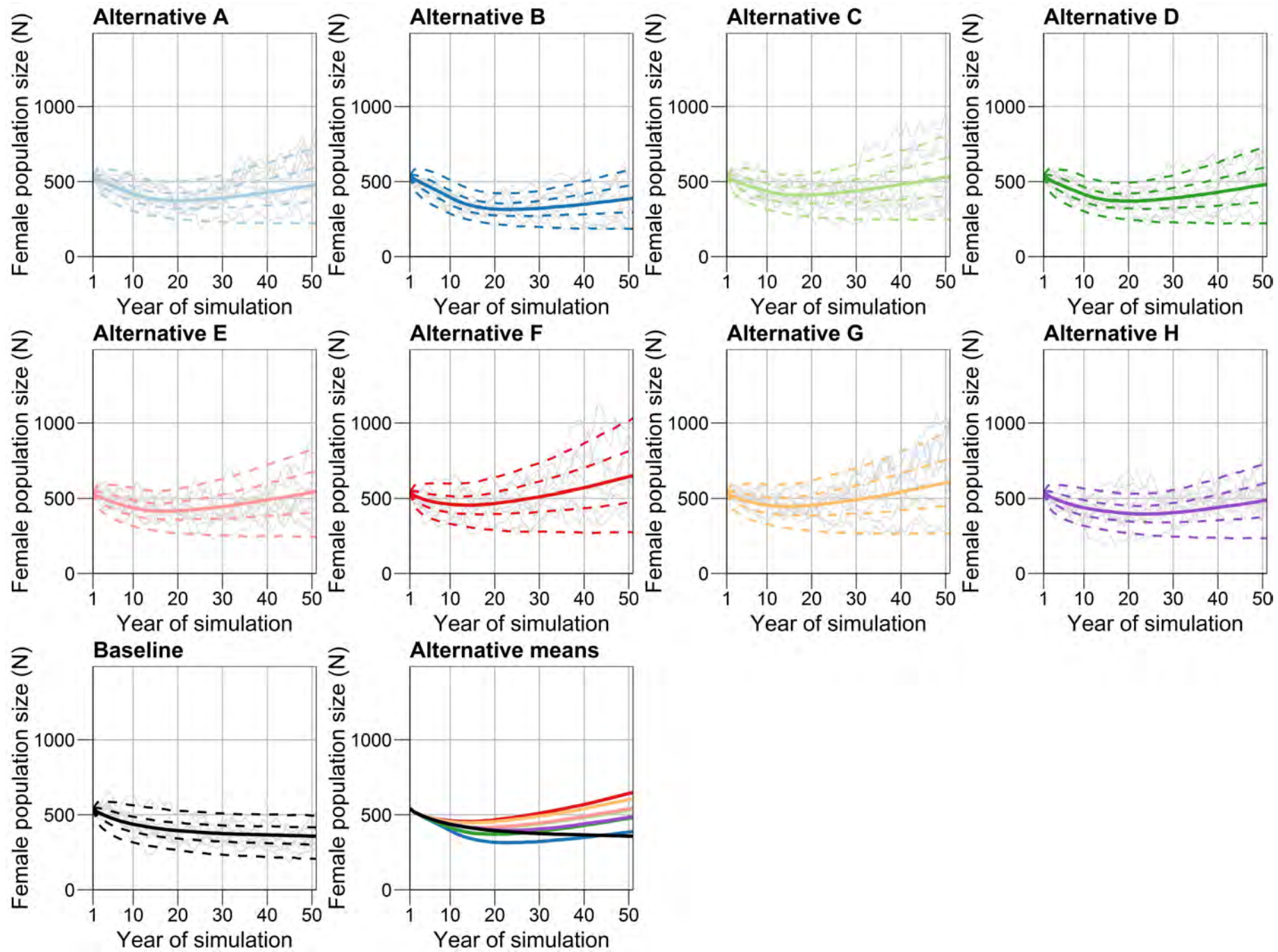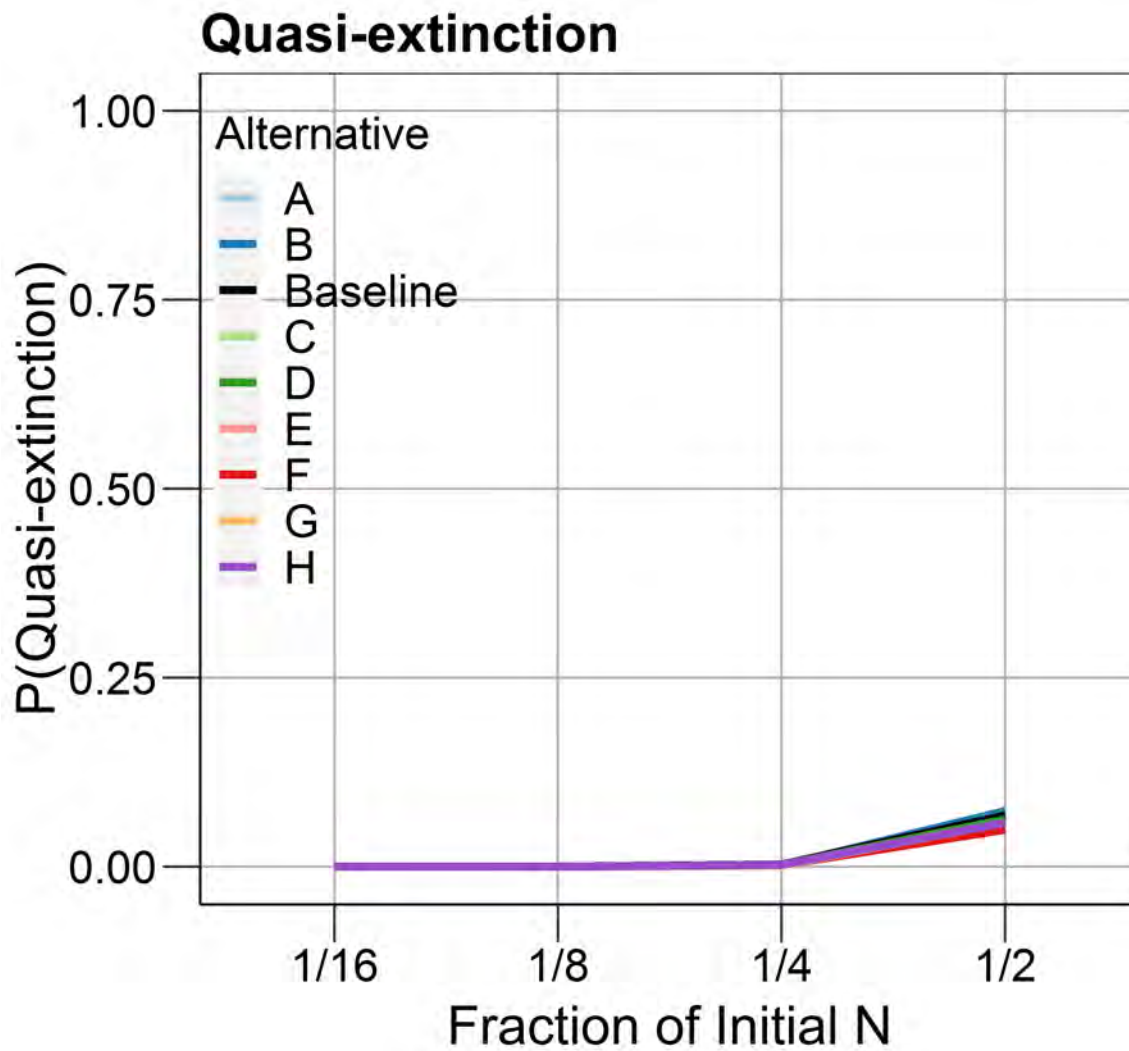
Figure 6. *Risk* analysis – Washington. Projected murrelet population sizes as a function of proposed management alternatives. In each panel the solid colored line represents the mean annual population size averaged over 10,000 simulations, the dashed colored lines represent the 5%, 25%, 50% (median), 75%, and 95% quantiles, and the grey lines represent a random subsample (n = 10) of individual simulation outcomes. The bottom-right panel ("Alternative means") plots the mean from each alternative on a single graph for the purposes of comparison.

Figure 7. *Enhancement* analysis – DNR lands. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the proposed management alternatives.

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Figure 8. *Enhancement* analysis – DNR lands. Projected murrelet population sizes as a function of proposed management alternatives. In each panel the solid colored line represents the mean annual population size averaged over 10,000 simulations, the dashed colored lines represent the 5%, 25%, 50% (median), 75%, and 95% quantiles, and the grey lines represent a random subsample (n = 10) of individual simulation outcomes. The bottom-right panel ("Alternative means") plots the mean from each alternative on a single graph for the purposes of comparison. Note that in this set of graphs the line representing the 50% quantile (median) is not visible because it is obscured by the line representing the mean.

Figure 9. *Enhancement* analysis – Washington. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the proposed management alternatives.

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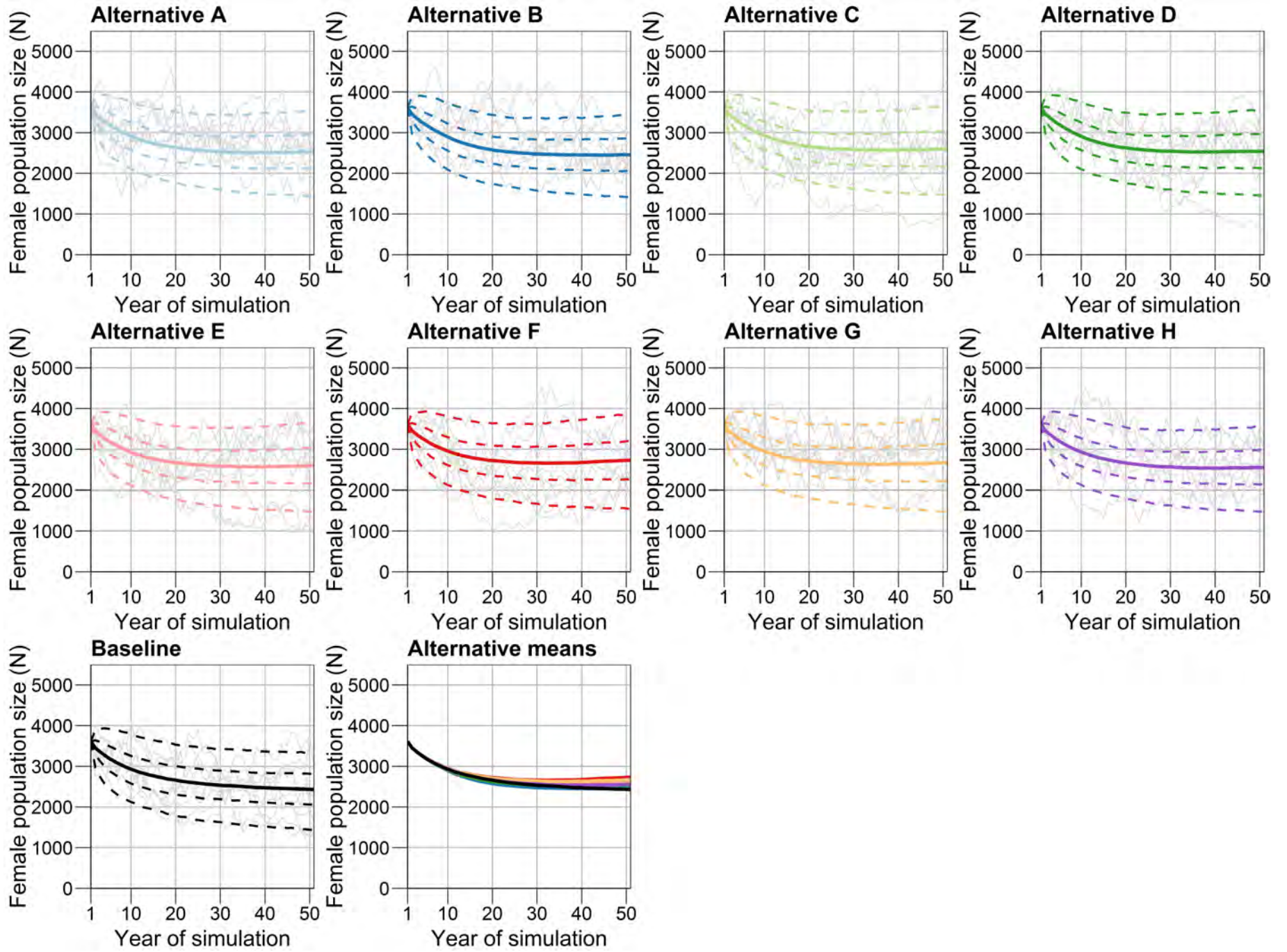
Figure 10. *Enhancement* analysis – Washington. Projected murrelet population sizes as a function of proposed management alternatives. In each panel the solid colored line represents the mean annual population size averaged over 10,000 simulations, the dashed colored lines represent the 5%, 25%, 50% (median), 75%, and 95% quantiles, and the grey lines represent a random subsample (n = 10) of individual simulation outcomes. The bottom-right panel ("Alternative means") plots the mean from each alternative on a single graph for the purposes of comparison.
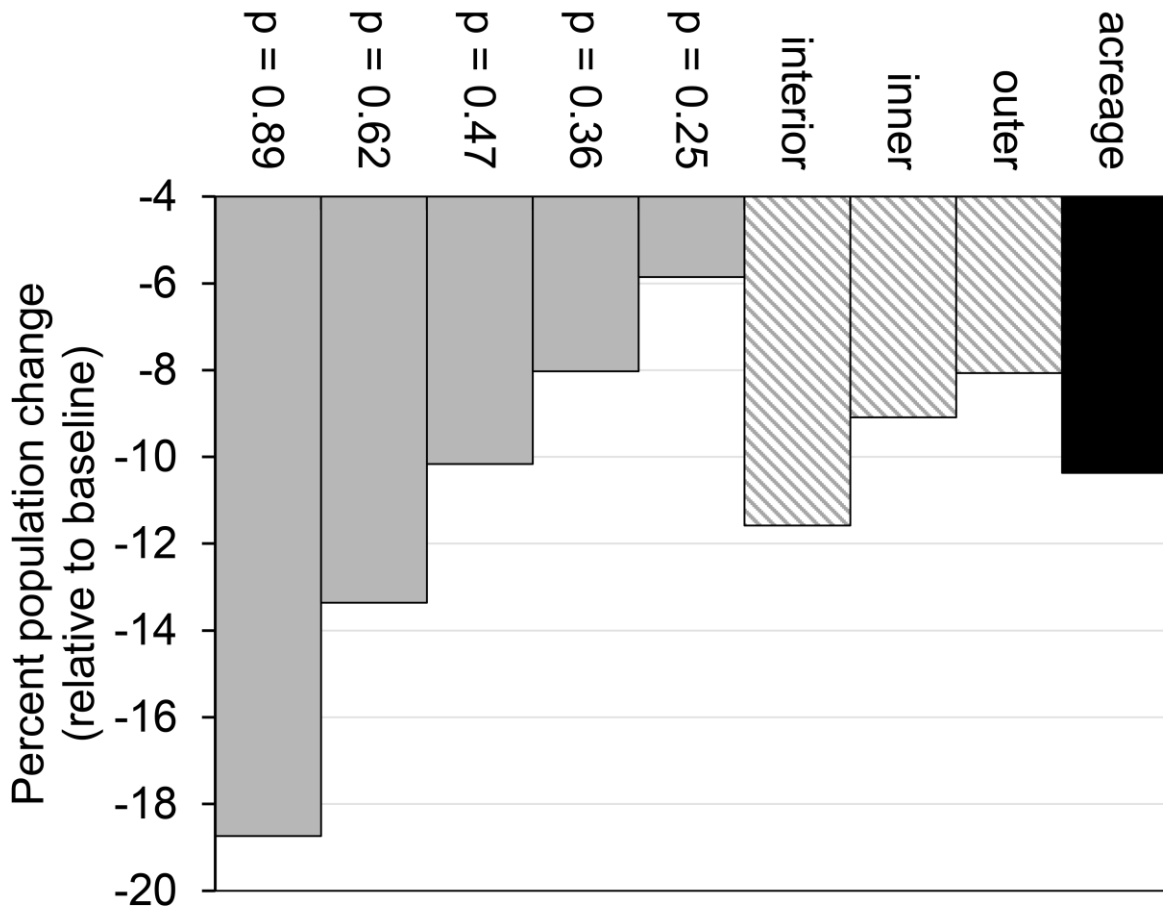
Figure 15. Sensitivity analysis. Grey solid bars represent habitat quality (Pstage), grey hatch-marked bars represent habitat configuration (edge conditions), and the black bar represents habitat amount (raw acreage).

APPENDIX A

Nest Density – Based on the assumptions that a threshold acreage of habitat is required to provide one nest site and that nesting habitat is limited so that there is just enough for the current statewide population, i.e., the population is at the carrying capacity, *K*, of its forest habitat. WA state habitat estimates are from Raphael et al. (2016) and the murrelet population is estimated as the average WA at-sea population over a 5 year monitoring period, 2011-2015. Due to reduced-sampling efforts implemented in 2014, state-scale estimates for Washington are not currently available for the 2016 or 2017 monitoring years (Lynch et al. 2016). Habitat quality, and consequently the availability of potential nest sites, is assumed to be influenced by stand condition, edge effects including lack of habitat capability in strings, and geography (see below). Adjusted acreages for non-DNR land are based on Science Team (Raphael et al. 2008) assumptions for habitat quality and accessory assumptions for edge conditions and strings (i.e., assume federal habitat consists of half as much edge and strings while private habitat consists of 50% more edge and strings than DNR-managed land). Adjusted acreages for DNR land are based on assumptions regarding the influence of stand development, edge effects, and geography on habitat quality (see below) applied to estimated habitat acreage (Raphael et al. 2016). Nest density, *D*, is estimated as the total number of murrelets in WA divided by the total adjusted habitat acreage, *A*.

Raw Habitat (DNR) – Acreage of habitat (*Pstage*>0) symbolized as *H*, based on interpretation and projection of DNR's spatially-explicit forest inventory. This estimate of current habitat (*Pstage*>0), 211,700 acres, differs slightly from that of Raphael et al. (2016) which was used to estimate nest density, 187,100 acres.

Adjustment for Habitat Quality (DNR) – This incorporates three influences on habitat quality as it relates to function in providing nesting opportunities and *K*: stand condition, edge effects,

and geography. DNR's spatially-explicit forest inventory summarizes acreage (*H*), composition, and structure for stands, contiguous forest patches with sufficiently uniform composition and structure to be distinguishable units. Each stand has a current and projected future *Pstage* value (0, 0.25, 0.36, 0.47, 0.62, 0.89) which reflects habitat quality, thus its capacity to provide nest sites as *H* * *Pstage*. Edge effects, *E*, are influenced by two factors, distance from edge and edge type as summarized in the table below. Edge type and distance were estimated with spatial analyses of DNR forest inventory and the proposed conservation alternatives. Geographic influence, *G*, was incorporated by mapping habitat over 5 km from the nearest occupied murrelet site where the diminished attractiveness and/or availability of nest sites was assumed to have a further effect, 0.25, on habitat quality at these isolated habitat patches. Less than 5% of DNR-managed habitat, *H*, is so isolated, thus *G* = 1 for the large majority of habitat.

		Interior (*t*)	Inner Edge (r)	Outer Edge(*o*)	String
Edge Type	None (*n*)	1	1	1	0
	Soft (*s*)	1	0.8	0.6	0
	Hard (*h*)	1	.585	.17	0

Stands of current and projected future habitat (*Pstage*>0) were spatially partitioned by multiple factors important to DNR forest management including edge distance and geography (approximately 1,000,000 partitions varying by time-step and alternative), so that each partition, *i*, had an unique acreage H_i, and was in one of twenty-four *Pstage*/Edge-distance categories. Habitat was configured either in small, often fairly linear fragments called *strings* that contained

no interior forest, or in larger blocks that contained habitat in outer (*o*) and inner (*n*) edges as well as in interior forest (*t*), >100 meters from edge. Edge effects were assumed to negate the value of habitat in strings. Depending on alternative, 13% - 24% of habitat was in strings. Edge effects on inner and outer edge habitat was estimated with spatial methods based on the location of p-stage, and estimates of forest growth in LTFC based on site index values from DNR's forest inventory. Edges outside of LTFC were assumed to be equal to current proportions of edge types due to the balance of growth and harvest across the land base. Thus, projected future edge effects to inner and outer edge forests varied by alternative over the 50 year modeling period.

Six of the eighteen, non-string *Pstage*/Edge-distance categories are interior (*t*) and not subject to edge effects. The habitat quality adjustments described above were applied to all *j* spatial partitions within the interior categories and estimate the "functional capability" of murrelet habitat over 100 meters from potential edge as the sum of adjusted habitat acreage:

$$A_t = \sum_{i=1}^{j} H_i * Pstage_i * G_i * E_t$$

where $E_t = 1$. The adjusted habitat acreage within inner and outer edge categories are calculated as:

$$A_r = \sum_{i=1}^{j} H_i * Pstage_i * G_i * ((E_{nr} * p_n) + (E_{sr} * p_s) + (E_{hr} * p_h))$$

and

$$A_o = \sum_{i=1}^{j} H_i * Pstage_i * G_i * ((E_{no} * p_n) + (E_{so} * p_s) + (E_{ho} * p_h)),$$

respectively. The sum of adjusted acreages in interior and the two edge categories estimates A_{DNR},

$$A_{DNR} = A_t + A_r + A_o.$$

K (DNR) – The estimated number of nest sites on DNR-managed land, calculated as $K_{DNR} = D *$ $A_{DNR} * 0.5$ to reflect a population that is half female.

Nest Success (DNR) – Based on the assumption that edge effects are a primary influence on nest success, f. High nest success, f_{high} is assumed to be 0.55 and low success, f_{low}, 0.38 (McShane et al. 2004), with intermediate success, f_{int}, halfway between. Edge effects are influenced by two factors, distance from edge and edge type as summarized in the table below (Malt and Lank 2009). Edge type and distance from edge were estimated with spatial analysis of DNR forest inventory.

		Interior	Inner Edge	Outer
Edge	None (n)	0.55	0.55	0.55
Type	Soft (s)	0.55	0.55	0.55
	Hard (h)	0.55	0.465	0.38

Similar to adjustments for habitat quality, nest success was estimated by a combination of spatial and non-spatial analyses. Seven of the nine Edge-distance/Edge-type categories are interior or influenced by no or soft edge and are not subject to edge effects. Their influence on nest success, f, was estimated for all j spatial partitions within those categories as

$$f_{t,n,s} = \sum_{i=1}^{j} H_i * f_{high}$$

The influence of inner and outer hard edges on nest success was estimated as

$$f_{hr} = \sum_{i=1}^{j} H_i * f_{int}$$

and

$$f_{ho} = \sum_{i=1}^{j} H_i * f_{low}$$

thus

$$f_{DNR} = f_{t,n,s} + f_{hr} + f_{ho}$$

Raw Habitat (Other) – Estimates from Raphael et al. (2016).

Adjustment Factor (Other) – Based on the same logic and edge effects described for the DNR adjustment factor but using Science Team (Raphael et al. 2008) assumptions for habitat quality and the assumptions for edge conditions and strings summarized above, i.e., federal habitat consists of half as much edge and strings while private habitat consists of 50% more edge and strings than DNR-managed land.

K (Other) – The estimated number of nest sites on federal and other non-federal land, calculated as described above.

Nest Success (Other) – Estimated as above, based on the assumptions about edge on non-DNR lands (federal habitat consists of half as much edge while private habitat consists of 50% more edge than DNR-managed land).

Additional references

Lynch, D. Falxa, G., J. Baldwin, M. M. Lance, S.K. Nelson, S.F. Pearson, M.G. Raphael, C.

Strong, and R.Young. 2016. Marbled murrelet effectiveness monitoring, Northwest

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