Appendix C. Population Viability Analysis (Peery and Jones 2016)

Note: This report is currently undergoing peer review. This review is expected to be complete before the final EIS for the marbled murrelet long-term conservation strategy.

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 – F) 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 alternative F 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 alternative F provided the greatest capacity to enhance murrelet populations. At the state level, alternative F was projected to lead to 53 and 295 more murrelets than alternative B under the *Risk* and *Enhancement* scenarios, respectively. In addition, 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. The same pattern was generally observed for quasi-extinction probabilities, although differences between alternative A and the other alternatives

were not quite as consistent as they were for projected mean population size. In a separate sensitivity analysis, we found that, acre-for-acre, murrelet population growth was most sensitive to changes in high-quality nesting habitat (Pstages 0.89 and 1), 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…” (US Fish and Wildlife Service 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 & 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, Miller & Ralph 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 (U.S. Fish and Wildlife Service 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 (Raphael and Falxa *In Press*).

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 (Washington Department of Natural Resources 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 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, provides a more direct means to "credit and debit" the DNR for expected increases and decreases in nesting habitat on their 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 (Washington Department of Natural Resources 2016a). 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 in a relative manner (Beissinger & 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 (≥3-year olds) nonbreeders that did not breed because of insufficient nesting habitat, and adult breeders (≥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 ≥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 & Doak 2002). The murrelet meta-population model $\mathbf{A}_t$ consisted of four submatrices that defined local demographic and dispersal processes (Hunter & Caswell 2005):

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

The two submatrices on the main diagonal ($\mathbf{A}_{\mathrm{L},t}$) governed local demographic processes on DNR and non-DNR lands, denoted $\mathbf{A}_{1,\mathrm{t}}$ and $\mathbf{A}_{2,\mathrm{t}}$, 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.* 2006) (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.

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 ($\mathrm{d}_{\mathrm{L,t}}$*) 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:

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

For example, if $L = 1$, then the matrix $\mathbf{M}_{\mathbf{1},t}$ 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 & 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:

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

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 ($\mathrm{n}_{\mathrm{x,L,0}}$*).* 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., In Press). The total number individuals (i.e., females) was allocated to DNR and non-DNR lands in proportion to the distribution of nesting habitat that currently exists on each of the two landownerships (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 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 ($\geq$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 (Washington Department of Natural Resources 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, Mack & Cooper 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 seven nesting habitat quality categories ("Pstage"), non-habitat (Pstage = 0) and six classes of habitat with Pstage values 0.25, 0.36, 0.47, 0.62, 0.89, and 1. 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. Pstage 1 is not inventory-based, that value was assigned to stands where murrelet use was observed during DNR-sponsored surveys. In our population model, the Pstage value represented the stand's maximum nesting density where, for example, four acres of Pstage 0.25 provide the same nesting opportunities as one acre of Pstage 1.

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, Franklin & Spies 1992; van Rooyen, Malt & Lank 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 (6 classes), edge distance (3 classes: outer, inner, interior), and edge type (hard and soft). This process resulted in 24 combinations of six Pstage classes by edge-distance (outer, inner) and edge-type (hard, soft) plus six Pstage classes in interior habitat providing 30 different nesting density adjustments applied to current and alternative-specific projected future habitat maps. For example, nesting density was assumed to be sixteen times greater in Pstage = 1, interior forest than in Pstage = 0.25 subject to the hard, outer edge effect of 0.25 (16 = 1 / (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.* 2015). 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, Mack & Cooper 2002; Malt & 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 six forest management alternatives, each involving different approaches to timber harvesting and habitat conservation on DNR-managed land in western Washington (see Washington Department of Natural Resources 2016b). 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 six alternatives are more thoroughly defined in DNR (2016) but they, and a baseline scenario (i.e., static forest conditions), are summarized below:

1. **Alternative A** is the “no-action” alternative, approximating continued DNR operations as authorized under the 1997 HCP. This alternative includes approximately 620,000 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 P-stage value >0 in decade 0.

2. **Alternative B** focuses on protecting the known locations of marbled murrelet occupied sites on DNR-managed land. Under this alternative, LTFC totals approximately 593,000 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 636,000 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 634,000 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 P-stage 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 P-stage 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 640,000 acres of long-term forest cover. This alternative includes the following murrelet-specific conservation: occupied sites, with 100 meter buffers; all habitat with a P-stage 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 LTFC 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 734,000 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. **Baseline** represents a static habitat scenario, where the raw amount of murrelet nesting habitat that presently exists on DNR lands (170,797 acres) remains constant over the 50-year modeling period. Carrying capacity ($K_{1,t}$ = 217) and nest success ($f_{1,t}$ = 0.509) 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 six proposed alternatives, the DNR and USFWS proposed an additional exploratory analysis which would show how the modeled murrelet population on DNR lands would respond to (i) delayed harvest implementation and (ii) including habitat in "stringers", where all the habitat is influenced by edge conditions (i.e., no interior habitat), under both *Risk* and *Enhancement* scenarios. These additional exploratory analyses were applied to the existing framework of alternative D (see above), and can be described as follows:

1. **Alternative D – 'M'** is the exploratory variant of alternative D in which habitat removal was 'metered' over two decades as opposed to all habitat harvest occurring in the first decade, as was the case in all six proposed alternatives above. The primary goal of this exploration was to gauge the extent to which slowing the rate of habitat decline in the near-term would allow habitat recovery in LTFC to "compensate" for that harvest. Delaying harvest of habitat could also be part of an expanded mitigation strategy.
2. **Alternative D – 'S'** is the exploratory variant of alternative D in which P-stage habitat completely influenced by edge conditions ('stringers') is credited as viable murrelet

habitat. In the six proposed alternatives above, ‘stringers’ have no habitat value. The primary goal of this exploration was to determine if ‘stringers’ have a net positive or negative effect on murrelet populations. This alternative begins with a higher value for nesting carrying capacity because ‘stringers’ are credited as potential nesting habitat.

For the six primary and two exploratory alternatives, 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:

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

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-year-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.* 2006). 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.* 2015). 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 and better model performance. 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.* 2006; Becker, Peery & Beissinger 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 six 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. For example, when exploring model sensitivity to changes in "inner edge", approximately 3,000 of the 10,000-acre simulated loss of "inner edge" habitat occurred within Pstage = 1, which represents its extent (30%) relative to the other Pstage classes within this edge class. We created one additional scenario ("acreage") in which the simulated 10,000-acre loss in habitat occurred proportionally across all 18 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.

We chose 10,000 acres (~5.9% of total raw acreage) because it represented the maximum habitat loss possible while meeting the "proportional loss" constraint of the sensitivity analysis; any larger amount would have required proportional losses to certain habitat classes that 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

All six of the primary management alternatives were projected to result in more nesting habitat, a greater carrying capacity, and expected nest success on DNR lands at the end of the 50-year modeling period (Figure 2a-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 habitat increased by 58% over the 50-

year modeling period. In contrast, the most pessimistic scenario for change in raw habitat was alternative B, which yielded an initial decline in habitat over the first decade but resulted in gradual increases thereafter, ending with a net 9% increase 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 six alternatives were bounded on the upper end by alternative F and on the lower end by alternative B. Carrying capacity increased by 137% under alternative F, while alternative B ended with a net 30% increase after 50 years following an initial decline. Carrying capacities for the remaining alternatives always fell between B and F (Figure 2b). Mean nest success, which contributed to estimates of annual fecundity, was similarly bounded by alternatives B (lower nest success) and F (higher nest success) with all other alternatives falling between the two (Figure 2c). In contrast to the six 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 two exploratory variants of alternative D (D –‘S’ and D – ‘M’) can be found in Figure 2d-f. Because alternative D – ‘S’ credited ‘stringers’ as potential murrelet nesting habitat, it had a greater amount of raw habitat and carrying capacity than either D or D – ‘M’ (Figure 2d-e). However, because ‘stringers’ are entirely adjacent to edge thus of lower habitat quality, the estimated average nest success for alternative D – ‘S’ was lower than any other scenario in this analysis (Figure 2f). Alternative D – ‘M’ tracked alternative D closely except over the first two decades for raw habitat and carrying capacity, because alternative D – ‘M’ was designed to implement a delayed harvesting strategy (Figure 2d-e).

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 six 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 0.8417 (alternative F) to 0.9721 (alternative B). Alternatives F and B continued to define the boundaries of quasi-extinction probabilities for smaller thresholds: at 1/4 of initial N, quasi-extinction probability ranged from 0.4515 (alternative F) to 0.8170 (alternative B); at 1/8 of initial N, quasi-extinction probability ranged from 0.1092 (alternative F) to 0.4203 (alternative B); and at 1/16 of initial N, quasi-extinction probability ranged from 0.0108 (alternative F) to 0.0974 (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 174.7 (most optimistic) and 95.4 (most pessimistic) under alternatives F and B representing a 67.7% and 82.4% 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 0.7978 (alternative F) to 0.8302 (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 0.3297 (alternative F) to 0.3618 (alternative B); at 1/8 of initial N, quasi-extinction probability ranged from 0.0538 (alternative F) to 0.0614 (alternative B). At 1/16 of initial N, quasi-extinction probability ranged from 0.0022 (alternative C) to 0.0042 (alternative F), although the difference between these probability estimates represents only 20 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 1,091 (most optimistic) and 1,076 (most pessimistic) under alternatives F and B (similar to the DNR population, see above) representing a 69.8% and 71.3% 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 0.0768 (alternative F) to 0.3462 (alternative B). At 1/4 of initial N, quasi-extinction probabilities among alternatives ranged from 0.0049 (alternative F) to 0.0412 (alternative B); at 1/8 and 1/16 of initial N, quasi-extinction probability was nearly equal to zero across all alternatives (i.e. 10 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 589.7 (most optimistic) and declined to 199 (most pessimistic) under alternatives F and B representing a 8.8% increase and 39.4% 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 0.0610 (alternative F) to 0.0903 (alternative B), with the remaining alternatives yielding quasi-extinction probabilities between F and B. Quasi-extinction probability was nearly equal to zero for all other thresholds among all alternatives (i.e. fewer than 30 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 2,663 (most optimistic) and 2,367.7 (most pessimistic) individuals under alternatives F and B (similar to the DNR population, see above) representing a 26.4% and 34.5% 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 variants of alternative D. We evaluated the exploratory variants of alternative D under the *Risk* and *Enhancement* scenarios for DNR lands only. In the *Risk* analysis, quasi-extinction probabilities were always highest for the D – 'S' alternative compared with alternatives D and D – 'M' (Figure 11, Table 4). The probability of the murrelet population on DNR lands reaching 1/2 its initial population size after 50 years was highest for alternative D – 'M' (0.9378) followed by alternative D (0.9315) and alternative D – 'S' (0.8893). At 1/4 of initial N, the quasi-extinction probability was again higher for alternative D – 'M' (0.6592) compared to alternative D (0.6393) and D – 'S' (0.5474) and the same pattern continued at 1/8 of initial N (Figure 11, Table 4). Female population size declined from 542 individuals to 151.3, 129.9, and 125.7 individuals under alternatives D – 'S', D, and D – 'M', respectively, after 50 years (Figure 12). A complete list of quasi-extinction probabilities is provided in Table 4, and mean female population sizes at 10-year intervals is provided in Table 5.

In the *Enhancement* analysis, quasi-extinction probability was generally highest for alternative D. At 1/2 of initial N, quasi-extinction probability was 0.1701 for alternative D followed by alternative D – ‘M’ (0.1419) and D – ‘S’ (0.1071). This pattern persisted at 1/4 of initial N but the differences among scenarios was smaller. At 1/8 and 1/16 of initial N, quasi-extinction probability was nearly zero for all three alternatives (Figure 13, Table 4). Mean female population size declined from 542 individuals to 537.5, 451.1, and 436.2 individuals under alternatives D – ‘S’, D – ‘M’, and D, respectively, after 50 years (Figure 14, Table 5). A complete list of quasi-extinction probabilities is provided in Table 4, and mean female population sizes at 10-year intervals is provided in Table 5.

Sensitivity Analysis

Murrelet population growth was most sensitive to changes in the highest Pstage (habitat quality) classes 1 and 0.89; reducing the prevalence of these habitat classes on the landscape by 10,000 acres resulted in population estimates that were 7.5% and 5.0% 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 4.0% lower than the baseline, which had a slightly stronger effect on murrelet population growth than removing 10,000 acres of interior forest (3.9% lower than baseline). Removing Pstages 0.62, 0.47, inner edge, and outer edge resulted in final populations 3.4%, 1.6%, 2.9%, and 1.6% lower than the baseline scenario, respectively. Removing 10,000 acres of Pstages 0.25 and 0.36 caused minor (<0.5%) changes to murrelet populations compared to the baseline (Figure 15).

DISCUSSION

Implications for Population Risk and Enhancement

We developed a stochastic, demographic meta-population model to evaluate the potential effects of 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 extent to which proposed management actions may 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. Only one alternative (B) was projected to reduce murrelet population size compared to the Alternative A ("no-action"; i.e., continued management under the 1997 HCP guidelines) 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). Conversely, our findings suggest that all other alternatives (C – F) are expected to lead to larger murrelet populations than alternative A should the population continue to decline as a results of these factors. Similarly, alternative B appeared to provide less capacity for murrelet populations to increase in size than alternative A, whereas alternatives C through F 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, although differences between alternative A and the other alternatives were not quite as consistent as they were for mean projected population size.

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), almost 1.5 times as many murrelets were expected to occur on DNR lands under alternative F according to both *Risk* and *Enhancement* analyses (i.e., almost a 50% 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 the “best” (alternative F) and “no-action” (alternative A) alternatives was 51.7 for DNR lands and 34.1 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. Moreover, and as discussed above, alternative B was also the only proposed alternative that resulted in lower murrelet numbers than the “no-action” alternative (alternative A) in both *Risk* and *Enhancement* analyses for both DNR lands and the state of Washington. This finding was, to a certain extent, consistent with the fact that alternative B would protect the least (593,000 acres) of LTFC among all alternatives. By comparison, the “no-action” alternative (A) would involve the protection of 620,000 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.

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 53.3 and 295.3 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, 94,000 more acres (734,000 acres total) of LTFC than any other alternative (alternative E being the second most conservative, involving the protection of 640,000 acres). Compared with others, alternative F is distinct in that it proposes the establishment of more extensive conservation areas in most planning units and includes existing, mapped low quality northern spotted owl habitat in designated owl conservation areas as LTFC (alternatives A through E only include high quality owl habitat as LTFC).

In sum, alternative B posed the greatest risk to murrelet populations and alternative F 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.

The exploratory analysis comparing alternative D with a delayed harvest variant (D – ‘M’) and a variant that included ‘stringers’ as potential murrelet habitat (D – ‘S’) provides several interesting observations and insights. First, while the quasi-extinction probability was generally highest for alternative D – ‘M’ in the *Risk* analysis, the quasi-extinction probability was highest for alternative D in the *Enhancement* analysis. By comparison, alternative D – ‘S’ consistently had the lowest quasi-extinction probabilities and highest average female population size across both analyses. This result was unsurprising given that alternative D – ‘S’ had a comparably larger amount of raw habitat and a higher carrying capacity than the other alternatives (Figure 2d-e) because ‘stringers’ were credited as murrelet habitat which, despite lowering mean nest success because of increased edge effects (Figure 2f), resulted in a net positive for murrelet populations. This suggests that if our assumptions about edge effects are sound, small habitat patches with high levels of edge effects may not pose a direct population risk when they occur in combination with more extensive amounts of intact forest habitat. Less clear is why ‘metering’ harvest activities – such that their implementation occurred over two decades as opposed to one (alternative D – ‘M’) – resulted in higher quasi-extinction probability in the *Risk* analysis and a lower quasi-extinction probability in the *Enhancement* analysis. This result is more nuanced for mean female population size, which remained higher for D – ‘M’ in both analyses compared to alternative D over the first two decades of simulation, remaining above D in the *Enhancement* analysis (Figure 12) but falling below D in the *Risk* analysis for all years thereafter (Figure 10). While the factors driving these differences are not entirely clear, we suspect that a delayed harvest under the *Enhancement* scenario, which was parameterized with more optimistic population vital rates, may have provided a greater capacity for murrelet population growth than in the *Risk* analysis. Regardless, the influence of delayed harvest on murrelets in our model appeared to be relatively small, resulting in an average of only 4.2 fewer individuals in the *Risk* analysis and 14.9 more individuals in the *Enhancement* analysis compared to the standard 10-year harvest schedule (Table 5).

Sensitivity of Marbled Murrelet Populations to Habitat Change

The sensitivity analysis suggested that murrelet populations were most sensitive to changes in the amount of high-quality nesting habitat (P-stages 0.89 and 1), 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, Mack & Cooper 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 (51%) than the other categories (29%) on DNR-managed land (Washington Department of Natural Resources & US Fish and Wildlife Service 2016).

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 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, five murrelets recruited into the breeding population, four would do so into Pstage = 1 habitat and one would recruit into Pstage = 0.25 habitat, even if additional nests were available in Pstage = 1 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 & 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	$\sum_{i=1}^{x} n_{x,1,0} = 542$	$\sum_{i=1}^{x} n_{x,2,0} = 3{,}074$	Falxa *et al.* (2015); Lance and Pearson (2015)
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	$f_{1,0} = 0.5090$ $f_{1,\geq 1}$ varies by management alternative	$f_{2,0} = 0.5418$ $f_{2,\geq 1}$ remains constant	See Appendix A
Fecundity rate ($m_{L,t}$)	Both	$m_{1,t} = \frac{b \cdot f_{1,t}}{2}$	$m_{2,t} = \frac{b \cdot f_{2,t}}{2}$	
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 (proportion of 10,000 simulations that reached a specified fraction of initial population size) for proposed forest management alternatives (A – F) under the *Risk* and *Enhancement* analyses. Note that a quasi-extinction probability of 0.0001 represents 1 single outcome of 10,000 simulations.

Risk - DNR lands

	Fraction of Initial Population Size			
Alternative	1/16	1/8	1/4	1/2
A	0.0479	0.2624	0.6617	0.9420
B	0.0974	0.4203	0.8170	0.9721
C	0.0126	0.1508	0.5391	0.9003
D	0.0404	0.2361	0.6393	0.9315
E	0.0160	0.1485	0.5402	0.8903
F	0.0108	0.1092	0.4515	0.8417
Baseline	0.0198	0.1670	0.5980	0.9363

Risk - Washington

	Fraction of Initial Population Size			
Alternative	1/16	1/8	1/4	1/2
A	0.0033	0.0605	0.3350	0.8201
B	0.0035	0.0614	0.3618	0.8302
C	0.0022	0.0553	0.3387	0.8066
D	0.0040	0.0562	0.3418	0.8168
E	0.0030	0.0554	0.3418	0.8062
F	0.0042	0.0538	0.3297	0.7978
Baseline	0.0044	0.0553	0.3367	0.8134

Enhancement - DNR lands

	Fraction of Initial Population Size			
Alternative	1/16	1/8	1/4	1/2
A	0	0.0006	0.0180	0.1950
B	0.0001	0.0010	0.0412	0.3462
C	0	0.0001	0.0095	0.1271
D	0	0.0004	0.0138	0.1701
E	0	0.0001	0.0088	0.1226
F	0	0.0004	0.0049	0.0768
Baseline	0	0.0008	0.0139	0.2355

Enhancement - Washington

	Fraction of Initial Population Size			
Alternative	1/16	1/8	1/4	1/2
A	0	0	0.0029	0.0710
B	0	0.0001	0.0024	0.0903
C	0	0	0.0018	0.0669
D	0	0.0001	0.0028	0.0754
E	0	0	0.0022	0.0650
F	0	0	0.0022	0.0610
Baseline	0	0	0.0029	0.0799

Table 3. Projected mean population sizes (average of 10,000 simulations) at each 10-year interval for proposed forest management alternatives (A – F) in the *Risk* and *Enhancement* analyses.

Risk - DNR lands

	Year of Simulation					
Alternative	0	10	20	30	40	50
A	542	294.0	219.6	181.2	149.8	123.0
B	542	257.8	165.3	139.5	115.9	95.4
C	542	340.6	268.8	222.3	183.6	150.7
D	542	299.4	229.1	190.8	158.0	129.9
E	542	341.6	274.7	227.7	187.5	153.9
F	542	381.4	314.1	258.9	213.4	174.7
Baseline	542	338.0	259.1	207.1	167.1	134.9

Risk - Washington

	Year of Simulation					
Alternative	0	10	20	30	40	50
A	3616	2303.9	1813.1	1495.5	1254.1	1057.8
B	3616	2271.5	1765.0	1468.6	1229.5	1038.6
C	3616	2337.2	1843.4	1524.3	1279.4	1077.6
D	3616	2313.0	1821.5	1507.5	1263.6	1066.4
E	3616	2327.2	1853.9	1534.3	1285.7	1083.2
F	3616	2353.9	1873.6	1548.5	1298.3	1091.9
Baseline	3616	2327.6	1834.2	1515.5	1268.0	1064.4

Enhancement - DNR lands

	Year of Simulation					
Alternative	0	10	20	30	40	50
A	542	393.2	342.7	349.8	375.4	405.5
B	542	354.9	275.9	276.9	302.1	328.4
C	542	419.9	391.9	408.1	445.1	481.7
D	542	397.0	354.4	367.8	401.8	436.2
E	542	423.3	401.1	418.5	455.4	490.5
F	542	466.8	466.4	495.6	540.5	589.7
Baseline	542	418.8	374.3	353.4	340.4	333.8

Enhancement - Washington

	Year of Simulation					
Alternative	0	10	20	30	40	50
A	3616	2858.1	2584.9	2488.1	2469.7	2470.2
B	3616	2807.7	2512.0	2410.8	2371.8	2367.7
C	3616	2889.4	2636.0	2542.3	2528.8	2541.7
D	3616	2856.1	2596.3	2507.0	2477.0	2481.2
E	3616	2884.9	2639.6	2553.8	2534.2	2554.9
F	3616	2923.3	2714.1	2637.0	2638.7	2663.0
Baseline	3616	2874.7	2631.0	2507.5	2437.5	2391.9

Table 4. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for alternative D and two variants D - 'M' and D - 'S' under *Risk* and *Enhancement* scenarios on DNR lands. Note that a quasi-extinction probability of 0.0001 represents 1 simulated population reaching a given threshold.

Risk - DNR lands

	Fraction of Initial Population Size			
Alternative	1/16	1/8	1/4	1/2
D	0.0404	0.2361	0.6393	0.9315
D – 'M'	0.0277	0.2418	0.6592	0.9378
D – 'S'	0.0286	0.1720	0.5474	0.8893

Enhancement – DNR Lands

	Fraction of Initial Population Size			
Alternative	1/16	1/8	1/4	1/2
D	0	0.0004	0.0138	0.1701
D – 'M'	0.0001	0.0004	0.0097	0.1419
D – 'S'	0	0.0003	0.0066	0.1071

Table 5. Projected mean population sizes (average of 10,000 simulations) at each 10-year interval for alternative D and two variants D - 'M' and D - 'S' under *Risk* and *Enhancement* scenarios on DNR lands.

Risk - DNR lands

	Year of Simulation					
Alternative	0	10	20	30	40	50
D	542	299.4	229.1	190.8	158.0	129.9
D – 'M'	542	341.2	224.4	184.7	153.0	125.7
D – 'S'	542	357.6	282.3	230.2	187.4	151.3

Enhancement – DNR lands

	Year of Simulation					
Alternative	0	10	20	30	40	50
D	542	397.0	354.4	367.8	401.8	436.2
D – 'M'	542	423.5	376.6	384.4	416.8	451.1
D – 'S'	542	462.7	434.3	455.1	497.1	537.5

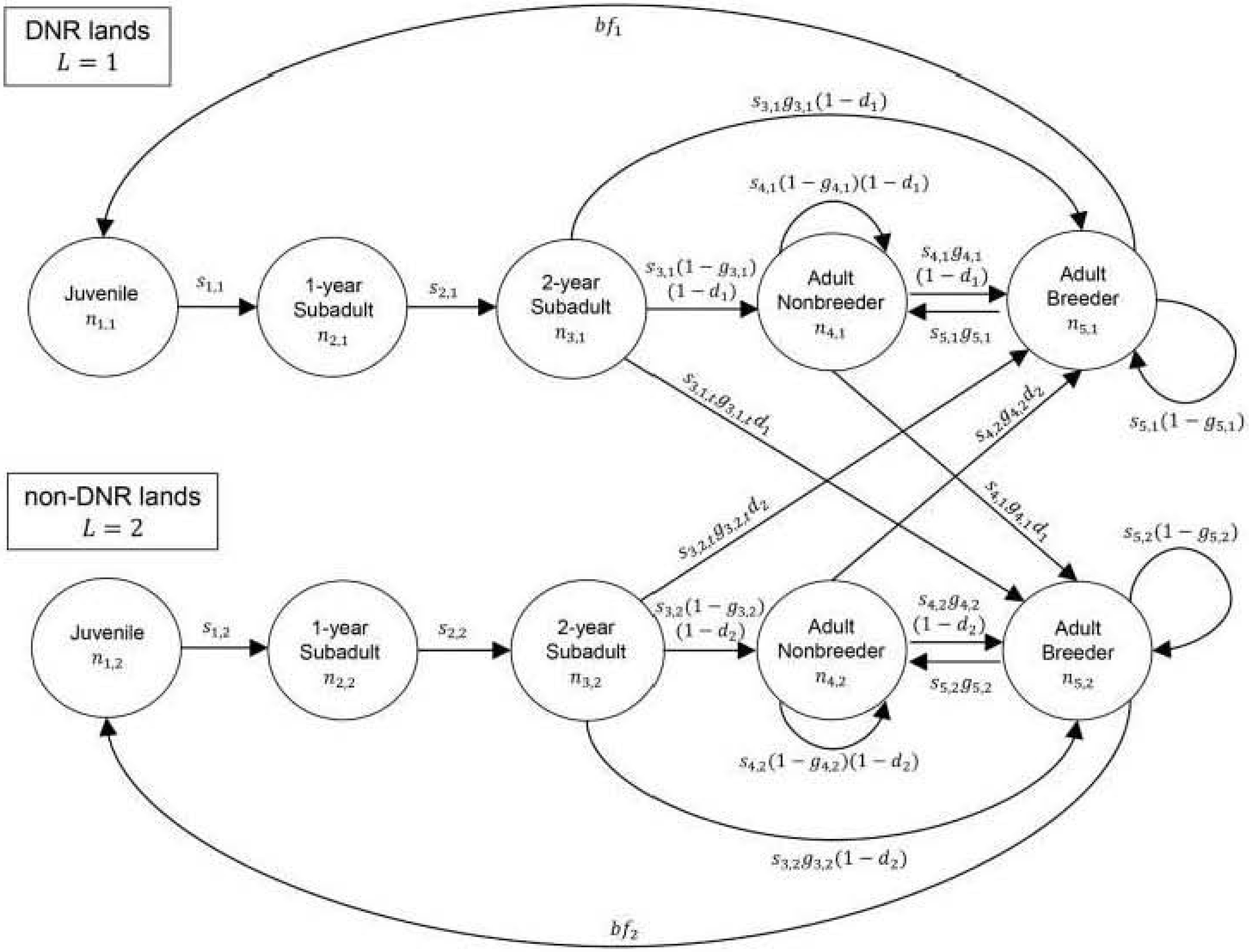
DNR lands
$L = 1$
bf_1
$s_{3,1}g_{3,1}(1-d_1)$
$s_{4,1}(1-g_{4,1})(1-d_1)$
Juvenile $n_{1,1}$
$s_{1,1}$
1-year Subadult $n_{2,1}$
$s_{2,1}$
2-year Subadult $n_{3,1}$
$s_{3,1}(1-g_{3,1})$ $(1-d_1)$
Adult Nonbreeder $n_{4,1}$
$s_{4,1}g_{4,1}$ $(1-d_1)$
$s_{5,1}g_{5,1}$
Adult Breeder $n_{5,1}$
$s_{3,1,t}g_{3,1,t}d_1$
$s_{4,2}g_{4,2}d_2$
$s_{5,1}(1-g_{5,1})$
non-DNR lands
$L = 2$
$s_{3,2,t}g_{3,2,t}d_2$
$s_{4,1}g_{4,1}d_1$
$s_{5,2}(1-g_{5,2})$
Juvenile $n_{1,2}$
$s_{1,2}$
1-year Subadult $n_{2,2}$
$s_{2,2}$
2-year Subadult $n_{3,2}$
$s_{3,2}(1-g_{3,2})$ $(1-d_2)$
Adult Nonbreeder $n_{4,2}$
$s_{4,2}g_{4,2}$ $(1-d_2)$
$s_{5,2}g_{5,2}$
Adult Breeder $n_{5,2}$
$s_{4,2}(1-g_{4,2})(1-d_2)$
$s_{3,2}g_{3,2}(1-d_2)$
bf_2

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,…,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.

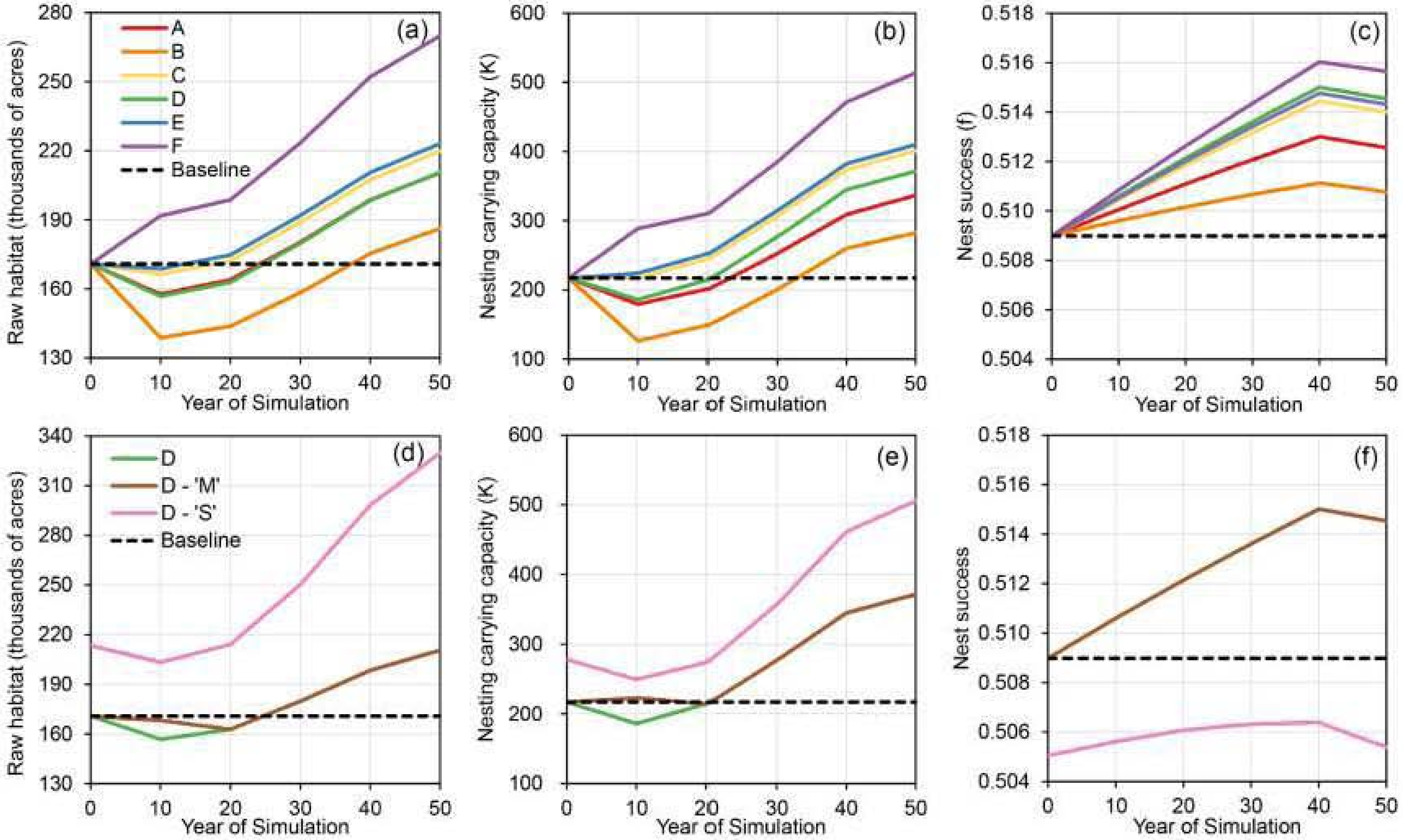
(a)
A
B
C
D
E
F
Baseline
Raw habitat (thousands of acres)
280
250
220
190
160
130
0
10
20
30
40
50
Year of Simulation
(b)
Nesting carrying capacity (K)
600
500
400
300
200
100
0
10
20
30
40
50
Year of Simulation
(c)
Nest success (f)
0.518
0.516
0.514
0.512
0.510
0.508
0.506
0.504
0
10
20
30
40
50
Year of Simulation
(d)
D
D - 'M'
D - 'S'
Baseline
Raw habitat (thousands of acres)
340
310
280
250
220
190
160
130
0
10
20
30
40
50
Year of Simulation
(e)
Nesting carrying capacity (K)
600
500
400
300
200
100
0
10
20
30
40
50
Year of Simulation
(f)
Nest success
0.518
0.516
0.514
0.512
0.510
0.508
0.506
0.504
0
10
20
30
40
50
Year of Simulation

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 – F) over the modeling period are presented in panels a – c, respectively. The same measures for the exploratory alternatives (D – 'M' and D – 'S') are shown in panels d – f, and include alternative D for the purposes of comparison.

Note: In panel F nest success is not significantly different between Alt D and D-M

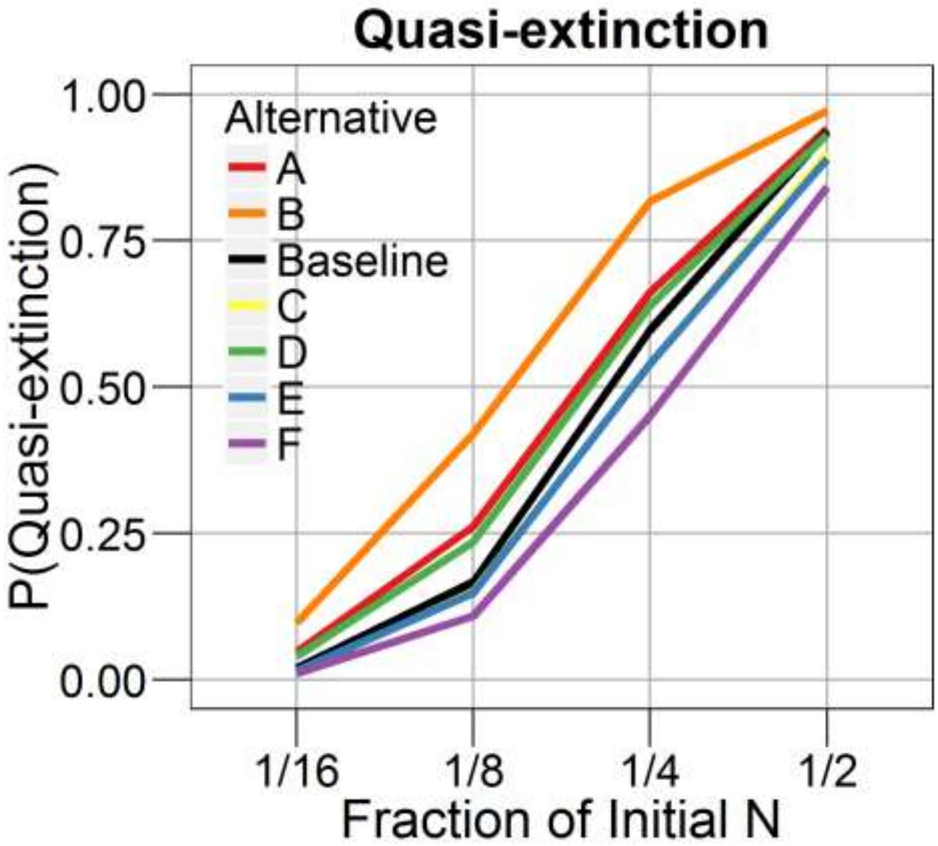

Figure 3. *Risk* analysis – DNR lands. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the primary proposed management alternatives (A – F).

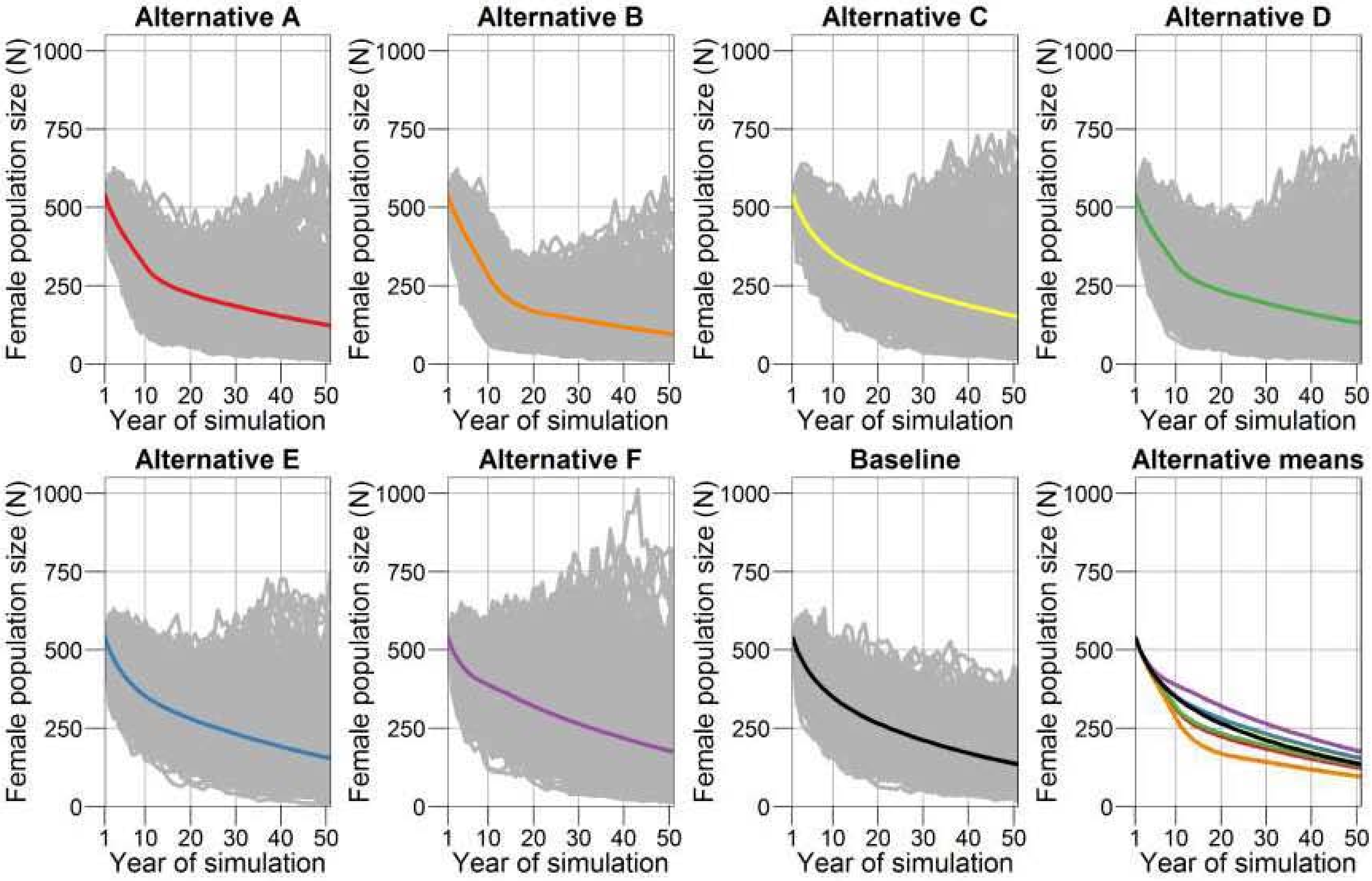

Figure 4. *Risk* analysis – DNR lands. Projected murrelet population sizes as a function of proposed management alternatives (A – F).

In each panel the colored line represents the mean annual population size averaged over 10,000 simulations, and the grey lines represent a subsample (n = 1,000) 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.

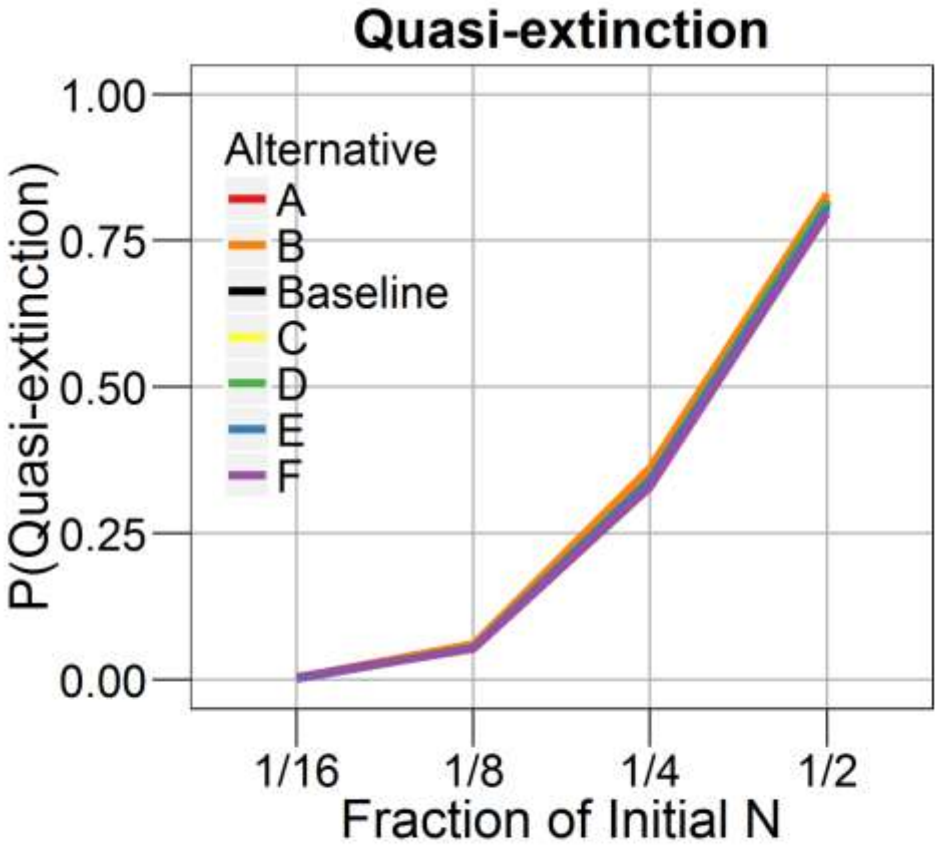

Figure 5. *Risk* analysis – Washington. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the primary proposed management alternatives (A – F).

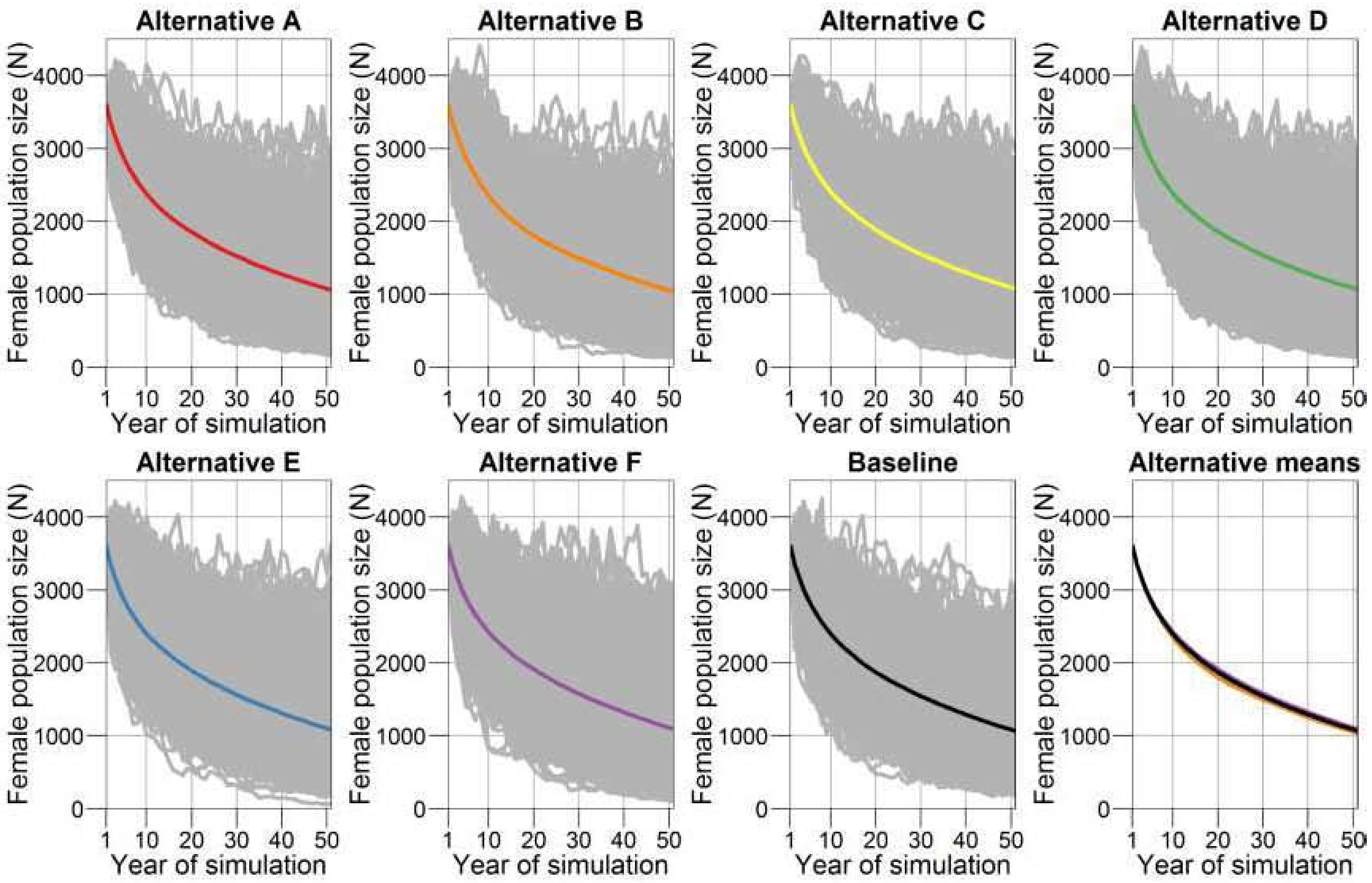
Alternative A
Alternative B
Alternative C
Alternative D
Alternative E
Alternative F
Baseline
Alternative means
Female population size (N)
0
1000
2000
3000
4000
Year of simulation
1
10
20
30
40
50

Figure 6. *Risk* analysis – Washington. Projected murrelet population sizes as a function of proposed management alternatives (A – F). In each panel the colored line represents the mean annual population size averaged over 10,000 simulations, and the grey lines represent a subsample (n = 1,000) 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.

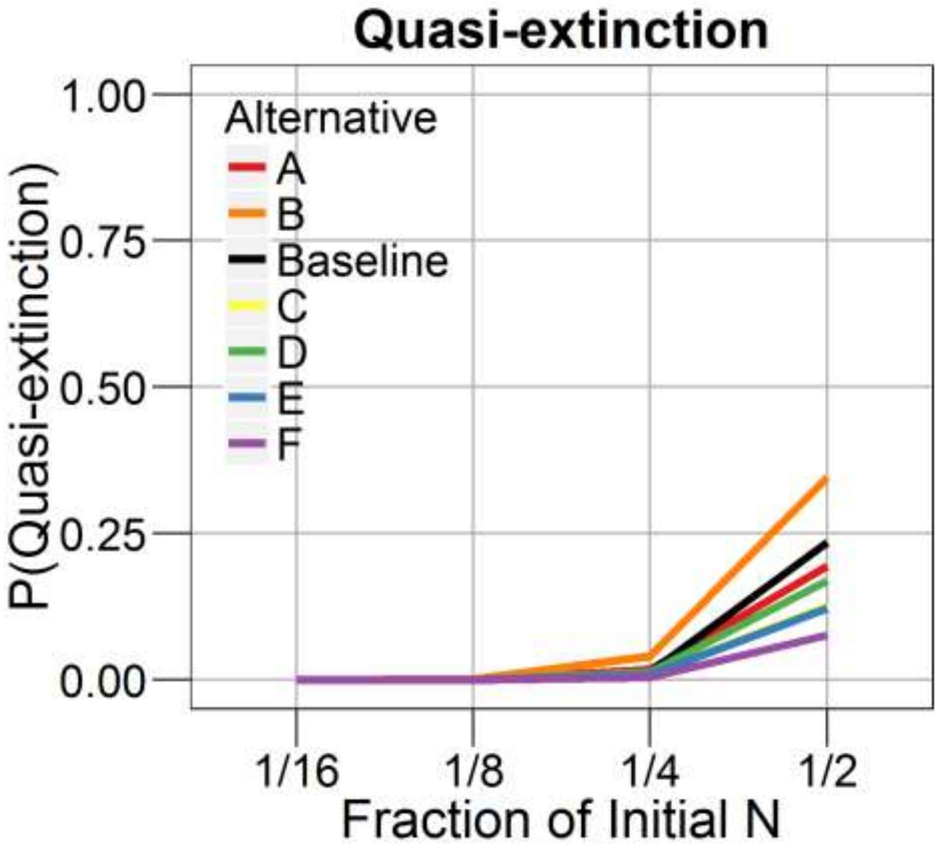

Figure 7. *Enhancement* analysis – DNR lands. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the primary proposed management alternatives (A – F).

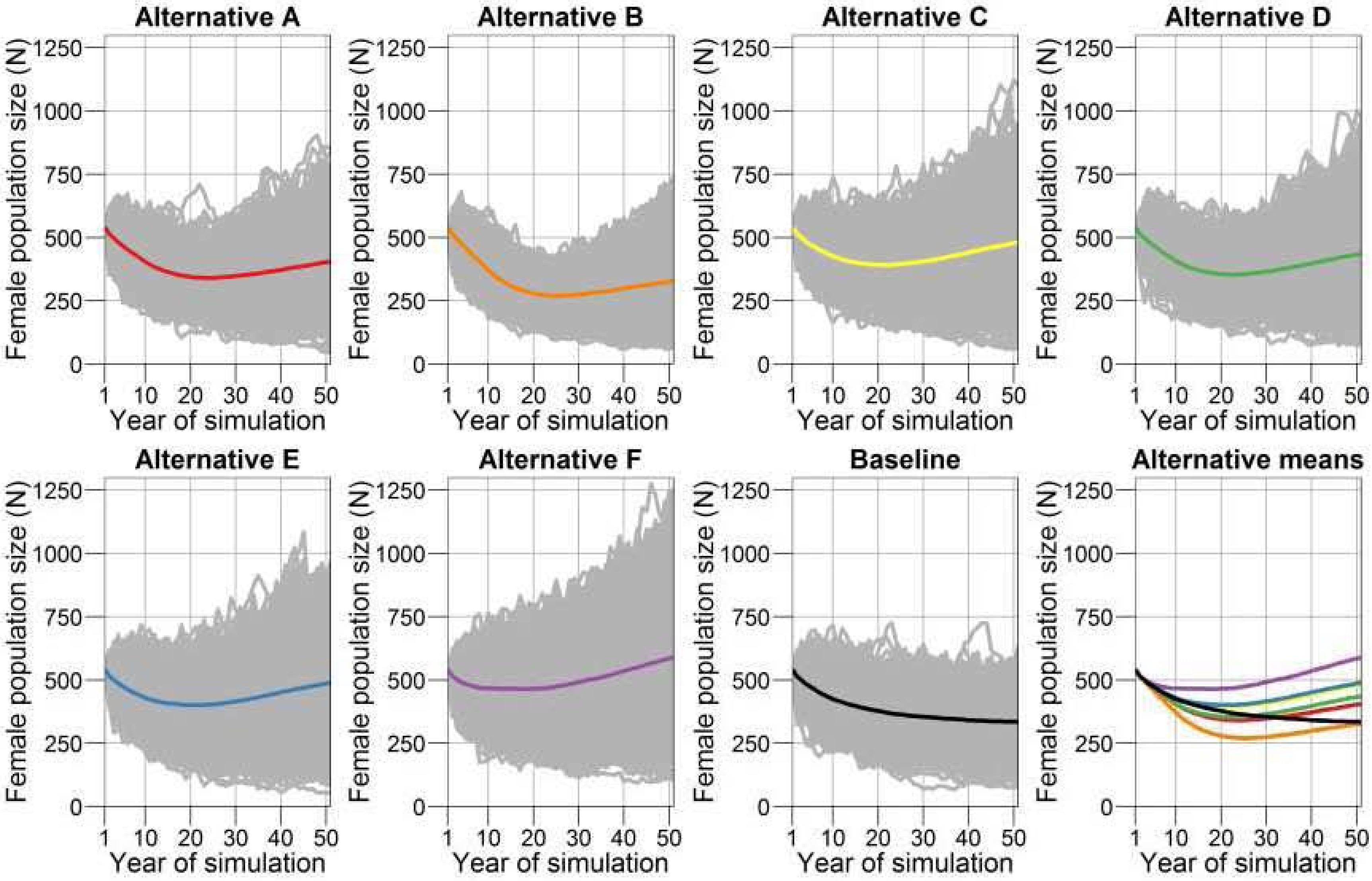
Alternative A
Alternative B
Alternative C
Alternative D
Alternative E
Alternative F
Baseline
Alternative means
Female population size (N)
0
250
500
750
1000
1250
Year of simulation
1
10
20
30
40
50

Figure 8. *Enhancement* analysis – DNR lands. Projected murrelet population sizes as a function of proposed management alternatives (A – F). In each panel the colored line represents the mean annual population size averaged over 10,000 simulations, and the grey lines represent a subsample (n = 1,000) 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.

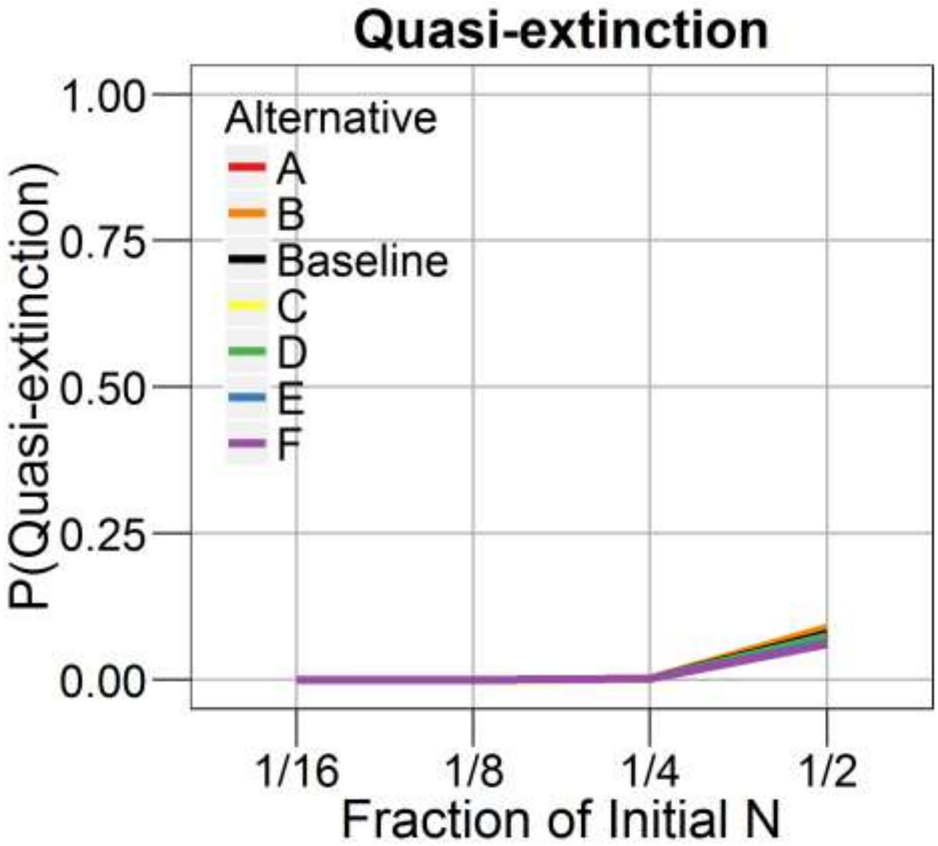

Figure 9. *Enhancement* analysis – Washington. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for the primary proposed management alternatives (A – F).

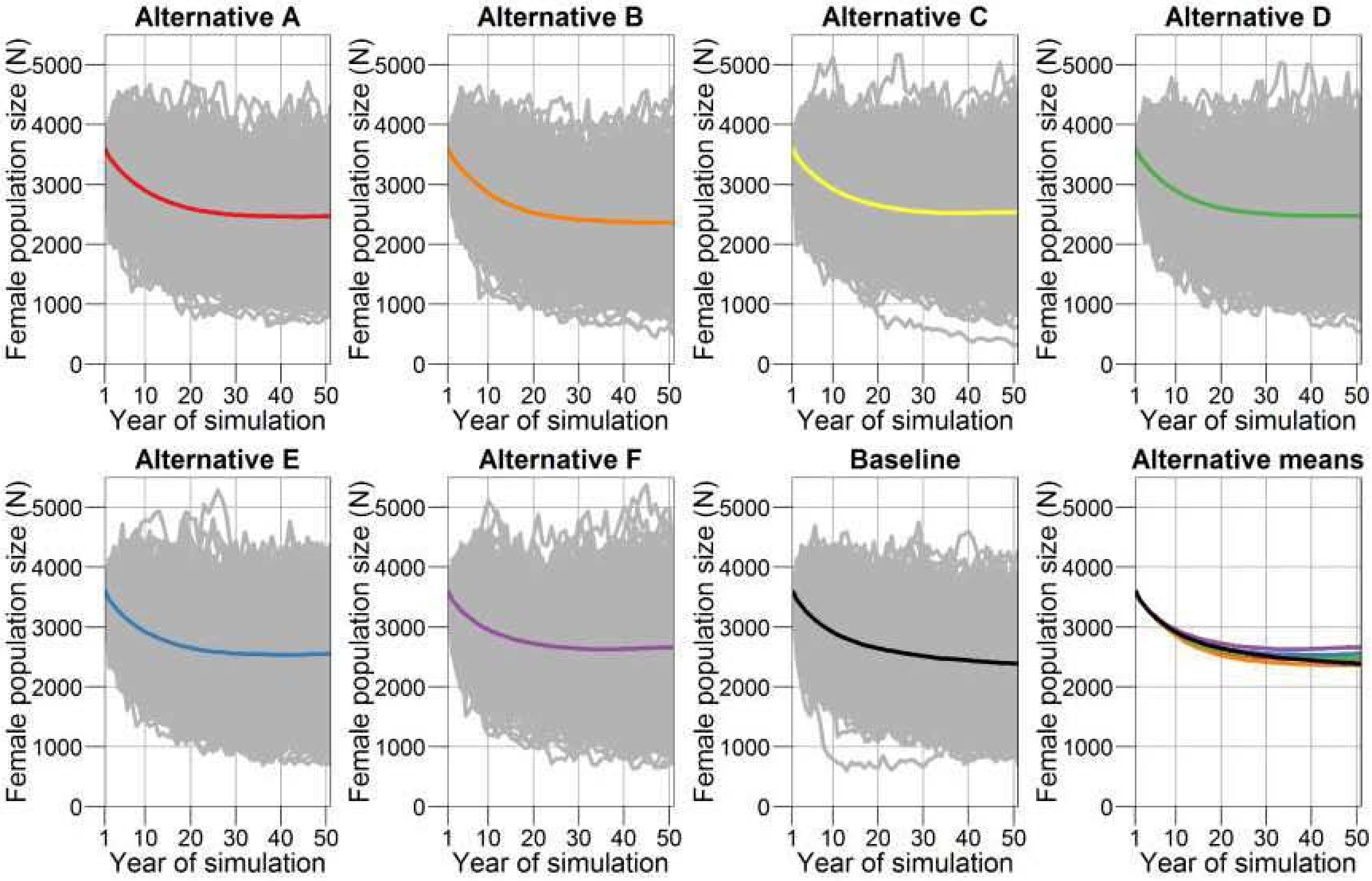
Alternative A
Alternative B
Alternative C
Alternative D
Alternative E
Alternative F
Baseline
Alternative means
Female population size (N)
0
1000
2000
3000
4000
5000
1
10
20
30
40
50
Year of simulation

Figure 10. *Enhancement* analysis – Washington. Projected murrelet population sizes as a function of proposed management alternatives (A – F). In each panel the colored line represents the mean annual population size averaged over 10,000 simulations, and the grey lines represent a subsample (n = 1,000) 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.

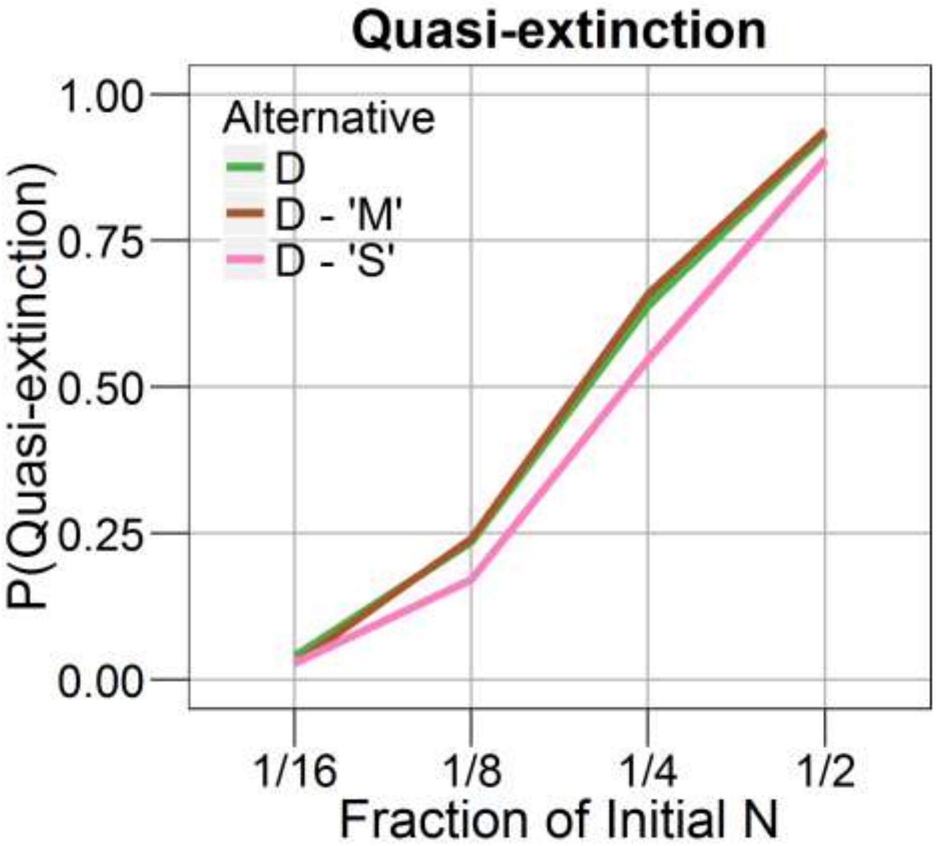

Figure 11. Exploratory *Risk* analysis – DNR lands. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for alternative D compared to its two exploratory variants (D – 'M' and D – 'S').

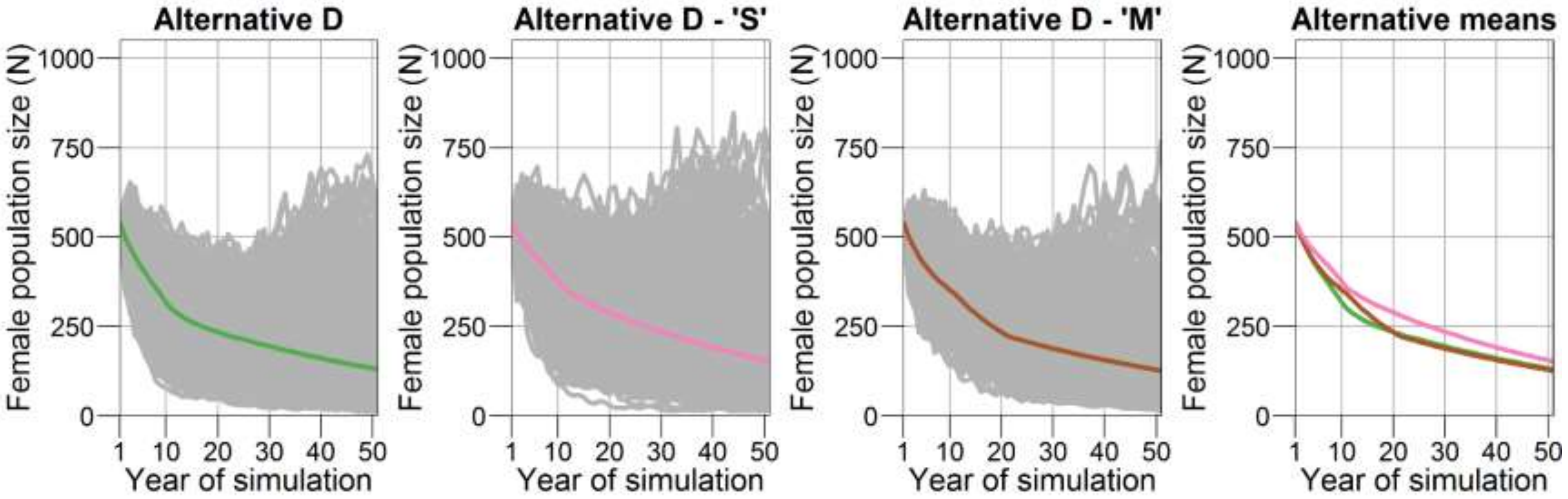

Figure 12. Exploratory *Risk* analysis – DNR lands. Projected murrelet population sizes as a function of alternative D compared to its two exploratory variants (D – 'M' and D – 'S'). In each panel the colored line represents the mean annual population size averaged over 10,000 simulations, and the grey lines represent a subsample (n = 1,000) of individual simulation outcomes. The far-right panel ("Alternative means") plots the mean from each alternative on a single graph for the purposes of comparison.

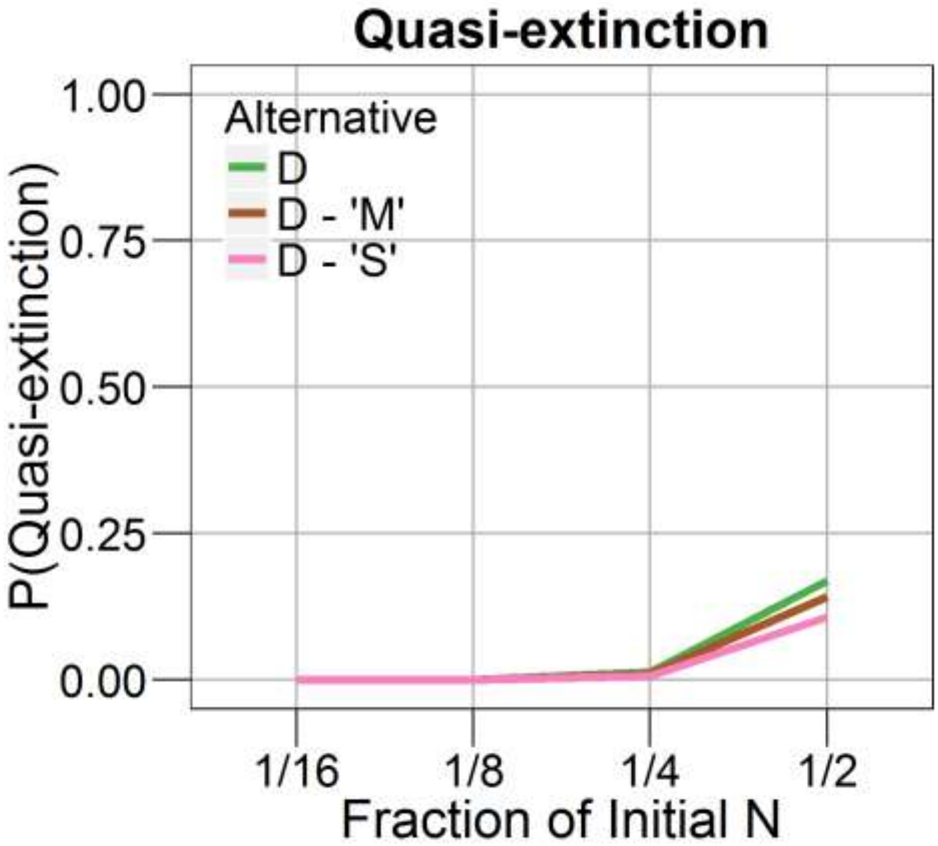

Figure 13. Exploratory *Enhancement* analysis – DNR lands. Quasi-extinction probabilities (proportion of 10,000 simulations that reached a specified fraction of initial population size) for alternative D compared to its two exploratory variants (D – 'M' and D – 'S').

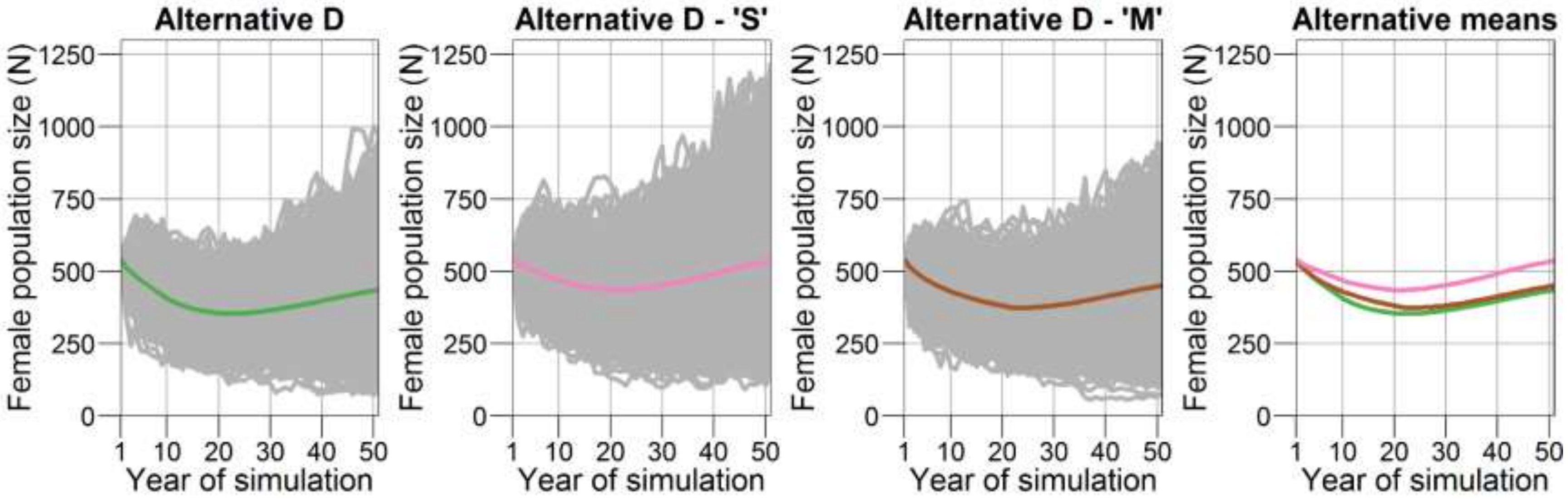

Figure 14. Exploratory *Enhancement* analysis – DNR lands. Projected murrelet population sizes as a function of alternative D compared to its two exploratory variants (D – 'M' and D – 'S'). In each panel the colored line represents the mean annual population size averaged over 10,000 simulations, and the grey lines represent a subsample (n = 1,000) of individual simulation outcomes. The far-right panel ("Alternative means") plots the mean from each alternative on a single graph for the purposes of comparison.

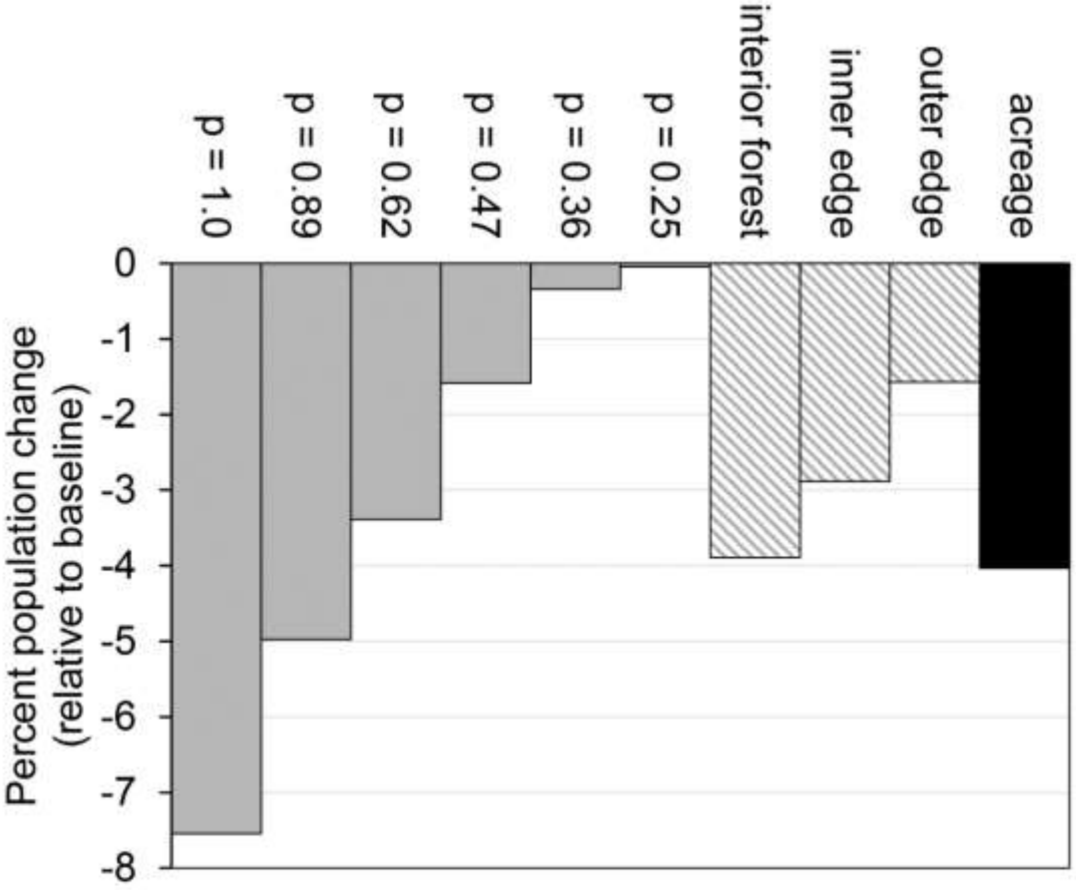

Figure 15. Sensitivity analysis. Grey solid bars represent habitat quality (Pstage), grey hatch-marked bars represent habitat configuration (edge conditions), and the black bar represents habitat amount (raw acreage).

Appendix

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 the latest 5 years of monitoring, 2011-2015 (Falxa et al. *in press*). 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), 213,400 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, 1) 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	0.625	0.25	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, 16% - 34% of habitat was in strings. Edge effects on inner and outer edge habitat was estimated with non-spatial methods based on the assumption that current proportions of edge types on conservation lands, averaged across their alternative designations approximate the long-term proportion of edge types due to the balance of growth and harvest across the land base. Thus, current and projected future edge effects to inner and outer edge forests were distributed across edge types according to the average proportions of no ($p_n = 0.422$), soft ($p_s = 0.307$), and hard ($p_h = 0.271$) edge.

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 $\mathrm{K}_{\mathrm{DNR}} = D * A_{DNR} * 0.5$ 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 Type	None (*n*)	0.55	0.55	0.55
	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).

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