



Estimating the Location and Quality of Marbled Murrelet Habitat

Focus
Paper
#3

The purpose of this paper is to describe how DNR and USFWS identify and classify marbled murrelet habitat for purposes of developing the long-term conservation strategy.

Identifying marbled murrelet nesting habitat

Marbled murrelets were proposed for listing under the Endangered Species Act in part because their nesting habitat in older, complex-structured forests was thought to be so diminished by timber harvest that nesting opportunities were limiting the population (USFWS 1992). Contemporary research continues to support the importance of both *quantity* and *quality* of nesting habitat to murrelet distribution and abundance (e.g., Raphael and others 2015). For the development of a long-term conservation strategy, DNR and USFWS require a credible method, a “habitat model,” to identify the current and potential future location and quality of marbled murrelet habitat across DNR-managed lands. Specific objectives for a habitat model were that it be:

1. Consistent with contemporary scientific findings on the relationships of murrelet nesting biology with forest characteristics,
2. Applicable to DNR-managed lands within the analysis area,
3. No more complex than necessary,
4. Geographic scale and resolution consistent with DNR forest inventory,
5. Appropriately consistent with independent habitat assessments on DNR-managed land, and
6. Consistent with data and models for forest structure and composition, growth, habitat quality and development.

Using forest inventory data

Murrelet nesting habitat is widely considered to have four components that interact to attract nesting murrelets and support their successful nesting: potential nest sites (platforms), flight access to the platforms, nest site- and neighborhood-level security from nest predators, and within commuting distance of marine habitat (considered to be 55 miles inland). The presence and abundance of platforms, and canopy complexity that enables flight access and provides site-level security are characteristics of forest stands¹ that can

Marbled murrelet nesting habitat key components:

- **Nest platforms**
- **Flight access to platforms**
- **Security from predators**
- **Located within 55 miles of marine habitat**

be evaluated using DNR's comprehensive forest inventory. This inventory includes data for stands across all DNR-managed forest lands. A variety of inventory measurements of live and dead trees, other plants, and site conditions are used to provide stand-level estimates of timber volume and value, growth potential, habitat potential, and other important attributes. These forest inventory data also provide the basis for identifying the location and quality of current and future murrelet habitat according to methods agreed upon by DNR and USFWS and described here. The resulting estimates are essential for purposes of conservation planning. Forest stands with high value as nesting habitat, or with the potential to develop nesting habitat characteristics within the HCP tenure, can be identified and incorporated in conservation strategies.² Likewise, these estimates can provide an objective basis for evaluating and adjusting forest management to arrive at a conservation strategy that meets the mandates of both DNR and USFWS.

What habitat classification models are available?

Since the marbled murrelet was listed under the Endangered Species Act in 1992, USFWS and DNR have used various methods to define and identify murrelet habitat.

Habitat modeling under the HCP interim strategy

The 1997 HCP includes an interim strategy that directs DNR to follow a stepwise process of increasingly focused identification and protection of habitat. The interim strategy has led to deferrals of harvest in the most important habitat (and some harvest deferrals in less important habitat) while DNR continues to gather knowledge about how and where marbled murrelets use habitat on DNR-managed lands. (See Focus Paper #4, "Occupied Sites," for a detailed description of the interim strategy.) The first step of the interim strategy is the identification of "suitable habitat blocks," which requires intensive fieldwork and has therefore been mostly applied to screen site-specific timber harvest proposals, rather than for comprehensive habitat inventory and conservation planning. This first step was followed by the development of habitat relationship models, planning-unit specific statistical models that used a suite of stand and neighborhood-level characteristics to predict the likelihood of murrelet use (occupancy) based on HCP-directed murrelet research in a sample of 54 forest stands in each planning unit (Prenzlow

¹ A forest stand is a contiguous group of trees sufficiently uniform to be a distinguishable unit. Definition provided by Society of American Foresters. 1998. Dictionary of Forestry. <http://dictionaryofforestry.org/dict/term/stand>

² See Focus Paper #2, "Areas of Long-Term Forest Cover," for a description of how the strategy delineates these areas; see Focus Paper #5, "Potential Impacts and Mitigation," for a discussion of activities that may impact the murrelet.

Escene 1999).³ Based on these models, habitat mapping (“reclassification”) was done across DNR-managed lands in four planning units, and audio-visual murrelet surveys were conducted in that habitat to determine the extent of marbled murrelet occupancy and further refine implementation of the interim strategy. Note that habitat relationship modeling was not successful in the North and South Puget planning units; the interim strategy continues to use suitable habitat blocks to identify and protect habitat in those units.

Northwest Forest Plan modeling

Other comprehensive, region-wide habitat models have been developed for habitat inventory and monitoring to support the federal Northwest Forest Plan (1994). The “*Biomapper*” model was published in the ten-year review of the plan (Raphael 2006) and was used by the Science Team (Raphael and others 2008) in their analysis of murrelet conservation opportunities. Further work by the NWFP team led to updates using a different habitat modeling technique, “*Maxent*,” the results of which were published in the fifteen-year and 20-year reviews of the Northwest Forest Plan (Raphael and others 2011; Falxa and Raphael 2015). The 20-year review provides the best available landscape scale estimate of the amount and location of murrelet habitat across all lands in Washington. It is not specific to DNR-managed lands.

Science Team modeling

In 2004, DNR convened a team of scientists to assess the state of knowledge on murrelets and their habitat on DNR-managed lands in order to provide recommendations on conservation opportunities. This “Science Team” published a report that included a habitat model that used DNR’s forest inventory to predict current and future locations and quality of murrelet habitat (Raphael and others 2008).

Why have we selected the Science Team’s classification model to estimate marbled murrelet habitat for the long-term conservation strategy?

For the long-term conservation strategy, DNR and USFWS sought a habitat classification model that would use DNR’s spatially-explicit forest inventory data to credibly estimate the current and future location and quality of habitat. To be credible, the model needed to generally identify habitat where it exists, avoid and minimize “false positives” (identifying non-habitat as habitat), avoid and minimize “false negatives” (model not predicting habitat where it actually exists), and distinguish lower-quality habitat in structurally-simple stands from higher-quality habitat in older, complex-structured stands. Additionally, model predictions needed to be reasonably consistent with observed patterns of murrelet habitat use. The model known as “P-stage” was developed by the DNR Science Team to meet these criteria and is modified slightly here to reflect updated information and understanding. Development of the P-stage habitat model was described in detail by Raphael and others (2008, pp. 4.1 – 4.19) and is briefly summarized here, as are the current modifications.

³ See Focus Paper #4, “Occupied Sites,” for a description of this survey and modeling work.

What is P-stage?

P-stage is based on a conceptual model of marbled murrelet nesting habitat (e.g., Nelson 1997) as it relates to stand development in natural forests (e.g., Franklin and Spies 2002). It attempts to generalize and classify levels of habitat quality as it relates to forest stand characteristics. The model was developed by the Science Team using information from DNR-commissioned murrelet surveys, forest inventory, and forest growth modeling as well as general murrelet and silvicultural science.

Probability of occupancy increased with stand development from the simple-structured, large-tree exclusion stage through the complex-structured, “fully-functional” stage.

Developing the P-stage model

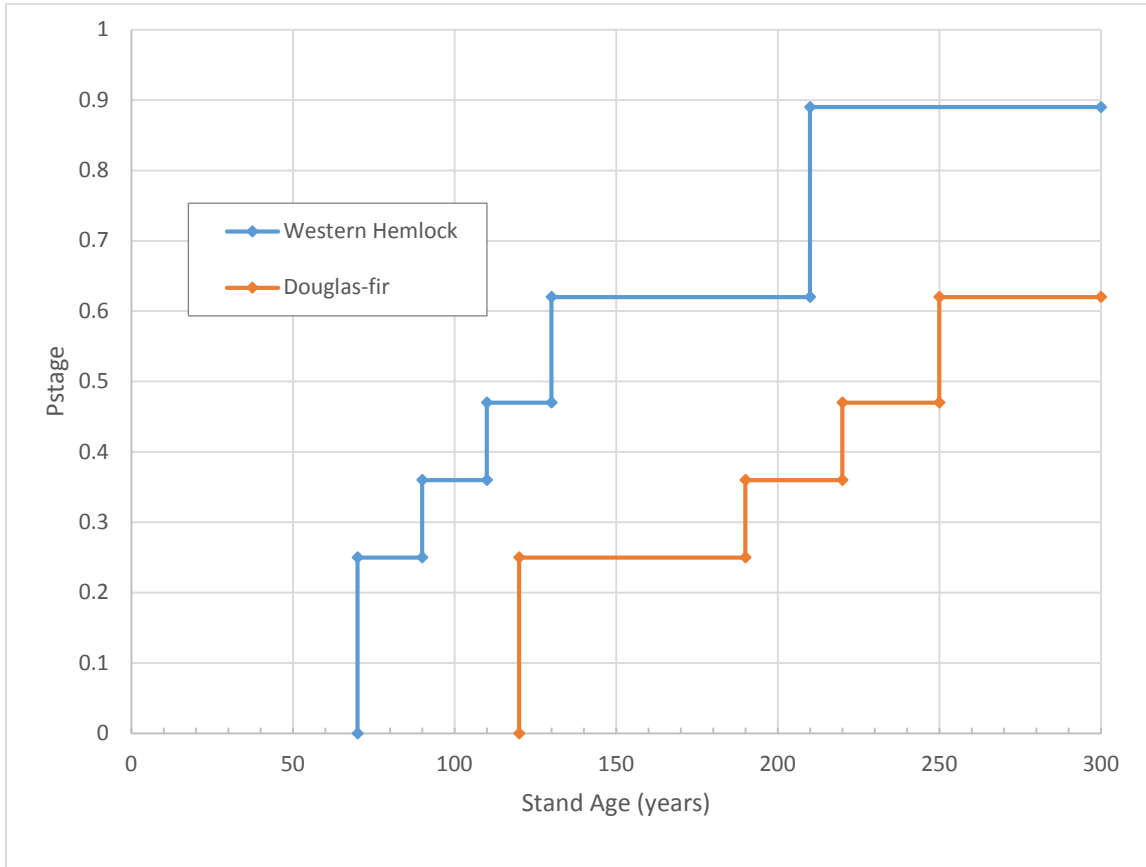
P-stage was developed by the Science Team in order to estimate murrelet habitat quality based on DNR’s forest inventory. DNR commissioned murrelet surveys⁴ to screen forest stands for murrelet use, resulting in their binary classification as occupied or not. Forest inventory data from 355 murrelet survey sites in southwest Washington were used in logistic regression analysis to estimate the probability of occupancy based on two forest attributes widely acknowledged to be important components of nesting habitat, platform abundance and canopy complexity. Platform abundance was estimated with the model used by Washington State Forest Practices (Duke 1997), which was developed with data from private forest lands in southwest Washington and is based on the relationships of platform presence and abundance with tree size. An algorithm that estimated canopy layering based on gaps in tree-height distribution (Crookston and Stage, 1999) provided an index to canopy complexity. Platform abundance, canopy layering, and their interaction (platforms * layers) were found to be associated with higher probabilities of occupancy, but were not perfect predictors. However, model predictions clearly supported that probability of occupancy (habitat quality) increased with stand successional development (DNR 2004) from the simple-structured “large-tree exclusion” stage at least through the complex-structured “fully-functional” stage (which provides functions of “old-growth”), as represented in the 355 sites in southwest Washington.

The Science Team examined this relationship of habitat quality increasing with platform abundance and canopy layering, observing that it paralleled patterns of stand successional development. The Team generalized a set of assumptions that quantified habitat quality as a function of stand age and dominant tree species composition (Raphael and others, 2008). Five stand development stages (DNR 2004) were assumed to have some value as murrelet habitat, and forest growth models were used to generalize the relationship of these five stages with stand age.⁵ Stands were classified into stages based on forest inventory estimates of age and species composition, which also predicted the age at which a stand would transition into a higher quality stage (Figure 1).

⁴ See Focus Paper #3, “Occupied Sites,” for more details about occupancy surveys.

⁵ See Figures 4-2 and 4-3 in the Science Team Report (Raphael and others, 2008).

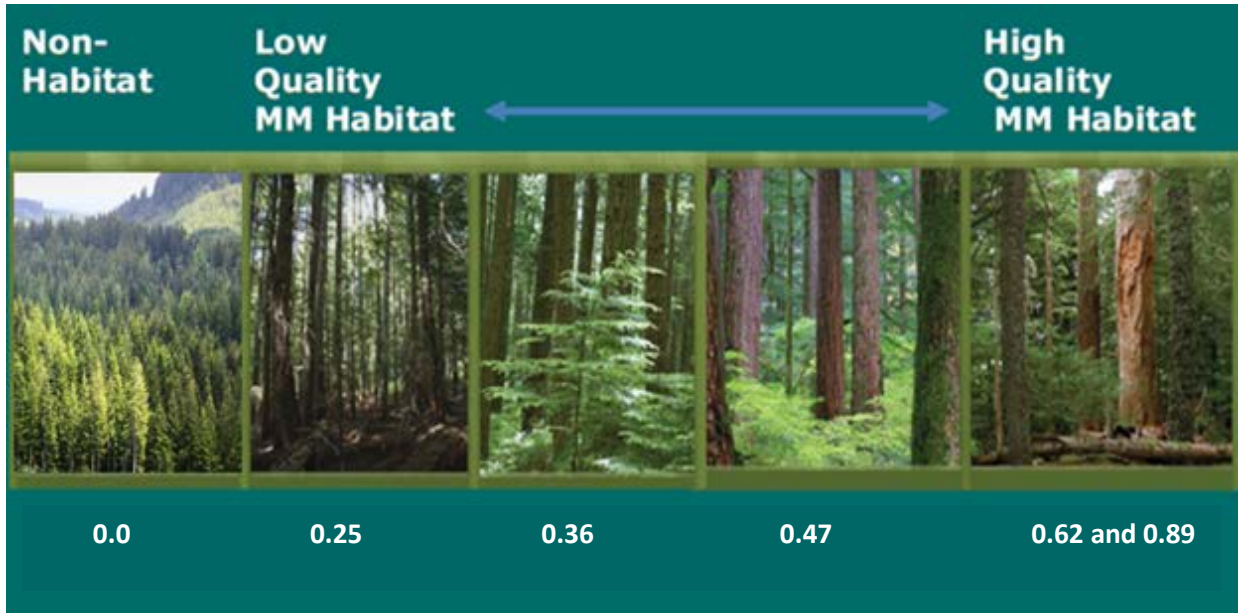
Figure 1. Ages at Which Naturally-Regenerated Forest Stands Transition among P-stage Categories according to the P-stage model



Stands dominated by Douglas-fir rather than western hemlock or other shade-tolerant species were predicted to develop habitat quality more slowly (Raphael and others, 2008). The value that indexed “habitat potential” based on stand development stage was called P-stage to reflect its origins in the logistic regression analysis that predicted “p,” the probability of use. Stands were classified as non-habitat (P-stage 0) or as one of five stages of increasing quality (.25, .36, .47, .62, .89), from the lowest-quality stage that had consistent use (large tree exclusion) to the stage with the highest usage rates (fully-functional) (Figure 2). Those assumptions were used to evaluate conservation opportunities on DNR-managed lands in southwest Washington and the Olympic Peninsula (Raphael and others, 2008).

The value that indexed “habitat potential” based on stand development stage was called “P-stage” to reflect its origins in the logistic regression analysis that predicted “p,” the probability of use.

Figure 2. How the P-stage Model Associates Key Stand Characteristics with Stepwise Development of High Theorized Marbled Murrelet Habitat



Updates to the P-stage model

The P-stage model of Raphael and others (2008) was modified slightly to apply more broadly across all DNR-managed forests in western Washington and to incorporate updated information and understanding of murrelet habitat and stand development. The most significant update was to the plan area, which was expanded beyond the four coastal HCP planning units analyzed by the Science Team to include the North and South Puget planning units. This approximately doubled the analysis area. Stand origin categories of naturally regenerated versus planted were included to avoid predicting that late 20th century plantations with few or no legacy trees would develop into habitat during the 50-year analysis projections. This would allow model predictions of habitat development in naturally-regenerated stands that often include considerable biological legacies due to historical timber harvest methods. Small adjustments were also

made to the predicted rates of transition among P-stage classes (Table 1). The Science Team applied P-stage values to forest habitat within 40 miles of high-use marine habitat (Raphael and others 2008) and discounted those values by 0.25 at greater distances; the current approach applies the values to all habitat within 55 miles of marine water, with discounts applied to some regions with little or no documented murrelet use (see Focus Paper #5, “Potential Impacts and Mitigation,” for a description of how P-stage values are adjusted for geography and edge effects across the landscape). An additional adjustment acknowledged the demonstrably high value of known *occupied* habitat, which was classified as P-stage 1 (a value not represented in the Science Team report).

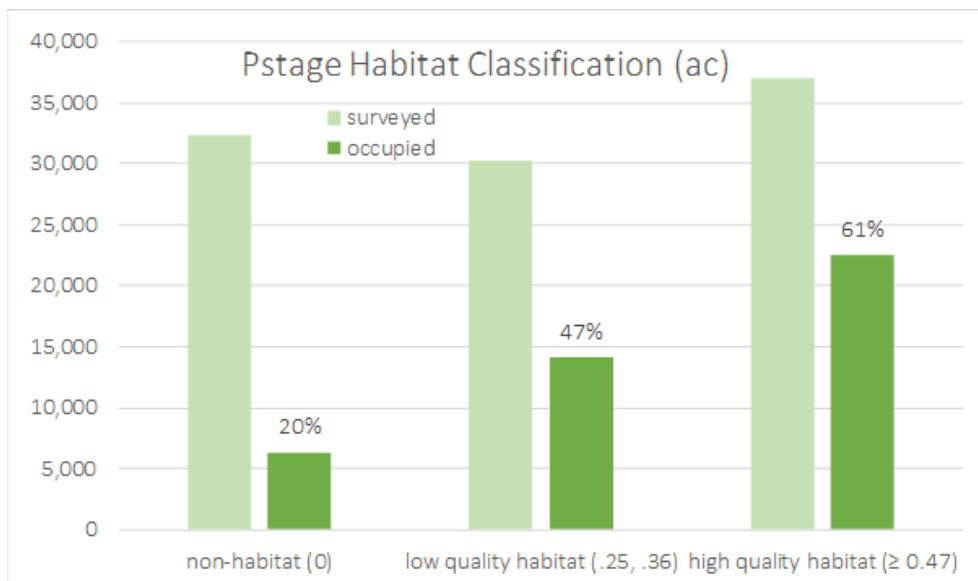
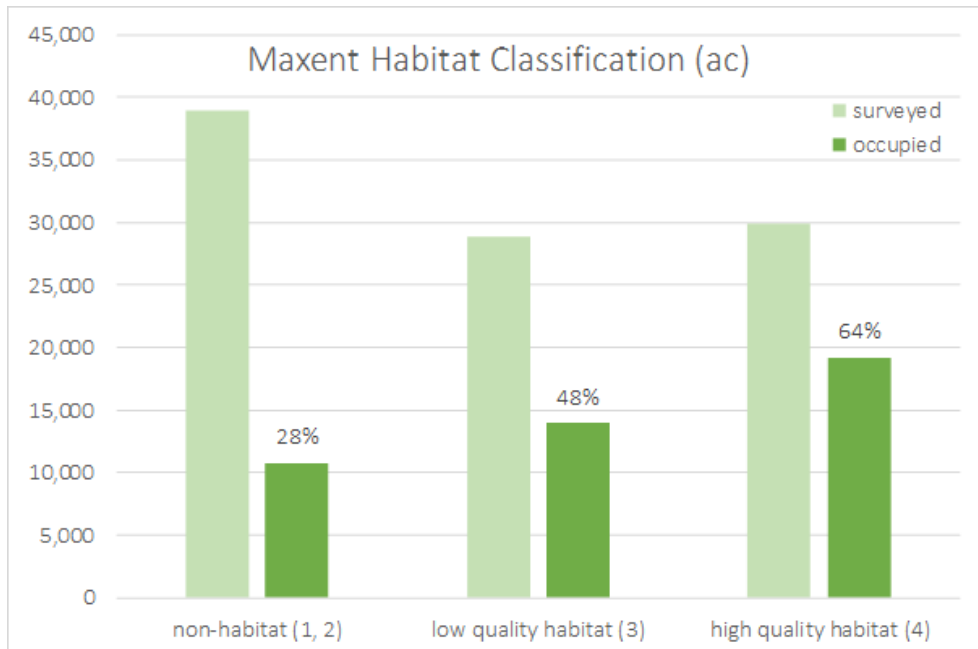
Table 1. Ages at which stands transition among P-stage categories, by dominant tree species, for modelling decisions

P-stage (value)	Relative Stand Age (years)	
	Western hemlock	Douglas-fir
0.25	70	120
0.36	90	190
0.47	110	220
0.62	130	250
0.89	210	NA

How does P-stage compare to other models in estimating habitat?

To evaluate a model’s performance, the normal procedure is to compare predicted results with an observed set. The ratio of observed over predicted results provides a measure of the model’s performance. Because there are no agreed upon biological definitions of murrelet habitat or habitat quality, it is not possible to have an observed data set that captures varying habitat quality. Instead, evidence regarding the accuracy of Maxent and P-stage predictions was gathered by examining model predictions at DNR murrelet survey sites comprising nearly 100,000 acres (see Focus Paper #4, “Occupied Sites,” for a description of these surveys). Given the hypothesis that murrelets avoid non-habitat and preferentially occupy higher-quality habitat, the ratio of occupied to surveyed acreage (occupied ÷ surveyed) should be near zero for non-habitat, and increase as model-predicted habitat quality increases. Falxa and Raphael (2015 in press) summarize Maxent categories 3 and 4 as habitat and categories 1 and 2 as non-habitat. They also consider categories 3 and 4 to represent a gradient in habitat quality. Figure 3 suggests that both P-stage and Maxent predictions are in accord with the murrelet’s hypothesized pattern of habitat use, although both models identify significant portions of occupied sites as non-habitat.

Figure 3. Habitat Classification by the Maxent and P-stage Models for DNR-Managed Land Surveyed for Murrelets and for Occupied Sites Located with those Surveys (percentages reflect occupied/surveyed acres within classes)

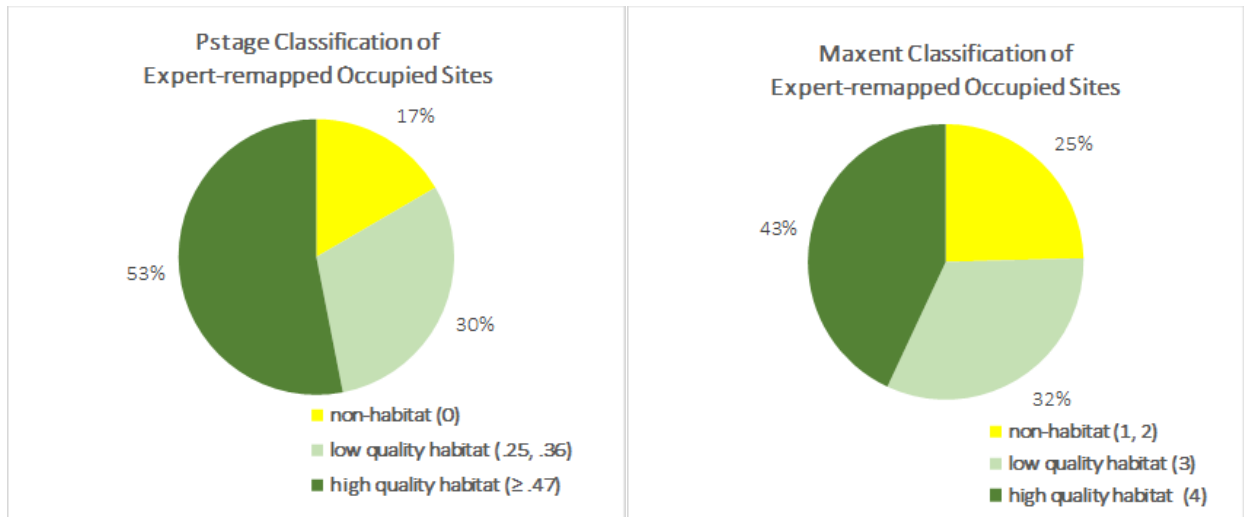


Expert review (Raphael and others 2008) of occupied sites as they were originally mapped under the HCP resulted in the delineation of approximately 16,000 more acres (including surveyed and unsurveyed areas) as occupied habitat. Assuming that this expert re-mapping provides a more biologically appropriate delineation of murrelet habitat, Maxent and P-stage habitat classifications of those re-mapped occupied sites can also be evaluated. Model-based estimates of the composition of those areas should conform to

the prediction that occupied murrelet sites are predominantly higher quality habitat, with lesser amounts of low quality habitat and little non-habitat.

As illustrated in Figure 4, both models do identify that predicted distribution, with higher quality habitat comprising the most abundant group under Maxent (43%) and P-stage (53%) classifications. However, both models identify significant amounts of occupied sites as non-habitat, Maxent 25% and P-stage 17%.

Figure 4. Maxent and P-stage Classifications of 61,000 acres of Expert-mapped Occupied Murrelet Sites on DNR-Managed Land (percentages are class/total area of occupied sites)



It appears that both Maxent and P-stage provide reasonably consistent habitat estimates for areas surveyed for murrelets and for areas found to be occupied. Model predictions of habitat classes at occupied sites provide information on the ability of the respective models to identify habitat where it exists and suggest that while both models perform “reasonably,” neither model can identify all habitat. While evidence is less direct, some of the model-predicted habitat by either model that was found unoccupied with surveys may actually be non-habitat. However, the general alignment of both models with predictions based on murrelet biology, the gradient of occupancy rates found with murrelet surveys and the composition of occupied sites, suggests that either model provides appropriate estimates of current location and quality of habitat.

Although no conclusive comparisons of model performance can be made, habitat predictions of the P-stage model align slightly better with hypothesized murrelet habitat relationships, with a lower occupancy rate in non-habitat (Figure 3) and higher proportions of habitat and high-quality habitat composing occupied sites (Figure 4). P-stage appears to be the best available stand-level murrelet habitat model for DNR-managed land because it is the only model that meets all requirements of USFWS and DNR for development and assessment of the long-term conservation strategy (Table 2).

Table 2. Criteria-based Comparison of Three Habitat Classification Models

Model Criteria	P-stage	Maxent	Interim Strategy (reclassified model)
1. Based on relationship between nesting biology and forest composition	✓	✓	
2. Applicable to all DNR-managed lands in the analysis area	✓	✓	
3. Simple rather than complex	✓		
4. Scale and resolution consistent with DNR forest inventory	✓		
5. Habitat classifications demonstrably consistent with contemporary murrelet science	✓	✓	✓
6. Consistent with DNR forest modeling	✓		

How do we address uncertainty in P-stage model predictions?

Hilborn and Mangel (1997) describe two broad types of uncertainty that influence our ability to make inference from ecological models: 1) uncertainty in generalizing and quantifying ecological *processes*, and 2) uncertainty in ecological data gathered from *observations*. Both process and observation uncertainty affect conclusions derived from the P-stage habitat model. Murrelet biological responses (processes like habitat selection, nesting rates, and nest success) are more variable and unpredictable than can be acknowledged within our simplistic model of habitat quality, or in the binary classification of murrelet habitat as “occupied” or not. Likewise, forest structure, composition, and growth are processes that are more complex and subject to many more influences than can be incorporated into the P-stage model. Findings from our sample-based forest inventory and murrelet surveys can be influenced by sampling and measurement error and other forms of observation uncertainty.

Predictions of the P-stage model cannot be perfectly accurate; the model classifies habitat quality by discrete groups, while habitat quality in nature is more likely a continuous gradient. Murrelets likely select habitat based on a more complex suite of environmental cues than platform abundance and canopy layering, and further specificity is lost in the generalization of those elements of stand structure by age-class. Because of these and other uncertainties, some habitat will be overlooked, some non-habitat will be mistakenly identified as habitat. Some habitat will also be mistakenly classified as higher or lower quality than its actual state, and transitions among habitat quality classes will not perfectly follow predictions. Some of these uncertainties and their possible influences on evaluating and selecting a conservation strategy are summarized and discussed below.

If P-stage predictions were consistently biased, there would likely be a directional effect on outcomes of the conservation strategy. For example, if model predictions consistently under-estimated habitat quality,

habitat conservation would likely be less effective because some current habitat and forests that would grow into habitat will be overlooked. If habitat quality were consistently over-estimated, habitat conservation would likely be less efficient because some non-habitat would be assigned to conservation pathways but would not serve its intended purpose. Unbiased error can also affect conservation outcomes with effects of under- and over-estimates as noted above, but if those errors were approximately balanced then their effects would be manifest but diluted compared to consistent, directional error. Key components of the P-stage model are examined for theory and/or evidence that could suggest its predictions are biased.

Scale and resolution. The scale at which murrelets select nesting habitat is not known. Clearly, these seabirds need an appropriate nest platform in a context that provides stability and security during the nesting season. Across the nearly 3,000 miles of coast they inhabit in North America, those fine-scale elements of nesting habitat are rather constant but as the view expands beyond the immediate nest site, the environment becomes increasingly indistinguishable from its surroundings (McShane et al. 2004). This uncertainty over the scale at which habitat is distinguished from non-habitat, and how to distinguish among levels of habitat quality is likely responsible for much uncertainty in all habitat modeling and delineation exercises. Raphael et al. (2015) discuss this source of uncertainty in their Maxent model which predicts and maps murrelet habitat across three states at the scale of 30 m square pixels (the resolution of their satellite imagery), generalized from characteristics of the target pixels and its immediate neighbors (9 pixels total, approximately 2 acres) although their multivariate habitat model also incorporates broader-scale influences from the surrounding 50 hectares (147 acres). The P-stage model predicts and maps habitat over DNR-managed land at the scale of forest inventory units (i.e., stands as footnoted above) which average 48.7 acres in western Washington with 82% of nearly 19,000 stands between 5 and 100 acres. Stand-level metrics are developed from on-ground measurements at a network of sample plots located at approximately one plot per five acres. The “suitable habitat block” model, which has been mainly used for project-level planning and implementation, identifies and delineates habitat based on tree-by-tree inspection and arbitrary thresholds for the density of platforms observed (two per acre), the inter-tree distance between platform-bearing trees (300 feet, 92 meters), and minimum patch size (five acres).

Wiens (1976) cautioned researchers to avoid our human preconceptions and focus habitat research at scales important to the organisms of interest. Absent knowledge of the scale, or scales at which murrelets recognize and select nesting habitat, the habitat models noted above mainly focus around human perceptions of forest habitat at scales appropriate to the geographic scope of their unique applications (range-wide, estate-wide, project-level) using the resolution of available data. Thus even if each model classified habitat similarly, their mappings would differ because small habitat areas or inclusions of non-habitat would be variously overlooked depending on resolution. If murrelet habitat consistently occurred in habitat patches too small to be recognized with DNR’s forest inventory, P-stage would fail to identify much habitat. However, the consistent broad-scale relationship of murrelet numbers with habitat area as identified with a variety of habitat models (Burger 2002, Raphael and others 2002, Raphael and others 2015) and the consistent patterns of murrelet inland habitat use in identifiable habitat patches (i.e., “stands”) as identified with a variety of methods (e.g., McShane and others 2004) suggest that the scale and resolution of P-stage predictions are appropriate to identify most murrelet habitat.

Forest stands. Forest stands, by definition, are a construct of human perception. DNR’s current forest inventory is collected at sample plots, which comprise approximately one percent of stand area for

overstory trees (where potential murrelet nest sites occur). Thus, even though stands were delineated from high-resolution aerial photography based on apparent similarity of vegetation and topography, considerable fine-grained heterogeneity within stands is obscured when stand level averages are compiled from plot data. Consequently, discrete areas of habitat could be missed within stands with average characteristics of non-habitat or vice-versa. Some murrelet nests have been located in what appear to be unsuitable forest conditions (Bradley and Cooke 2001, Bloxton and Raphael 2009) although they were generally in landscapes dominated by older forest. These discoveries probably reflect the inability of coarse-grained, stand-level classifications to recognize rare structural elements or small patches of murrelet habitat. However, the great majority of murrelet nests have been located within forests more broadly recognizable as murrelet habitat (e.g., McShane and others, 2004), lending confidence that stand-level habitat classification can identify most murrelet habitat.

Forest growth, stand characteristics, and habitat development. The P-stage model simplifies the relationship of murrelet habitat quality with stand development to three stand characteristics: origin, dominant species, and age. But forest growth and the development of murrelet habitat that accompanies it are much more complex and unpredictable processes than represented by that simple model. Observation uncertainty in the forest inventory-based estimates of stand characteristics adds to the uncertainty that accompanies P-stage predictions of habitat quality. However, comparison of P-stage classifications with murrelet survey findings (Fig. 3) and habitat mapping at occupied sites (Fig. 4) do not suggest that P-stage provides biased estimates of murrelet habitat quality.

Field observations. Some areas predicted as murrelet habitat by P-stage appear to lack abundant trees with platforms and/or individual trees with abundant platforms. Likewise, some predicted non-habitat contains trees with platforms and some of the area mapped as occupied is classified by P-stage as non-habitat. These observations can be proposed as evidence that P-stage mistakenly classifies some non-habitat as habitat and overlooks other habitat. However some areas mapped as occupied were found to lack platforms as well, lending an additional dimension of uncertainty to comparisons of expert- and model-based habitat predictions. While some habitat is certainly overlooked just because of the scale issues summarized above, it is more difficult to contend that non-habitat is mistakenly classified as habitat because of the probabilistic nature of P-stage predictions. For example, P-stage 0.25 is so classified because stands with that general suite of characteristics are occupied about one-fourth as frequently as the highest quality habitat. The generalized probability of use that P-stage classes represent encompasses within-class, among-stand variability in habitat quality, behavioral variability among murrelets, and other sources of variability. Thus the lack of observable habitat characteristics in some P-stage habitat can be considered to be within the scope of model predictions. The overall patterns of “selection” among P-stage classes found with DNR murrelet surveys (Fig. 3) and the classification of habitat identified as belonging to occupied sites (Fig. 4) demonstrates the general applicability of the model even though some predictions do not conform to field observations.

Planning with uncertainty

The Joint Agencies conclude that there is an unknown level of uncertainty in P-stage predictions of current and future habitat. However, the general applicability of the P-stage model predictions outweigh their uncertainty for this conservation planning effort. We can acknowledge this uncertainty and proceed with developing and implementing a conservation strategy using P-stage habitat predictions for three basic reasons: 1) the apparent prevalence of reliable model predictions relative to those clouded by uncertainty, 2) the need to develop and implement a conservation strategy with this uncertainty in mind, and 3) existing policies and management procedures, as well as conservation planning approaches safeguard against high levels of risk associated with this uncertainty. Those additional cautions include:

The Joint Agencies conclude that there is an unknown level of uncertainty in P-stage predictions of current and future habitat, but also that the general applicability of P-stage model predictions outweigh their uncertainty.

1. Habitat conservation is geographically extensive in all alternatives.
2. Occupied sites were expanded to include sites where above-canopy circling was observed, and to include expert-identified contiguous habitat regardless of survey findings or previous habitat classification. Protection of expanded occupied sites and buffers are a component of all but one alternative.
3. All alternatives propose to retain the majority of identified current and potential future habitat.
4. Current and future habitat is abundant in LTFC. It is likely that much of the “overlooked habitat” is prevalent in LTFC and is already in conservation status.
5. Some alternatives propose the retention of all “higher quality” habitat.
6. Under most alternatives, the majority of habitat conservation and development occurs nearby but outside of occupied sites.
7. Estimation of impacts and mitigation are based on the same assumptions so there is an intrinsic balance.

How is P-stage applied in the development of the long-term strategy?

P-stage is being used for the long-term conservation strategy as a baseline for determining habitat quantity and quality on DNR-managed lands over the life of the HCP. P-stage values are used to identify key areas to focus conservation, as well as in the calculation of take and mitigation. It is important to recognize that there are other factors that influence the probability of occupancy of a forest stand by murrelets, including proximity to high-quality marine habitat, proximity to other occupied sites, and habitat fragmentation. The P-stage model does not, by itself, account for these factors when evaluating habitat. However, the analytical framework adjusts P-stage values to reflect edge effects, geographic location, and other important factors affecting habitat quality (see Focus Paper #5, “Potential Impacts and Mitigation”). In addition, the conservation alternatives being developed account for these factors when designating potential habitat for long-term protection under the HCP.

Literature cited

- Bloxton, T. D., and M. G. Raphael. 2009. Breeding ecology of the marbled murrelet in Washington State: five year project summary (2004-2008). USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington.
- Bradley, R. W., & Cooke, F. 2001. Clief and Deciduous Tree Nests of Marbled Murrelets in Southwestern British Columbia. *Northwestern Naturalist*, 82(2), 52–57.
- Crookston, N. L., and A. R. Stage. 1999. Percent canopy cover and stand structure statistics from the Forest Vegetation Simulator. Gen. Tech. Rep. RMRS-GTR-24. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 11 p.
- Duke, S. 1997. An inventory-based procedure for estimating the abundance of Marbled Murrelet platforms. Unpublished report, Weyerhaeuser. Tacoma, WA.
- Falxa, GA and M.G. Raphael, Tech. cords. 2015 (in press). Northwest Forest Plan- the first twenty years (1994-2013): Status and trend of marbled murrelet populations and nesting habitat. Gen.Tech.Rep., USDA Forest Service Draft 26 May 2015. <http://www.reo.gov/monitoring/reports/index.shtml>
- Franklin, J.F. and T.A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications*, 2(4) pp. 387-396.
- McShane, C., T. Hamer, H. Carter, G. Swartzman, V. Friesen, D. Ainley, R. Tressler, K. Nelson, A. Burger, L. Spear, T. Mohagen, R. Martin, L. Henkel, K. Prindle, C. Strong, and J. Keany. 2004. Evaluation report for the 5-year status review of the marbled murrelet in Washington, Oregon, and California. Unpublished report. EDAAW, Inc. Seattle, Washington. Prepared for the U.S. Fish and Wildlife Service, Region 1., Portland, Oregon.
- Nelson, S.K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). In: Poole, A.; Gill, F., eds. *Birds of North America*. No. 276. Philadelphia, PA: Academy of Natural Sciences; Washington, DC: American Ornithologists Union. 32 p.
- Prenzlów-Escene, D. 1999. Marbled murrelet forest habitat relationships studies. Washington Department of Natural Resources, Olympia, Washington
- Raphael, M.G., D. Evans-Mack, and B.A. Cooper. 2002. Landscape-scale relationships between abundance of marbled murrelets and distribution of nesting habitat. *Condor* 104:331-342.
- Raphael, M. G. 2006. Conservation of the Marbled Murrelet under the Northwest Forest Plan. *Conservation Biology*, 20: 297–305.
- Raphael, M. G., S. K. Nelson, P. Swedeen, M. Ostwald, K. Flotlin, S. Desimone, S. Horton, P. Harrison, D. P. Escene and W. Jaross. 2008. Recommendations and Supporting Analysis Marbled Murrelet Science Report Recommendations (Science Team Report) Washington State Department of Natural Resources
- Raphael, M.G., Gary A. Falxa, Katie M. Dugger, Beth M. Galleher, Deanna Lynch, Sherri L. Miller, A. Kim Nelson, Richard D. Young. 2011. Northwest Forest Plan- the first 15 years (1994-2008): status and trend of nesting habitat for the marbled murrelet. Gen.Tech.Rep. PNW-GTR-848. Portland, OR: USDA Forest Service, PNW Research Station. 52 p.
- Raphael, Martin G., Andrew J. Shirk, Gary A. Falxa, Scott F. Pearson . 2015. Habitat Associations of Marbled Murrelets During The Nesting Season In Nearshore Waters Along The Washington To California Coast. *Journal of Marine Systems*. 146:17-25.
- Washington State Department of Natural Resources. 2004. Final Environmental Impact Statement on Alternatives for Sustainable Forest Management of State Lands in Western Washington and for Determining the Sustainable Harvest Level. Washington State Department of Natural Resources, Olympia, Washington

Wiens, J.A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7:81-120.