DRAFT Appendix C: Development of a Modeling Framework to Support Recovery Implementation and Habitat Conservation Planning

Introduction by U.S. Fish and Wildlife Service

The Service believes a spatially explicit demographic model would greatly improve recovery planning and implementation for the spotted owl. Peer reviewers were critical of the 2008 Recovery Plan's habitat conservation network strategy and the general lack of updated habitat modeling capacity. The Service considered this criticism and concluded that a spatially explicit demographic model would greatly improve recovery implementation for the spotted owl, as well as other land use management decisions.

For this Revised Recovery Plan, the Service appointed a team of experts to develop and test a modeling framework that can be used in numerous spotted owl management decisions. This spatially-explicit approach is designed to allow for a more in-depth evaluation of various factors that affect spotted owl distribution and populations**.** This approach also allows for a unique opportunity to integrate new data sets, such as information from the NWFP 15-year Monitoring Report (Davis and Dugger, in press) and the recent spotted owl population meta-analysis (Forsman *et al.*, in press).

The Service expects this modeling framework will be applied by Federal, State, and private scientists to make better informed decisions concerning what areas should be conserved or managed to achieve spotted owl recovery. Specifically, the modeling framework can be applied to various spotted owl management challenges, such as to:

1) Inform evaluations of meeting population goals and Recovery Criteria.
2) Develop reliable analysis and modeling tools to enable evaluation of the influence of habitat suitability and barred owls on spotted owl demographics.
3) Support future implementation and evaluation of the efficacy of spotted owl conservation measures described in various Recovery Actions.
4) Provide a framework for landscape-scale planning by both Federal and non-federal land managers that enables evaluation of potential demographic responses to various habitat conservation scenarios, including information that could be used in developing a proposed critical habitat rule.

These and other potential applications of the modeling framework described herein represent a significant advancement in spotted owl recovery planning. Although the completed model framework will be included in the Revised Recovery Plan, the Service hopes that future application of this modeling approach will lead to refinement and improvements, such as incorporation of population connectivity and source-sink dynamics, over time as experience and new scientific insights are realized.

To meet these objectives, the Service established the Spotted Owl Modeling Team (hereafter the "modeling team") to develop and apply modeling tools for the Service's use in designing and evaluating various conservation options for achieving spotted owl recovery. The modeling team was informally organized along lines of function and level of participation. Jeffrey Dunk (Humboldt State University), Brian Woodbridge (USFWS), Bruce Marcot (USFS, Pacific Northwest Research Station), Nathan Schumaker (USEPA), and Dave LaPlante (a contractor with Natural Resource Geospatial) composed the primary group which was responsible for conducting the data analyses and modeling. They were assisted by spotted owl researchers, agency staff and modeling specialists who individually provided data sets and advice on particular issues within their areas of expertise, and reviewed modeling processes and outputs. These experts were: Robert Anthony (Oregon State University), Katie Dugger (Oregon State University), Marty Raphael (USFS, Pacific Northwest Research Station), Jim Thrailkill (USFWS), Ray Davis (USFS, Northwest Forest Plan Monitoring Group), Eric Greenquist (BLM), and Brendan White (USFWS). Additionally, technical specialists—Craig Ducey (BLM), Karen West (USFWS) and Dan Hansen and M.J. Mazurek (contractors with Humboldt State University Foundation) conducted literature reviews and assisted with data collection and analyses.

To ensure that the modeling effort was based on the most current information and scientific knowledge and opinion, the modeling team also sought the assistance of numerous individual scientists and habitat managers from government, industry and a non-profit conservation organization (listed in acknowledgements) in development of habitat descriptions, modeling regions and many other aspects of spotted owl and forest ecology. To facilitate this effort, the Service held a series of meetings with spotted owl experts (habitat expert panels) to obtain additional information, data sets, and expertise regarding spotted owl habitats.

Representatives of the modeling team have prepared this Appendix to provide a thorough description of the modeling framework developed by the team, the results of model development and testing, and examples of preliminary modeling process outputs that demonstrate how the model can be used to evaluate habitat conservation scenarios.

While this framework represents state-of-the-art science, it is not intended to represent absolute spotted owl population numbers or be a perfect reflection of reality. Instead, it provides a comparison of the relative spotted owl responses to a variety of potential conservation measures and habitat conservation networks. The implementation of spotted owl recovery actions should consider the results

of the modeling framework as one of numerous sources of information to be incorporated into the decision-making process.

General Approach

The modeling team (hereafter "we") employed state-of–the-art modeling tools in a multi-step analysis similar to that proposed by Heinrichs *et al.* (2010) and Reed *et al.* (2006) for designing habitat conservation networks and evaluating their contributions to spotted owl recovery. In addition to this objective, the modeling tools in this framework, individually or in combination, are designed to enable evaluation of the efficacy of spotted owl conservation measures such as Recovery Action 10 and management of barred owls**.**

Our conservation planning framework integrates a spotted owl habitat model, a habitat conservation planning model, and a population simulation model. Collectively, these modeling tools allow comparison of estimated spotted owl population performance among alternative habitat conservation network scenarios under a variety of potential conditions. This will enable the Service and other interested managers to use relative population viability (timing and probability of population recovery) as a criterion for evaluating habitat conservation network scenarios and other conservation measures for the spotted owl.

The evaluation approach the modeling team developed consists of three main steps (Figure C1):

> **Step 1** – Create a map of spotted owl habitat suitability throughout the species' U.S. range, based on a statistical model of spotted owl habitat associations.
>
> **Step 2** – Develop a spotted owl conservation planning model, based on the habitat suitability model developed in Step 1, and use it to design an array of habitat conservation network scenarios.
>
> **Step 3** – Develop a spatially explicit spotted owl population model that reliably predicts relative responses of spotted owls to environmental conditions, and use it to test the effectiveness of habitat conservation network scenarios designed in step 2 in recovering the spotted owl. The simulations from this spotted owl population model are not meant to be estimates of what will occur in the future, but provide information on trends predicted to occur under differing habitat conservation scenarios.

The Service or other practitioners can use the population simulation model developed in Step 3 to test the degree to which various recovery actions and habitat conservation network scenarios contribute to recovery of the spotted owl. For example, it can be used to evaluate modeled population size and trend, as well as distribution and connectivity of modeled spotted owl populations through time.

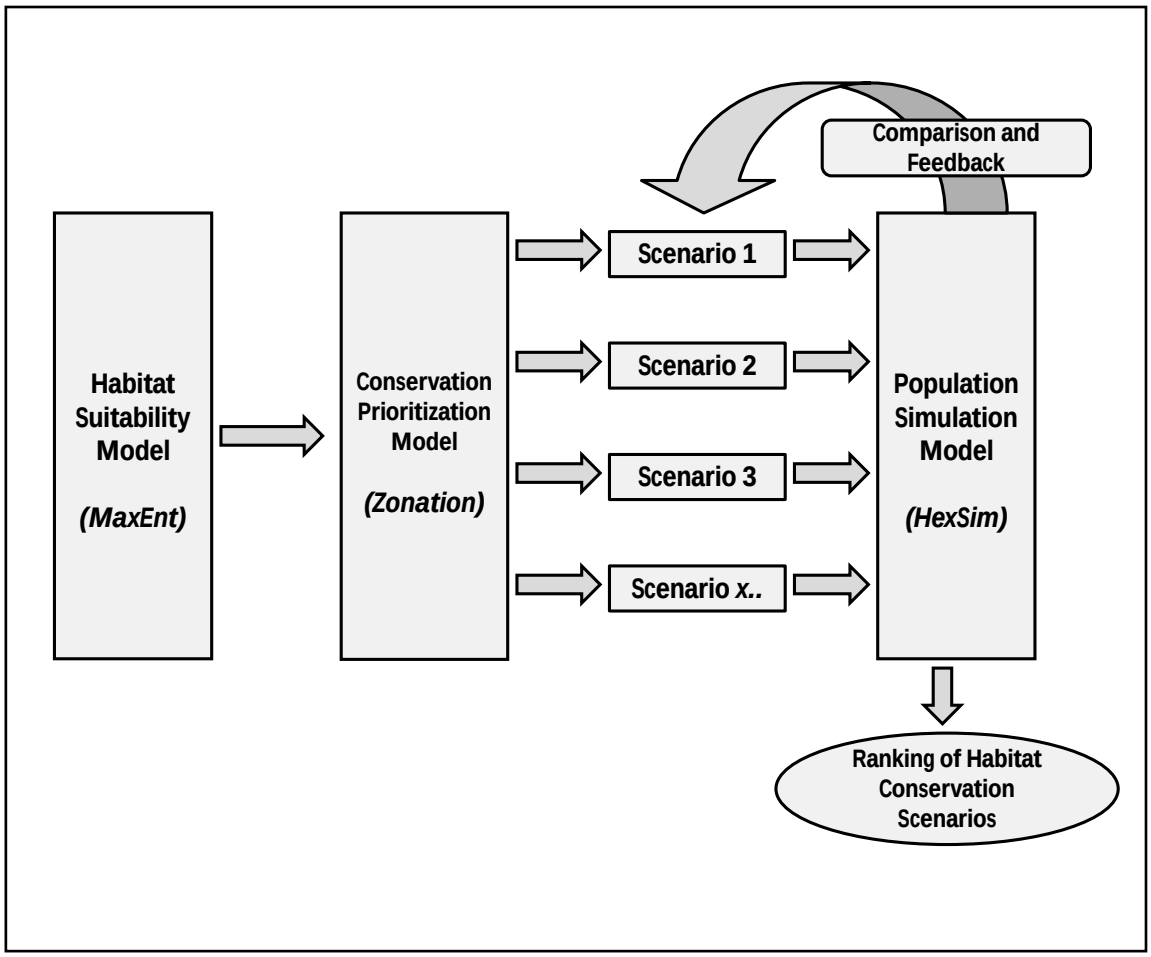
Each of the steps noted above involved statistical and / or mathematical modeling and is not meant to be exact predictions of what currently exists or what will

occur in the future, but represent our best estimates of current conditions and relationships. These models allow the use powerful, up-to-date scientific tools in a repeatable and scientifically accepted manner to develop and evaluate habitat conservation networks and other conservation measures to recover the spotted owl. We view the benefit and utility of such models in the same way that Johnson (2001) articulated, "*A model has value if it provides better insight, predictions, or control than would be available without the model*." The modeling tools described herein meet this standard.

The overall framework and evaluations outlined in Figure C1 are somewhat similar to Raphael *et al.* (1998). Our modeling process differs fundamentally from the conservation planning approach used by the ISC (Thomas *et al*. 1990), 1992 Draft Recovery Plan (USFWS 1992b), FEMAT (1993), and the 2008 Recovery plan (USFWS 2008b), which were based on *a priori* rule sets derived from best expert judgment regarding the size of reserves or habitat conservation blocks, target number of spotted owl pairs per reserve or block, and targeted spacing between reserves or blocks. The new modeling framework we developed instead uses a series of spatially explicit modeling processes to develop habitat conservation networks (or "reserves") based on the distribution of habitat value. Issues of habitat connectivity and population isolation are identified within the population simulation model outputs.

The spotted owl modeling team has completed the development and evaluation of the overall modeling framework described in Steps 1 through 3 above. The *use* of the modeling framework, for example, to inform design and evaluation of various habitat conservation network scenarios (including potential effects of barred owl management), other conservation measures described in Recovery Actions, and evaluate potential effects of climate change will be completed as a part of recovery plan implementation or other analytical and regulatory processes.

Figure C1. Diagram of stepwise modeling process for developing and evaluating habitat conservation scenarios for the spotted owl.



Modeling Process Step 1 – Create a spotted owl habitat suitability map covering the U.S. range of the subspecies based on a statistical model of spotted owl habitat associations.

Habitat modeling objective and overall approach:

Species distributional models are used to evaluate species-habitat relationships, evaluate an area's suitability for the species, and to predict a species' presence (Elith and Leathwick 2009). These models, also called environmental (or ecological) niche models, correlate environmental conditions with species distribution and thereby predict the relative suitability of habitat within some geographic area (Warren and Seifert 2011). When translated into maps depicting the spatial distribution of predicted habitat suitability, these models have great utility for evaluating conservation reserve design and function (Zabel *et al.* 2002,

Zabel *et al*. 2003, Carroll and Johnson 2008, Carroll *et al.* 2010). In this context, we defined relative habitat suitability (RHS) as the relative similarity of environmental conditions, including both biotic (forest composition and structure) and abiotic (terrain, climate) components at spotted owl sites to the distribution of those conditions across the landscape. The spotted owl is one of the most studied raptors in the world; hundreds of peer-reviewed papers have been published on various aspects of the species' ecology, including habitat use and selection (see reviews by Gutiérrez *et al.* 1995, Blakesley 2004). Only a few range-wide (in the U.S.) evaluations of habitat association (Carroll and Johnson 2008) or habitat distribution (Davis and Lint 2005) have been conducted. While we capitalized on this large body of literature and other information to build models for conservation planning purposes, we were primarily interested in using such models to map habitat suitability rather than to provide new ecological understanding of spotted owl habitat associations.

Meetings with spotted owl habitat experts and review of literature and data sets:

Because the spotted owl is among the most-studied birds in the world, there is a wealth of information on its ecology and habitat associations. To ensure that the modeling effort was based on this scientific foundation, our first step was to conduct an extensive review of published and unpublished information on the species. Concurrent with this effort, team members travelled throughout the spotted owl's range and met with researchers and biologists with extensive experience studying spotted owls. Some of these meetings were one-on-one, and at other times we held meetings with several experts at one time to seek their individual advice. We have sometimes referred to these meetings as "expert panels." At these meetings, biologists were each asked to identify (1) the environmental factors to which spotted owls respond within particular physiographic provinces (*e.g.* Klamath Mountains of southern Oregon and northern California, Olympic Peninsula, Redwood Coast), and (2) regions believed to be distinct where spotted owls may be responding to conditions uniquely. In order to identify distinct modeling areas and definitions of spotted owl habitat (see below), we used both empirical findings (*i.e.*, published information) and the professional judgment of spotted owl experts.

Modeling regions - Partitioning the species' range:

Several authors have noted that spotted owls exhibit different habitat associations in different portions of their range, which is often attributed to regional differences in forest environments and factors such as important prey species (Carey *et al.* 1992, Franklin *et al.* 2000, Noon and Franklin 2002, Zabel *et al.* 2003), or presence of Douglas-fir dwarf mistletoe (expert panels). The distribution of these features is likely influenced by relatively large east-west and north-south gradients in ecological conditions (*e.g.*, temperature, precipitation, net primary productivity) and subsequent variation in forest environments. Hence, we developed and evaluated region-specific habitat suitability models

under the assumption that spotted owls *within* a modeling region respond to habitat conditions more similarly than do spotted owls *between* modeling regions where conditions differ.

For monitoring, management and regulatory purposes, the spotted owl's range has historically been divided into 12 physiographic provinces (USDI 1992, Davis and Lint 2005) based largely on the regional distribution of major forest types and state boundaries. Based on differences and similarities in spotted owl habitat, we combined some provinces (California and Oregon Klamath provinces), retained others, and divided some provinces into smaller modeling regions (see Figure C2). We did not establish modeling regions or develop models for the Puget Lowlands, Southwestern Washington, and Willamette Valley, where spotted owls are almost completely absent and sample sizes were too small to support for model development. Instead, we projected the models developed for the closest adjacent area to those areas. This decision had the influence of allowing those regions to have at least some potential value to simulated spotted owls as opposed to assuming zero value.

The predictive ability and accuracy of habitat suitability models are influenced by the range of environmental conditions that are incorporated into the training data used in model development. Models developed from data sets encompassing broad environmental gradients tend to be overly general; conversely, models developed with data representing a small subset of conditions have limited applicability across the species' larger distribution. The practice of partitioning a species' range into "modeling regions" that encompass relatively dissimilar subsets of species-habitat relationships and developing models specific to each region was used to reduce this source of variability. The challenge is balancing the high degree of variability within large regions against the tendency to create many small modeling regions (with potentially small sample sizes) based on locally unique environmental conditions.

We queried experts to suggest potential modeling region boundaries, and they provided input on broad-scale patterns in climate, topography, forest communities, spotted owl habitat relationships, and prey-base that supported delineation of the draft spotted owl modeling regions (Figure C2). Franklin and Dyrness (1973), Kuchler (1977) and other published sources of information on the distribution of major ecological boundaries were also consulted. Using information provided through our discussions with the expert panels and existing ecological section and subsection boundaries (McNab and Avers 1994), we delineated 11 spotted owl modeling regions (Figure C2).

In general, the spotted owl modeling regions varied in terms of these ecological features:

1) Degree of similarity between structural characteristics of habitats used by spotted owls primarily for nesting/roosting and habitats used for foraging and other nocturnal activities. This similarity is largely influenced by habitat characteristics of the spotted owl's dominant prey (proportion of flying squirrels versus woodrats).

2) Latitudinal patterns of topography and climate. For example, in the WA Cascades, spotted owls are rarely found at elevations above 1,219-1,372 m, whereas in southern Oregon and the Klamath province spotted owls commonly reside up to 1,830 m.
3) Regional patterns of topography, climate, and forest communities.
4) Geographic distributions of habitat elements that influence the range of conditions occupied by spotted owls. For example, several panelists pointed out that the distribution of dwarf mistletoe influences the range of stand structural values associated with spotted owl use. Other examples include the geographic distribution of elements such as evergreen hardwoods, Oregon white oak woodlands, and ponderosa pine-dominated forests.

Modeling Region Descriptions:

North Coast Ranges and Olympic Peninsula (NCO): This region consists of the Oregon and Washington Coast Ranges Section M242A (McNab and Avers 1994). This region is characterized by high rainfall, cool to moderate temperatures, and generally low topography (448 to 750 m). High elevations and cold temperatures occur in the interior portions of the Olympic Peninsula, but spotted owls in this area are limited to the lower elevations (<900 m.). Forests in the NCO are dominated by western hemlock, Sitka spruce, Douglas-fir, and western red cedar. Hardwoods are limited in species diversity (consist mostly of bigleaf maple and red alder) and distribution within this region, and typically occur in riparian zones. Root pathogens like laminated root rot (*Phellinus weirii*) are important gap formers, and vine maple, among others, fills these gaps. Because Douglas-fir dwarf mistletoe is unusual in this region, spotted owl nesting habitat consists of stands providing very large trees with cavities or deformities. A few nests are associated with western hemlock dwarf mistletoe. Spotted owl diets are dominated by species associated with mature to late-successional forests (flying squirrels, red tree voles), resulting in similar definitions of habitats used for nesting/roosting and foraging by spotted owls. This region contains the Olympic Demographic Study Area (DSA).

Oregon Coast Ranges (OCR): This region consists of the southern 1/3 of the Oregon and Washington Coast Ranges Section M242A (McNab and Avers 1994). We split the section in the vicinity of Otter Rock, OR, based on gradients of increased temperature and decreased moisture that result in different patterns of vegetation to the south. Generally this region is characterized by high rainfall, cool to moderate temperatures, and generally low topography (300 to 750 m.). Forests in this region are dominated by western hemlock, Sitka spruce, and Douglas-fir; hardwoods are limited in species diversity (largely bigleaf maple and red alder) and distribution, and are typically limited to riparian zones. Douglas-fir and hardwood species associated with the California Floristic Province (tanoak, Pacific madrone, black oak, giant chinquapin) increase toward the southern end of the OCR. On the eastern side of the Coast Ranges crest,

habitats tend to be drier and dominated by Douglas-fir. Root pathogens like laminated root rot (*P. weirii*) are important gap formers, and vine maple among others fills these gaps. Because Douglas-fir dwarf mistletoe is unusual in this region, spotted owl nesting habitat tends to be limited to stands providing very large trees with cavities or deformities. A few nests are associated with western hemlock dwarf mistletoe. Spotted owl diets are dominated by species associated with mature to late-successional forests (flying squirrels, red tree voles), resulting in similar definitions of habitats used for nesting/roosting and foraging by spotted owls. One significant difference between OCR and NCO is that woodrats comprise an increasing proportion of the diet in the southern portion of the modeling region. This region contains the Tyee and Oregon Coast Range DSAs.

Redwood Coast (RDC): This region consists of the Northern California Coast Ecological Section 263 (McNab and Avers 1994). This region is characterized by low-lying terrain (0 to 900 m.) with a maritime climate; generally mesic conditions and moderate temperatures. Climatic conditions are rarely limiting to spotted owls at all elevations. Forest communities are dominated by redwood, Douglas-fir-tanoak forest, coast liveoak, and tanoak series. The vast majority of the region is in private ownership, dominated by a few large industrial timberland holdings. The results of numerous studies of spotted owl habitat relationships suggest stump-sprouting and rapid growth rates of redwoods, combined with high availability of woodrats in patchy, intensively-managed forests, enables spotted owls to maintain high densities in a wide range of habitat conditions within the Redwood zone. This modeling region contains the Green Diamond and Marin DSAs.

Western Cascades North (WCN): This region generally coincides with the northern Western Cascades Section M242B (McNab and Avers 1994), combined with western portion of M242D (Northern Cascades Section), extending from the U.S. - Canadian border south to Snoqualmie Pass in central Washington. It is similar to the Northern Cascades Province of Franklin and Dyrness (1974). This region is characterized by high mountainous terrain with extensive areas of glaciers and snowfields at higher elevation. The marine climate brings high precipitation (both annual and summer) but is modified by high elevations and low temperatures over much of this modeling region. The resulting distribution of forest vegetation is dominated by subalpine species, mountain hemlock and silver fir; the western hemlock and Douglas-fir forests typically used by spotted owls are more limited to lower elevations and river valleys (spotted owls are rarely found at elevations greater than 1,280 m. in this region) grading into the mesic Puget lowland to the west. Root pathogens like laminated root rot (*P. weirii*) are important gap formers, and vine maple, among others, fills these gaps. Because Douglas-fir dwarf mistletoe occurs rarely in this region, spotted owl nests sites are limited to defects in large trees, and occasionally nests of other raptors. Diets of spotted owls in this northern region contain higher proportions of red-backed voles and deer mice than in the region to the south, where flying squirrels are dominant (expert panels). There are no Demographic Study Areas in this modeling region.

Western Cascades Central (WCC): This region consists of the midsection of the Western Cascades Section M242B (McNab and Avers 1994), extending from Snoqualmie Pass in central Washington south to the Columbia River. It is similar to the Southern Washington Cascades Province of Franklin and Dyrness (1974). We separated this region from the northern section based on differences is spotted owl habitat due to relatively milder temperatures, lower elevations, and greater proportion of western hemlock/Douglas-fir forest and occurrence of noble fir to the south of Snoqualmie Pass. Because Douglas-fir dwarf mistletoe occurs rarely in this region, spotted owl nest sites are largely limited to defects in large trees, and occasionally nests of other raptors. This region contains the Rainier DSA and portions of the Wenatchee and Cle Elum DSAs.

Western Cascades South (WCS): This region consists of the southern portion of the Western Cascades Section M242B (McNab and Avers 1994) and extends from the Columbia River south to the North Umpqua River. We separated this region from the northern section due to its relatively milder temperatures, reduced summer precipitation due to the influence of the Willamette Valley to the west, lower elevations, and greater proportion of western hemlock/Douglas-fir forest. The southern portion of this region exhibits a gradient between Douglas-fir/western hemlock and increasing Klamath-like vegetation (mixed conifer/evergreen hardwoods) which continues across the Umpqua divide area. The southern boundary of this region is novel and reflects a transition to mixed conifer sensu Franklin and Dyrness (1974). The importance of Douglas-fir dwarf mistletoe increases to the south in this region, but most spotted owl nest sites in defective large trees, and occasionally nests of other raptors. The HJ Andrews DSA occurs within this modeling region.

Eastern Cascades North (ECN): This region consists of the eastern slopes of the Cascade range, extending from the Canadian border south to the Deschutes National Forest near Bend, OR. Terrain in portions of this region is glaciated and steeply dissected. This region is characterized by a continental climate (cold, snowy winters and dry summers) and a high-frequency/low-mixed severity fire regime. Increased precipitation from marine air passing east through Snoqualmie Pass and the Columbia River results in extensions of moist forest conditions into this region (Hessburg *et al.* 2000). Forest composition, particularly the presence of grand fir and western larch, distinguishes this modeling region from the southern section of the eastern Cascades. While ponderosa pine forest dominates lower and middle elevations in both this and the southern section, the northern section supports grand fir and Douglas fir habitat at middle elevations. Dwarf mistletoe provides an important component of nesting habitat, enabling spotted owls to nest within stands of relatively younger, small trees.

Eastern Cascades South (ECS): This region incorporates the Southern Cascades Ecological Section M261D (McNab and Avers 1994) and the eastern slopes of the Cascades from the Crescent Ranger District of the Deschutes National Forest south to the Shasta area. Topography is gentler and less dissected than the glaciated northern section of the eastern Cascades. A large expanse of recent

volcanic soils (pumice region: Franklin and Dyrness 1974), large areas of lodgepole pine, and increasing presence of red fir and white fir (and decreasing grand fir) along a south-trending gradient further supported separation of this region from the northern portion of the eastern Cascades. This region is characterized by a continental climate (cold, snowy winters and dry summers) and a high-frequency/low-mixed severity fire regime. Ponderosa pine is a dominant forest type at mid-to lower elevations, with a narrow band of Douglas-fir and white fir at middle elevations providing the majority of spotted owl habitat. Dwarf mistletoe provides an important component of nesting habitat, enabling spotted owls to nest within stands of relatively younger, smaller trees. The Warm Springs DSA and eastern half of the South Cascades DSA occur in this modeling region.

Western Klamath Region (KLW): This region consists of the western portion of the Klamath Mountains Ecological Section M261A (McNab and Avers 1994). A long north-south trending system of mountains (particularly South Fork Mountain) creates a rainshadow effect that separates this region from more mesic conditions to the west. This region is characterized by very high climatic and vegetative diversity resulting from steep gradients of elevation, dissected topography, and the influence of marine air (relatively high potential precipitation). These conditions support a highly diverse mix of mesic forest communities such as Pacific Douglas-fir, Douglas-fir tanoak, and mixed evergreen forest interspersed with more xeric forest types. Overall, the distribution of tanoak is a dominant factor distinguishing the Western Klamath Region. Douglas-fir dwarf mistletoe is uncommon and seldom used for nesting platforms by spotted owls. The prey base of spotted owls within the Western Klamath is diverse, but dominated by woodrats and flying squirrels. This region contains the Willow Creek, Hoopa, and the western half of the Oregon Klamath DSAs.

Eastern Klamath Region (KLE): This composite region consists of the eastern portion of the Klamath Mountains Ecological Section M261A (McNab and Avers 1994) and portions of the Southern Cascades Ecological Section M261D in Oregon. This region is characterized by a Mediterranean climate, greatly reduced influence of marine air, and steep, dissected terrain. Franklin and Dyrness (1974) differentiate the mixed conifer forest occurring on the "Cascade side of the Klamath from the more mesic mixed evergreen forests on the western portion (Siskiyou Mountains), and Kuchler (1977) separates out the eastern Klamath based on increased occurrence of ponderosa pine. The mixed conifer/evergreen hardwood forest types typical of the Klamath region extend into the southern Cascades in the vicinity of Roseburg and the North Umpqua River, where they grade into the western hemlock forest typical of the Cascades. High summer temperatures and a mosaic of open forest conditions and Oregon white oak woodlands act to influence spotted owl distribution in this region. Spotted owls occur at elevations up to 1,768 m. Dwarf mistletoe provides an important component of nesting habitat, enabling spotted owls to nest within stands of relatively younger, small trees. The western half of the South Cascades

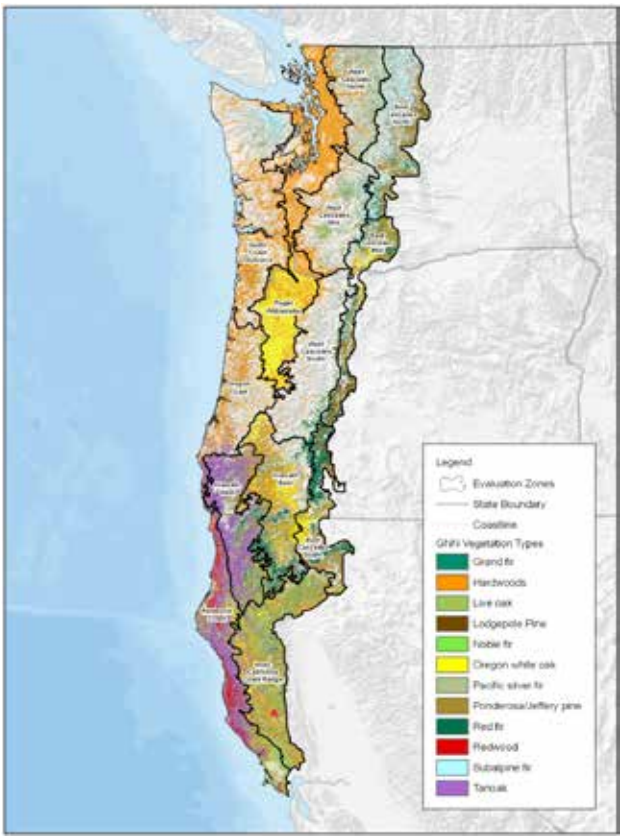
DSA and the eastern half of the Klamath DSA are located within this modeling region.

Northern California Interior Coast Ranges Region (ICC): This region consists of the Northern California Coast Ranges ecological Section M261B (McNab and Avers 1994), and differs markedly from the adjacent redwood coast region. Marine air moderates winter climate, but precipitation is limited by rainshadow effects from steep elevational gradients (100 to 2,400 m.) along a series of north-south trending mountain ridges. Due to the influence of the adjacent Central Valley, summer temperatures in the interior portions of this region are among the highest within the spotted owl's range. Forest communities tend to be relatively dry mixed conifer, blue and Oregon white oak, and the Douglas-fir-tanoak series. Spotted owl habitat within this region is poorly known; there are no DSAs and few studies have been conducted here. Spotted owl habitat data obtained during this project suggests that some spotted owls occupy steep canyons dominated by liveoak and Douglas-fir; the distribution of dense conifer habitats is limited to higher-elevations on the Mendocino National Forest.

Figure C2. Modeling regions used in development of relative habitat suitability models for the spotted owl.

Modeling Regions

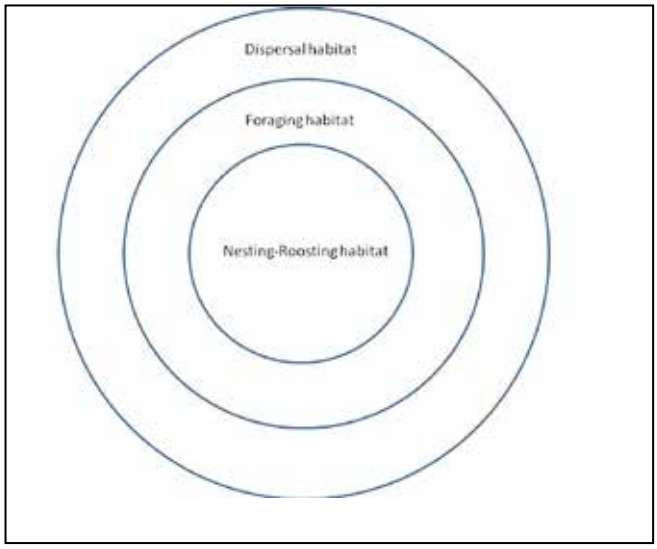
CODE	Description
NCO	North Coast and Olympic
OCR	Oregon Coast
RDC	Redwood Coast
WCN	Western Cascades - North
WCC	Western Cascades - Central
WCS	Western Cascades - South
ECN	Eastern Cascades - North
ECS	Eastern Cascades - South
KLW	Klamath-Siskiyou - West
KLE	Klamath-Siskiyou - East
ICC	Interior California Coast



Habitat Modeling Process:

Because spotted owl habitat use is influenced by factors occurring at different spatial scales, we developed habitat suitability models in two stages. In the first stage we used information from our literature review and experts to develop a series of alternative models of forest conditions corresponding to nesting-roosting habitat and foraging habitat within each modeling region. We used a modeling program called MaxEnt (Phillips *et al.* 2006, Phillips and Dudik 2008) to test the effectiveness of these models and identify the forest structural models that best predicted the relative likelihood of a spotted owl territory being present. Spotted owl habitat is often subdivided into distinct components including: nesting habitat, roosting habitat, foraging habitat, and dispersal habitat. Habitats used for nesting and roosting are very similar, and so we combined them into nesting-roosting. Such areas are used for nesting, roosting, foraging, and dispersal by spotted owls, and are usually forests with more late-seral forest characteristics than "foraging" or "dispersal" habitat. Foraging habitat is thought to be largely used for foraging and other nocturnal activities, but also for dispersal (USFWS 1992; see Figure C3). Dispersal habitat is thought to largely have value for dispersal, to lack nest/roost sites and to provide few foraging opportunities. These categories are not absolutes, but instead represent generalizations (*e.g.*, one should not infer that spotted owls never roost in

Figure C3. Venn diagram of relationships among spotted owl nesting-roosting, foraging, and dispersal habitats.



"foraging" habitat). That said, it is important to understand that nesting-roosting habitat is generally considered to provide all or most habitat requirements, whereas foraging and dispersal habitats are considered to provide only a subset of the spotted owl's habitat requirements. For this effort, we attempted to accurately model the suitability of breeding habitat for spotted

owls. Thus, we evaluated nesting-roosting and foraging habitat, but not dispersal habitat.

Spatial scale for developing and evaluating models:

Spotted owls have been found to respond to habitats at a variety of spatial scales (Solis and Gutiérrez 1990, Meyer *et al.* 1998, Franklin *et al*. 2000, Swindle *et al.* 1999, Thome *et al*. 1999, Zabel *et al.* 2003). Spotted owls do not build their own nests, but primarily utilize broken-top snags, tree cavities, dwarf mistletoe witch's brooms, or nests made by other species (Gutiérrez *et al.* 1995). Spotted owl habitat selection in the immediate vicinity of the nest (tens of meters around the nest tree) has been found to be strongly non-random, and largely associated with late-seral forest characteristics (Solis and Gutiérrez 1990, Meyer *et al.* 1998, Swindle *et al.* 1999) . Areas at this small spatial scale are necessary, but often not sufficient to be selected by spotted owls because areas at larger spatial scales around the nest-site must contain attributes that also contribute to their survival and reproductive success (*e.g.*, Franklin *et al*. 2000, Olson *et al.* 2004, Dugger *et al.* 2005). Carey *et al.* (1992), Hunter *et al.* (1995), Thome *et al.* (1999), Meyer *et al.* (1998), and Zabel *et al.* (2003) all evaluated spotted owl habitat selection at a variety of spatial scales beyond the nest site itself. All studies found differences between spotted owl-centered (nest or core areas) locations and random or unoccupied locations at a variety of spatial scales. However, the largest differences were often found in what Bingham and Noon (1997) defined as "core areas" (areas of the home range that received disproportionately more use than would be expected). An area of 200-ha has been used to describe / define spotted owl core areas, especially in the Klamath Mountains portion of their range (Zabel *et al*. 2003).

200-ha spatial scale:

Using the 200-ha (800-m radius circle) scale to conduct modeling throughout the spotted owl's range effectively makes the assumption that although home range sizes are known to vary dramatically in size from south to north (Gutiérrez *et al.* 1995, Schilling 2009), core area sizes are relatively stable and somewhat constant throughout the range. Spotted owls are central place foragers (Rosenberg and McKelvey 1999), and it is possible that the ~200-ha area Bingham and Noon (1997) reported is a function of the spotted owl's energetic (*i.e.*, areas nearby the nest are more efficient, energetically, to hunt and spend time in – being closer to nests) or perceptive abilities. Because spotted owl home ranges are very large (>1,000 ha), it is unlikely they are able to evaluate the entire home range equally well, and areas nearby nests are evaluated more thoroughly than other areas within the home range. Furthermore, even if core areas are not identically-sized throughout the spotted owl's geographic range, it is likely that modeling at the 200-ha scale effectively identifies patterns that would be found with slightly smaller or larger scales. Based on the literature and these considerations, we evaluated the amount of habitat at the 200-ha spatial scale.

Data Used for Model Development and Testing

Vegetation data – the GNN-LT Database:

To develop rangewide models of relative habitat suitability for spotted owls, we required maps of forest composition and structure of sufficient accuracy to allow discrimination of attributes used for nesting, roosting and foraging by spotted owls. Past efforts to model, map and quantify habitat selection by spotted owls at regional scales have often suffered from lack of important vegetation variables, inadequate spatial coverage, and/or coarse resolution of available vegetation databases (Davis and Lint 2005). However, recent development of vegetation mapping products for the NWFP's Effectiveness Monitoring program (Hemstrom *et al*. 1998, Lint *et al.* 1999) provided detailed maps of forest composition and structural attributes for all lands within the NWFP area (coextensive with the range of the spotted owl). These maps were developed using Gradient Nearest Neighbor (GNN) imputation (Ohmann and Gregory 2002) and LandTrendr algorithms (Kennedy *et al.* 2007, 2010) and were available for two "bookend" dates (1996 and 2006 in Oregon and Washington, 1994 and 2007 in California).

The GNN approach is a method for predictive vegetation mapping that uses direct gradient analysis and nearest-neighbor imputation to ascribe detailed attributes of vegetation to each pixel in a digital landscape map (Ohmann and Gregory 2002). Forest attributes from inventory plots (Forest Inventory and Analysis, Current Vegetation Surveys, etc.) are imputed to map pixels based on modeled relationships between plots and predictor variables from Landsat thematic mapper imagery, climatic variables, topographic variables, and soil parent materials. The assumption behind GNN methods is that two locations with similar combined spatial "signatures" should also have similar forest structure and composition. The GNN models were developed for habitat modeling regions used for the NWFP northern spotted owl effectiveness monitoring modeling (Davis and Dugger, in press). For the NWFP Effectiveness Monitoring program, GNN maps were created for the two bookend time periods mentioned above to 'frame' their analysis period for habitat status and trends. This novel bookend mapping approach presents challenges associated with spectral differences due to different satellite image dates, which might produce false vegetation changes. To minimize the potential for this, the bookend models were based on Landsat imagery that was geometrically rectified and radiometrically normalized using the LandTrendr process (Kennedy *et al.* 2007, 2010)

The large list of forest species composition and structure variables provided by GNN vegetation maps constitute an improvement in vegetation data for modeling and evaluating spotted owl habitat. For our modeling, we selected from a set of 163 variables, including basal area and tree density by size class and species, canopy cover of conifers and/or hardwoods, stand height, age, mean diameter and quadratic mean diameter by dominance class, stand density index, and measures of snags and coarse woody debris. Additional variables pertaining

to stand structural diversity and variability proved particularly useful for modeling spotted owl habitat.

The reliability or accuracy of vegetation databases poses a primary concern for wildlife habitat evaluation and modeling. The GNN maps come with a large suite of diagnostics detailing map quality and accuracy; these are contained in model region-specific accuracy assessment reports available at the LEMMA website (http://www.fsl.orst.edu/lemma/). For developing *a priori* models of spotted owl nesting/roosting habitat and foraging habitat, we considered these accuracies when selecting our habitat modeling variables with relatively high Kappa coefficients and low correlation with other selected variables. In addition, because we were also interested in the accuracy of GNN at the core area (500 acre) spatial scale, we conducted less formal assessments where we compared the distribution of GNN variable values at a large sample of actual locations (known spotted owl nest sites and foraging sites) to published estimates of those variables at the same scale. In addition, we received comparisons of GNN maps to a number of local plot-based vegetation maps prepared by various field personnel. Based on these evaluations, we determined that GNN represents a dramatic improvement over past vegetation databases used for modeling and evaluating spotted owl habitat, and used the GNN-LandTrendr maps as the vegetation data for our habitat modeling.

Spotted owl location data:

Spotted owl data used in model development consisted of site center locations documented within three years (plus or minus) of the date of the GNN vegetation data. Site centers are the location of spotted owl nests or daytime roosts containing paired spotted owls. Site center data for the habitat suitability modeling was made available through the cooperation of a variety of sources throughout the spotted owl's range. Data come from long-term demographic studies as well as locations from other research projects, public, private, and tribal sources.

Substantial effort was expended on verification of both the spatial accuracy and territory status of each site center in the data set. We specifically requested and received very high-quality data from spotted owl demography study areas (DSAs). For areas outside of DSAs, we obtained a large set of additional locations from NWFP Effectiveness Monitoring program (Davis and Dugger, in press); the majority of these site centers had been evaluated for spatial accuracy. We also obtained and verified data sets from private timber companies, USFS Region 5 NRIS database and a number of research and monitoring projects across the species' range.

Because of the spatial extent of our analysis area (>23 million ha), we do not have the luxury of having equal survey effort throughout the region. Instead we have data from research studies, monitoring of demographic rates, management efforts, and other sources. While spotted owl demographic study areas have been intensively and extensively studied for long periods of time (see Anthony *et*

al. 2006 and Forsman *et al.*, in press) and provide the highest- quality data sets, they comprise ~12% of the spotted owl's geographic range. Outside of DSAs, the quantity and density of site center data varies widely. While we have attempted to compile a large sample of site centers that is broadly representative of the entire distribution of spotted owls, the overall distribution of sample sites is somewhat clumped. Areas with few nest locations are a result of: 1) few surveys being conducted, 2) the absence of spotted owls, or 3) data being unavailable. We did not want the modeling results to be a function of the intensity of spotted owl sampling throughout the region, but to be as close of an approximation as possible of spotted owl-habitat relationships. Phillips *et al.* (2009) noted that spatially biased survey data present major challenges to distributional modeling by over-weighting areas where intensive sampling has occurred. Therefore, within each modeling region we "thinned" the spotted owl nest locations such that the minimum distance between nest locations would be 3.0 km (thinning with a 3 km distance resulted in removing ~25% of the locations available to us). Carroll *et al.* (2010) used a similar approach in their modeling of other species whereby clusters of records were identified and one record from the cluster was randomly selected from the set. Using a 3 km thinning distance retained 75% of the total data, and did not have a large effect on those modeling regions with small initial sample sizes (<100) of site center locations (Table C1).

Table C1. Sample size of spotted owl site center locations (1993-1999) by modeling region and the impact of various thinning distances (minimum allowable distance between site centers) on sample size.

		Thinning Distance					
Modeling Region	**Total Sites**	**1 km**	**1.5 km**	**2 km**	**2.5 km**	**3 km**	**4 KM**
NCO	241	236	229	221	209	196	162
OCR	454	430	414	371	325	281	202
RDC	724	716	670	547	461	392	284
WCN	80	80	79	78	77	77	74
WCC	214	211	205	195	182	173	144
WCS	489	489	487	482	477	470	342
ECN	216	215	209	203	195	184	155
ECS	123	122	119	112	104	93	67
KLW	462	460	454	440	414	358	275
KLE	472	468	463	455	434	381	285
ICC	308	308	307	300	286	253	199
Total	**3783**	**3735**	**3636**	**3404**	**3164**	**2858**	**2189**
Percentage of total	**100**	**98.7**	**96.1**	**90.0**	**83.6**	**75.5**	**57.9**

Due to the increased influence of the barred owl on spotted owls, we followed, in part, the modeling approach used by Davis and Dugger (in press) to reduce the influence of barred owls on apparent habitat associations of spotted owls. For our effort, we wanted our models to identify areas with more or less nesting suitability for spotted owls. Because barred owls have apparently displaced many spotted owls from previously-occupied nesting areas, sometimes into habitat types/conditions that spotted owls only rarely used prior to the barred owl's invasion (Gremel 2005, Gutiérrez *et al.* 2007), we did not want to evaluate their "displaced habitat use", but instead their use of habitat without the larger, current impact of barred owls. Although barred owls were known to be widely distributed in the northern portion of the spotted owl's range in 1996, Gremel (pers. comm. 2010) suggested barred owl densities were substantially lower in 1996 than in 2006. Pearson and Livezey (2003) reported that barred owls had increased by an average of 8.6% per year between 1982 and 2000 on parts of the Gifford Pinchot National Forest (GPNF), Washington. Subsequently, Livezey *et al.* (2007) reported that the 98 known barred owl sites on the GPNF in 2001 had increased to 143 sites in 2006. Thus, in an attempt to reduce the influence of barred owls on spotted owl habitat use, we developed and tested models using GNN vegetation data from 1996 (assumed to be the period with lower barred owl influence) along with spotted owl location information plus or minus three years from 1996. Those models were then projected to the most current (2006) GNN layer to predict contemporary relative habitat suitability (RHS). Each region's model was then tested by comparing with RHS values at independent sites from the 2006 spotted owl locations (only those that did not overlap with the 1996 locations).

Developing Habitat Definitions:

Nesting and roosting habitat

Prior to developing models, we attempted to synthesize both the literature and information from experts. From the literature, we emphasized studies evaluating habitat selection over those that described habitat features (associations) around spotted owl locations, but did not evaluate selection. This synthesis resulted in the development of a series of definitions of spotted owl nesting-roosting and foraging habitat. For example, several published studies concluded that nesting spotted owls strongly select for areas with canopy cover >70% and many large trees nearby and strongly select against areas with lower amounts of canopy cover and few or no large trees nearby. We therefore created definition "NR_1" (nesting-roosting definition number 1) based on canopy cover and density of large trees (*e.g.*, trees >75 cm dbh). Because experts and/or other published studies typically supported several (i) alternative NR definitions, we created roughly ten alternative NR habitat definitions (NR_2, NR_3, NR_i, etc.) per modeling region. We used an identical process to develop a series of foraging (F) habitat definitions for each modeling region (Tables C2 and C3 provide an example of this process). It is important to recognize that these habitat definitions are binary for each pixel; either the pixel contained each of the

features in the definition (and was therefore considered habitat), or it did not (it was considered non-habitat).

Table C2. Spotted owl nesting-roosting habitat variables for the northern Coast Ranges and Olympic Peninsula

Habitat characteristics from expert panel, literature	GNN Variable expression
Canopy cover of conifers is ≥ than 80%	CANCOV_CON_GE_80
Mean stand diameter is ≥ than 50cm	MNDBHBA_CON_GE_50
Structure should include ≥ 70 medium trees/ha	TPH_GE_50_GE_70
Structure should include ≥ 20 larger trees/ha	TPH_GE_75_GE_20
Very large remnant trees are important (≥5/ha)	TPH_GE_100_GE_5
Canopy layering/diversity is important	DDI_GE_6 *

*DDI = Diameter Diversity Index (ranges from 1-10)

Table C3. Sample definitions of spotted owl nesting-roosting habitat based on variables and values from Table 2.

	Candidate nesting/roosting habitat definitions
NR_1	CANCOV_CON_GE_80 + MNDBHBA_CON_GE_50 + DDI_GE6
NR_2	CANCOV_CON_GE_80 + MNDBHBA_CON_GE_50 + TPH_GE_75_GE_20 + TPH_GE_100_GE_5 + DDI_GE_6
NR_3	CANCOV_CON_GE_80 + TPH_GE_50_GE_70 + TPH_GE_75_GE_20 + TPH_GE_100_GE_5 + DDI_GE_6
NR_4	CANCOV_CON_GE_70 + MNDBHBA_CON_GE_50 + TPH_GE_75_GE_20 + DDI_GE_5

Foraging habitat

Foraging habitat definitions were informed by published and unpublished literature and input from experts. In this process, foraging habitat was, by definition, different than nesting-roosting habitat. This is not to suggest that spotted owls do not forage in nesting-roosting habitat, but for the sake of being explicit in this process, foraging habitat was distinct from nesting-roosting habitat. In general, foraging habitat definitions had lower thresholds of canopy cover, tree size, and canopy layering than nesting-roosting definitions (Tables C4 and C5 provide an example of this process).

Table C4. Spotted owl foraging habitat variables for the northern Coast Ranges and Olympic Peninsula.

Habitat characteristics from expert panel, literature	GNN Variable expression
Canopy cover of conifers is ≥ than 70%	CANCOV_CON_GE_70
Mean stand diameter is ≥ than 40 cm	MNDBHBA_CON_GE_40
Structure should include ≥ 50 medium trees/ha	TPH_GE_50_GE_50
Structure should include ≥ 8 larger trees/ha	TPH_GE_75_GE_8
Canopy layering/diversity is important	DDI_GE_4 *

*DDI = Diameter Diversity Index (ranges from 1-10)

Table C5. Sample definitions of spotted owl foraging habitat based on variables and values from Table C4.

	Candidate nesting/roosting habitat definitions
F_1	CANCOV_CON_GE_70 + MNDBHBA_CON_GE_40 + DDI_GE_4
F_2	CANCOV_CON_GE_70 + MNDBHBA_CON_GE_40 + TPH_GE_75_GE_8 + DDI_GE_6
F_3	CANCOV_CON_GE_70 + TPH_GE_50_GE_50 + TPH_GE_75_GE_8 + DDI_GE_4
F_4	CANCOV_CON_GE_60 + MNDBHBA_CON_GE_40 + TPH_GE_75_GE_8 + DDI_GE_4

Because attributes of habitat such as amount of edge and core area have been shown to influence both habitat selection and fitness (Franklin *et al.* 2000) of spotted owls, we also included NR "core" and "edge" metrics.

Abiotic variables:

Because published literature and information from experts suggested that abiotic features might be important in determining spotted owl habitat use and selection, we evaluated a series of abiotic features known or suspected to influence spotted owl habitat selection and use (Table C6). Numerous studies have shown that local geographic features such as slope position, aspect, distance to water, and elevation have been found to influence spotted owl site selection (Stalberg *et al.* 2009, Clark 2008). Several authors (Blakesley *et al.* 1992, Hershey *et al.* 1998, LaHaye and Gutiérrez 1999) have noted the absence of spotted owls above particular elevational limits (whether this limit is due to forest structure, prey, competitors, parasites, diseases, and/or extremes of temperature or precipitation is not known). At broader scales, temporal variation in climate has been shown to be related to fitness (Franklin *et al.* 2000, Olson *et al.* 2004, Dugger *et al.* 2005, Glenn *et al.* 2010), suggesting that spatial variation in climate may also influence habitat suitability for spotted owls. Ganey *et al.* (1993) found that

Mexican spotted owls (*S. o. lucida*) have a narrow thermal neutral zone and others (*e.g.*, Franklin *et al.* 2000) have assumed the northern spotted owl to be similar in this regard. Furthermore, the spotted owl's selection for areas with older-forest characteristics has been hypothesized to, in part, be related to its needing cooler areas in summer to avoid heat stress (Barrows and Barrows 1978). Temperature extremes (winter low and summer high) as well as potential breeding-season specific stressors (spring low temperature and high spring precipitation) are also considered potentially useful predictor variables for our purposes (Carroll 2010, Glenn *et al.* 2010). By including climate variables as candidate variables in our habitat suitability modeling, we evaluated whether climate effects on spotted owl fitness are translated into patterns of the species' distribution.

Developing models:

We used the MaxEnt program (Phillips *et al*. 2006, Phillips and Dudik 2008) to model spotted owl habitat suitability because it is specifically designed for presence-only data, like much of the data we used. Moreover, MaxEnt has been thoroughly evaluated on a number of taxa, geographic regions, and sample sizes and has been found to perform extremely well (Elith *et al.* 2006, Wisz *et al*. 2008). MaxEnt compares the characteristics (variables included in the models) of the training data sites to a random selection of ~10,000 random "background" (available) locations. We only used the linear, quadratic, and threshold features within MaxEnt (*i.e.*, hinge and product features were not used).

We used the following model-building and evaluation process within each modeling region

1) Each nesting-roosting habitat definition is a single-variable model. Thus, if we developed 10 nesting-roosting habitat definitions for a region, we compared 10 nesting-roosting habitat models for that region. We used MaxEnt to determine the best nesting-roosting habitat definition within each region (see model evaluation, below).

2) Within each modeling region that has foraging habitat definitions, we combined the best nesting-roosting habitat definition(s) with each foraging habitat definition to evaluate whether the addition of foraging habitat improved model performance. Models were considered to have been improved if the addition of foraging habitat increases the ranking of the model. If the addition of foraging habitat improved the model's performance, we used the nesting-roosting + foraging habitat model for step 3 (below). If not, we used the best nesting-roosting model(s) for step 3.

3) For abiotic variables, we developed univariate or multivariate models using the variables in Table C6. Carroll (2010) found that mean January precipitation, mean July precipitation, mean January temperature, and mean July temperature were the variables in the best, of 30, climate models he evaluated. He found the two precipitation metrics were the

most influential of the four. Franklin *et al.* (2000) also found climate variables to influence spotted owl survival and reproduction. We included three climate models: 1) the four variables Carroll (2010) reported, 2) mean January precipitation and mean July precipitation, 3) mean January precipitation and mean January temperature. We "challenged" the best model(s) after step 2 by adding each abiotic model to it (*sensu* Dunk *et al.* 2004), in an attempt to improve its predictive ability. The abiotic models were not compared to each other, but were compared in order to see if their addition to the best biotic (nesting-roosting or nesting-roosting + foraging) model resulted in an improved model (see step 2). If the biotic plus abiotic model was an improvement over the biotic-only model, we used the combination model, otherwise we used the biotic-only model. The reason abiotic-only models were not evaluated is that it is illogical to suggest that spotted owls (a species that nests in trees) might only respond to abiotic factors when selecting nesting areas. In contrast, we could develop a logical biological argument that spotted owls might respond only to biotic features when selecting nesting areas. We could also develop logical biological arguments articulating how a combination of biotic and abiotic factors might influence the selection of nesting areas.

Model-building hierarchy

The spatial distribution of spotted owl territories is influenced by a wide variety of environmental gradients operating at different spatial scales. At the smallest scale we evaluated, features such as the amount of nesting-roosting and / or foraging habitat within a core area, the amount of edge between spotted owl habitat and non-habitat, or amount of "core habitat" (*sensu* Franklin *et al*. 2000) have all be shown to influence spotted owl distribution, abundance, or fitness. Each of those variables, however, is a structural variable. That is, they are based on habitats comprised of various structural elements (*e.g.*, large trees, high canopy cover). However important and influential these variables are to spotted owls, other variables such as plant species composition (broadly speaking), topographic position, climate, and / or elevation are also likely to influence their distribution, abundance, and perhaps fitness (Franklin *et al.* 2000, Olson *et al*. 2004, Dugger *et al.* 2005, Glenn 2009).

In part, the partitioning of the spotted owl's geographic range into 11 modeling regions should act to reduce the influence of broad patterns in plant species composition, climate and / or elevation on the species. Nonetheless, we were interested in evaluating whether habitat suitability is influenced by local variation in these non-structural variables.

Stand structure and the spatial arrangement of forest patches have been found to influence spotted owl fitness (Franklin *et al*. 2000, Olson *et al*. 2004, Dugger *et al*. 2005). Edge between nesting-roosting habitat and other habitat types is thought to afford foraging spotted owl opportunities when habitats, but which are rarely used, are juxtaposed closely with habitats spotted owls use. "Core" habitat

includes those areas of spotted owl nesting habitat not subjected to edge-effects. Franklin *et al*. (2000) estimated core habitat by buffering all spotted owl habitat (largely mature forest areas) by 100 m and estimating the size of the habitat excluding the 100 m buffer.

Spotted owl experts noted that mid-scale or landscape level patterns such as tree species composition and topography may also influence the local distribution and density of spotted owls. For example, within many of the modeling regions, there exists variation in tree species composition, but forests with different species compositions may still have similar structural attributes (*e.g.*, high canopy cover, multi-storied, large trees). Some forest types (regardless of their structural attributes) are rarely, if ever, used by spotted owls, so we attempted to account for this variation by evaluating models that include some compositional variables.

Many of our 11 modeling regions contain high-elevation areas above the elevational extremes normally used by spotted owls. In some higher elevation areas there exists structurally complex, multi-storied forests with large trees – areas with similar structural characteristics to those used by spotted owls. However, spotted owls rarely if ever use such areas. Our intention was to attempt to account for this in our modeling.

We recognize the hierarchical nature of these environmental factors and their possible influence on spotted owl distribution. Our model building approach took this into consideration, by starting at the smallest scale and sequentially "challenging" models with variables from larger spatial scales. In order to focus on environmental features most directly linked to territory location, habitat selection, and individual fitness of spotted owls, we employed a bottom-up approach to building models (Table C6).

Table C6. Categories of candidate variables, variable names, and order of the entry of variables into modeling process.

Category	Variable	Order
Best climate / elevation model	Mean July Precipitation	↑
	Mean July Temperature	
	Mean July Precipitation	
	Mean July Temperature	
	Mean Elevation	
Topographic position	Curvature	
	Insolation	
	Slope Position	
Compositional variables (percent of basal area)	Redwood	
	Oak Woodland	
	Pine-dominated	
	Northern Deciduous Hardwoods	
	Evergreen Hardwoods	
	Douglas-fir	
	Subalpine forest	
Habitat pattern	Core of NR habitat	
	Edge of NR habitat	
Habitat structure	Foraging Habitat Amount	
	Nesting / Roosting Habitat	

Model Evaluation

Our goal for developing the MaxEnt relative habitat suitability models was to find models that accurately and consistently discriminated among areas of

varying suitability to spotted owls. We sought models that were not so over-fit to the developmental data that they did not have good generality (*i.e.*, we wanted models that worked well in the modeling regions in general, not simply at classifying the developmental/training data). MaxEnt attempts to balance model fit and complexity through the use of regularization (see Elith *et al.* 2011). Elith *et al.* (2011) noted that MaxEnt fits a penalized maximum likelihood model, closely related to other penalties for complexity such as Akaike's Information Criterion (AIC, Akaike 1974).

Model discrimination

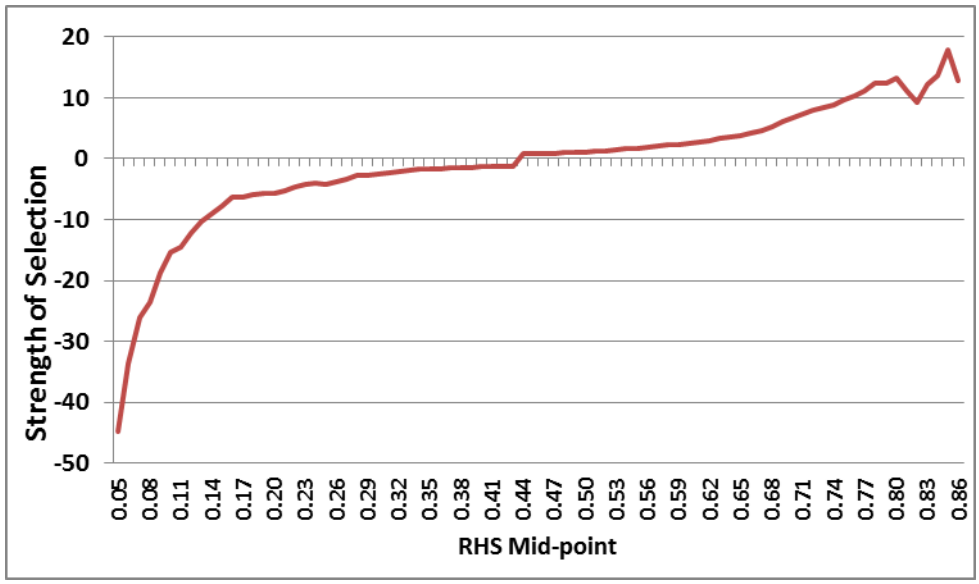
Once the best model was found for each region, we conducted a cross-validation of each model to evaluate how robust the model was. Each of 10 times we removed a random subset of 25% of the spotted owl locations, developed the model with the remaining 75% and classified using the withheld 25%. The area under the receiver operating characteristic curve (AUC) was evaluated for both training and test data within each region. AUC is a measure of a model's discrimination ability; in our case discrimination between spotted owl-presence locations and available locations (not discrimination of presence versus absence locations). AUC values, theoretically, range between 0 and 1.0, with values less than 0.5 having worse discriminatory ability than expected by chance, values closer to 0.5 suggesting no to poor discriminatory ability, and values closer to 1.0 suggesting excellent discriminatory ability. For these analyses, AUC values essentially describe the proportion of times one could expect a random selection of an actual spotted owl nest site location to have a larger relative habitat suitability value than a random selection from available locations. It is therefore a threshold-independent measure of model discriminatory ability. Because our evaluation represents use versus availability and not use versus non-use, AUC values have an upper limit somewhat less than 1.0 (because some of the available locations are actually used by spotted owls). Furthermore, AUC values may be somewhat lower in areas where the background areas contain larger amounts of suitable habitat. Two contrasting examples are provided to make this point: 1) a model estimating a riparian-dependent bird species' distribution in the Great Basin may have a very high AUC value because there is large contrast between riparian vegetation where the bird nests and the vast majority of background locations in sage-steppe, vs. 2) a model estimating the distribution of a generalist omnivore (like a black-bear) in a national forest may have a lower AUC because so much of the background habitat is suitable for the species. The point is that AUC is a measure of discrimination, but that a use-versus-availability model's ability to discriminate is a function of both the animal's habitat specificity and the abundance of the animal's habitat in the region of interest.

Model Calibration

Model calibration refers to the agreement between predicted probabilities of occurrence (habitat suitability for our study) and observed proportions of sites occupied (Pearce and Ferrier 2000, Phillips and Elith 2010). Phillips and Elith

(2010) note that model discrimination and model calibration are independent measures. Hirzel *et al.* (2006) (whose work Phillips and Elith [2010] expand upon), developed "strength of selection" metrics for species distribution models using a moving-window approach. Strength of selection (SOS) evaluations allow for an understanding of the use that areas with various habitat suitability values receive (by nesting spotted owls in our case) relative to the abundance of such areas in the study area (see Figure C4 below). Essentially, a well-calibrated model will show the species to use higher suitability areas disproportionately more and lower suitability areas disproportionately less. The shape of the relationship provides insights into the degree to which the species avoids or is attracted to areas with particular habitat suitability values.

Figure C4. This *example* of the strength of selection (SOS) evaluation shows a well-calibrated model. Areas with a mid-point RHS (*i.e.*, relative habitat suitability value) of 0.05 (the moving window size here was 0.1) were used ~45-times *less* than would be expected based on its extent in the study area. Similarly, areas with a mid-point RHS of 0.8 (window of 0.75-0.85) were used ~12-times *more* than expected based on its extent in the study area. This figure was developed from a model trained on >3,000 spotted owl night locations (many presumed to be foraging).



Habitat Modeling Results:

The following section provides summary descriptions of the final "best" models for each modeling region; including information on the relative contribution of each covariate to the model, model evaluation metrics, and the results of validation against independent data sets conducted to date. Because the primary objective of this habitat modeling step was to provide accurate prediction of relative habitat suitability and subsequent likelihood of spotted owl occupancy, we focus on presenting evaluation of model performance, rather than description of spotted owl habitat associations. Tables C7 to C14 provide descriptions of the

best nesting-roosting habitat model, foraging habitat model, and full model for each modeling region, as well as model evaluation metrics (AUC and Gain) and the relative contribution of each variable to the full model (a heuristic estimate provided in the standard output from MaxEnt). See Table C15 for codes and descriptions of variables used in the models.

Table Series C7. Nesting/Roosting habitat, foraging habitat, and full models for coastal Washington, Oregon and California modeling regions.

North Coast and Olympics Modeling Region (N= 196 training sites):

Model	Best	AUC	GAIN
Nesting	DDI (≥6) + TPH ≥ (>25/ha) + BAA GE3 (≥ 55 m^2/ha)	0.8365	0.7667
Foraging	MNDBHBA_CON (≥40); TPH_GE75 (≥10)	0.8619	0.8817
Full Model	NR06 + NR06EDGE + FORAGING HAB04 + SLOPE POSITION+ ELEVATION + CURVATURE + SUBALPINE FOREST+JULY MAX TEMP+JANUARY PRECIP + JULY PRECP + INSOLATION + JANUARY MIN TEMP + NORTHERN HARDWOODS	0.8989	1.057

Oregon Coast Ranges Modeling Region (N = 281training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV_CON (≥55) + DDI (≥6) + TPH_GE75 (≥20)	0.7683	0.4498
Foraging	DDI (≥4) + TPH_GE50 (≥30)	0.7787	0.467
Full Model	NR08 + NR08 EDGE + SLOPE POSITION + JULY MAX TEMP + JANUARY MIN TEMP + FORAGING HAB04 + CURVATURE + INSOLATION + JULY PRECIP + JANUARY PRECIP + ELEVATION + NR08 CORE + NORTHERN HARDWOODS + EVERGREEN HARDWOODS	0.864	0.811

Redwood Coast Modeling Region (N = 389 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥70) + MNDBHBA_CON (≥44)	0.5928	0.0509
Foraging	CANCOV (≥65) + BAC_GE50 (≥3)	0.6256	0.0785
Full Model	SLOPE POSITION + CURVATURE + NR03 EDGE + FORAGING HAB05 + NR03 + REDWOOD + ELEVATION + JANUARY PRECIP + OAK WOODLAND + JULY MAX TEMP + INSOLATION + JANUARY MIN TEMP + NR03 CORE + JULY PRECIP	0.760	0.335

Table C8. Individual covariates and their contribution to full model.

North Coast / Olympics		Oregon Coast Ranges		Redwood Coast	
Full Model	**%**	**Full Model**	**%**	**Full Model**	**%**
NR 06	42.4	NR 08	29.4	Slope Position	48.2
NR06Edge	21.5	NR08 Edge	24.2	Curvature	11.2
NR06+F04	20.1	Slope position	11.9	NR03 Edge	10.3
Slope position	6.0	July Max Temp	10.1	NR03 + F05	6.1
Elevation	3.6	Jan Min Temp	8	NR 03	5.7
Curvature	1.8	NR08 + F04	5.5	Redwood (%BA)	4.8
Subalpine	1.1	Curvature	4.1	Elevation	4.1
July Max Temp.	0.9	Insolation	3.1	January Precip.	3.2
Jan Precip.	0.9	July Precip	1.5	Oak Woodland	2.6
July Precip.	0.8	Jan Precip	1.3	July Max Temp	1.3
Insolation	0.6	Elevation	0.4	Insolation	0.9
Jan Min Temp	0.3	NR08 Core	0.2	Jan Min Temp	0.7
Northern Hdwd	0.1	Northern Hdwd	0.2	NR03 Core	0.7
		Evergreen Hdwd	0.1	July precip.	0.4

Table Series C9. Nesting/Roosting habitat, foraging habitat, and full models for Western Cascades modeling regions.

Western Cascades Modeling Region (Northern Section) (N = 76 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥80) + MNDBHBA_CON (≥60) + TPHC_GE100 (≥7)	0.8377	0.7555
Foraging	CANCOV (≥70); DDI (≥5); TPH_GE50 (≥42); BAA_GE3 (≥40)	0.8417	0.7698
Full Model	NR05 EDGE + NR05 + SLOPE POSITION + CURVATURE + ELEVATION + JANUARY PRECIP + NORTHERN HARDWOODS + JULY MAX TEMP + SUBALPINE FOREST + INSOLATION + JULY PRECIP + FORAGING HAB01 + JANUARY MIN TEMP + NR05 CORE	0.931	1.393

Western Cascades Modeling Region (Central Section) (N = 171 training sites)

Model	Best	AUC	GAIN
Nesting	TPH_GE50 (≥ 64) + TPH_GE75 (≥ 16) + TPHC_GE100 (≥ 4)	0.7965	0.5825
Foraging	CANCOV (≥70) + DDI (≥4) + TPH_GE50 (≥37) + BAA_GE3 (≥ 37)	0.816	0.6575
Full Model	NR09 EDGE + FORAGING HAB01 + CURVATURE + ELEVATION + NORTHERN HARDWOODS + SUBALPINE + SLOPE POSITION + JANUARY MIN TEMP + NR09 + JULY PRECIP + JULY MAX TEMP + INSOLATION + NR09 CORE + JANUARY PRECIP	0.892	1.024

Western Cascades Modeling Region (Southern Section) (N = 470 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥ 70) + MNDBHBA_CON (≥ 50) + TPH_GE75 (≥ 22)	**0.6877**	**0.2343**
Foraging	CANCOV (≥ 60) + DDI (≥ 4) + QMDC_DOM (≥ 37)	**0.6931**	**0.2385**
Full Model	NR02 + SLOPE POSITION + CURVATURE + FORAGING HAB01 + JANUARY MIN TEMP + NORTHERN HARDWOODS + INSOLATION + JULY PRECIP + JANUARY PRECIP + JULY MAX TEMP + ELEVATION	**0.762**	**0.355**

Table C10. Individual covariates and their contribution to full model.

Western Cascades North		Western Cascades Mid		Western Cascades South	
Full Model	**%**	**Full Model**	**%**	**Full Model**	**%**
NR05 Edge	34.4	NR09 Edge	44.8	NR 02	62.9
NR 05	17.2	NR09 + F01	13.9	Slope Position	17.8
Slope Position	13.0	Curvature	8.5	Curvature	4.7
Curvature	12.6	Elevation	7.6	NR02 + F01	3.9
Elevation	8.0	Northern Hdwd	7.4	Jan Min Temp	3.9
Jan Precip	4.3	Subalpine	4.2	Northern Hdwd	1.9
Northern Hdwd	3.7	Slope Position	4.1	Insolation	1.5
July Max Temp	2.2	Jan Min Temp	2.4	July Precip	1.5
Subalpine	1.4	NR 09	1.8	January Precip	0.9
Insolation	0.9	July Precip	1.5	July Max Temp	0.5
July Precip	0.9	July Max Temp	1.4	Elevation	0.5
NR05 + F01	0.8	Insolation	1.0		
Jan Min Temp	0.5	NR09 Core	0.7		
NR05 Core	0.2	Jan Precip	0.7		
NR05 Edge	34.4				

Table Series C11: Nesting/Roosting habitat, foraging habitat, and full models for Eastern Cascades modeling regions.

Eastern Cascades Modeling Region (Northern Section) (n = 182 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥ 70) + DDI (≥ 5) + MNDBHBA_CON (≥ 42)	0.685	0.2263
Foraging	CANCOV (≥52) + QMDC_DOM (≥30) + BAA_GE3 (≥23)	0.7347	0.3114
Full Model	NR06 + SLOPE POSITION + DOUGLAS-FIR + JANUARY MIN TEMP + ELEVATION + FORAGING HAB03 + NR06 EDGE + JULY MAX TEMP + SUBALPINE FOREST + JANUARY PRECIP + CURVATURE + INSOLATION + JULY PRECIP + PINE	0.879	0.843

Eastern Cascades Modeling Region (Southern Section) (N = training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥ 70) + MNDBHBA_CON (≥ 45) + TPH_GE75 (≥ 9)	0.7263	0.2912
Foraging	MNDBHBA_CON(≥ 38) + DDI(≥ 4) + QMDC_DOM(≥ 32)	0.7868	0.4797
Full Model	FORAGING HAB03 + NR07 + NR07 EDGE + PINE + DOUGLAS-FIR + JANUARY MIN TEMP + ELEVATION + SLOPE POSITION + NR07 CORE + JULY MAX TEMP + INSOLATION + JANUARY PRECIP + CURVATURE + SUBALPINE FOREST + JULY PRECIP	0.889	0.957

Table C12. Individual covariates and their contribution to full model.

Eastern Cascades South		Eastern Cascades North	
Full Model	**%**	**Full Model**	**%**
NR07 + F03	18.4	NR06	20
NR 07	13.9	Slope Position	14.6
NR07 Edge	11.7	Douglas-fir	13.6
Pine	10.7	Jan Min Temp	10.6
Douglas-fir	10.7	Elevation	8.3
Jan Min Temp	9.5	NR06 + F03	6.8
Elevation	5.4	NR06 Edge	5.7
Slope Position	4.6	July Max Temp	4.1
NR07 Core	4.5	Subalpine	4.0
July Max Temp	3.3	January Precip	3.3
Insolation	3.2	Curvature	2.9
January Precip	1.6	Insolation	2.7
Curvature	1.5	July Precip	2.1
Subalpine	0.6	Pine	1.5
July Precip	0.4		

Table Series C13. Nesting/Roosting habitat, foraging habitat, and full models for Klamath-Siskiyou Mountains and Interior California modeling regions.

Western Klamath Mountains (N = 357 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥75) + DDI (≥6) + QMDC_DOM (≥50)	0.6608	0.1677
Foraging	DDI (≥4) + BAH_PROP (0.25 - 0.70) + BAC_GE3 (≥18)	0.6751	0.1886
Full Model	SLOPE POSITION + NR01 EDGE + NR01 + CURVATURE + JANUARY PRECIP + JULY PRECIP + NR01 CORE + JANUARY MIN TEMP + ELEVATION + INSOLATION + JULY MAX TEMP + FORAGING HAB03 + OAK WOODLAND + EVERGREEN HARDWOODS	0.769	0.396

Eastern Klamath Mountains Modeling Region (N = 378 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥65) + DDI (≥5.5) + QMDC_DOM (≥42)	0.7052	0.2601
Foraging	CANCOV_CON (≥45) + TPH_GE50 (≥23) + QMDC_DOM (≥30)	0.7075	0.2613
Full Model	NR01 + SLOPE POSITION+ DOUGLAS-FIR+ ELEVATION + NR01 EDGE + INSOLATION + JAN PRECIP+ FORAGING HAB05 + CURVATURE + JULY MAX TEMP+ JAN MIN TEMP+ NR01 CORE + OAK WOODLAND+ PINE + SUBALPINE	0.830	0.605

Interior California Coast Ranges (N = 251 training sites)

Model	Best	AUC	GAIN
Nesting	CANCOV (≥65) + MNDBHBA_CON (≥46) + BAA_GE ≥75)	0.7136	0.2975
Foraging	DDI (≥3.5) + QMDC_DOM (≥30) + BAH_3_25 (≥5)	0.7296	0.3286
Full Model	NR02 + NR02 EDGE + SLOPE POSITION + JULY MAX TEMP + CURVATURE + FORAGING HAB04 + NR02 CORE + JULY PRECIP + JAN PRECIP + INSOLATION + JAN MIN TEMP + EVERGRN HDWD + PINE +OAK WOODLAND + ELEVATION	0.820	0.540

Table C14. Individual covariates and their contribution to full model.

Western Klamath		Eastern Klamath		Interior CA Coast Ranges	
Full Model	**%**	**Full Model**	**%**	**Full Model**	**%**
Slope Position	33.0	NR01	28.3	NR02	29.9
NR01 Edge	32.2	Slope Position	24.6	NR02 Edge	19.8
NR01	10.9	Douglas-fir	12.1	Slope Position	12.4
Curvature	6.6	Elevation	9.2	July Max Temp	11.1
January Precip	6.1	NR01 Edge	6.8	Curvature	5.6
July Precip	4.4	Insolation	5.4	NR02 + F04	4.9
NR01 Core	1.6	Jan Precip	4.9	NR02 Core	3.3
Jan Min Temp	1.3	NR01 + F05	3.3	July Precip	2.6
Elevation	1.1	Curvature	2.2	Jan. Precip	2.4
Insolation	1.0	July Max Temp	1.2	Insolation	2.0
July Max Temp	0.8	Jan Min Temp	0.8	Jan. Min Temp	1.8
NR01 + F03	0.5	NR01 Core	0.5	Evergrn Hdwd	1.7
Oak Woodland	0.2	Oak Woodland	0.2	Pine	1.3
Evergrn Hrdwd	0.2	Pine	0.2	Oak Woodland	0.7
		Subalpine	0.1	Elevation	0.5

Table C15. Codes and descriptions of stand structural variables from GNN and compositional variables used in relative habitat suitability models.

Variable	Definition
CANCOV	Canopy cover of all live trees
CANCOV_CON	Canopy cover of all conifers
DDI	Diameter diversity index (structural diversity within a stand, based on tree densities within different DBH classes)
SDDBH	Standard deviation of DBH of all live trees
MNDBHBA_CON	Basal area weighted mean diameter of all live conifers
TPH_GE_50	Live trees per hectare greater than or equal to 50 cm DBH
TPHC_GE_50	Conifers per hectare greater than or equal to 50 cm DBH
TPH_GE_75	Live trees per hectare greater than or equal to 75 cm DBH
TPHC_GE_75	Conifers per hectare greater than or equal to 75 cm DBH
TPHC_GE_100	Conifers per hectare greater than or equal to 100 cm DBH
QMDC_DOM	Quadratic mean diameter of all dominant and co-dominant conifers
BAA_GE_3	Basal area of all live trees greater than or equal to 2.5 cm DBH
BAA_3_25	Basal area of all live trees 2.5 to 25 cm DBH
BAA_GE_75	Basal area of all live trees greater than or equal to 75 cm DBH
BAC_GE_3	Basal area of conifers greater than or equal to 2.5 cm DBH
BAC_GE_50	Basal area of conifers greater than or equal to 50 cm DBH
BAH_PROP	Proportion of BAA_GE_3 that is hardwood
BAH_3_25	Basal area of all live hardwoods 2.5 to 25 cm DBH
Compositional Variables	
Evergreen Hardwoods	Basal area of tanoak, canyon, coast and interior live oaks, giant chinquapin, California bay and Pacific madrone
Subalpine	Basal area of silver fir, mountain hemlock, subalpine fir, red fir, Englemann spruce,
Pine	Basal area of ponderosa pine, Jeffrey pine, lodgepole pine, and Bishop pine
Northern Hardwoods	Basal area of red alder and bigleaf maple
Oak Woodland	Oregon white oak and blue oak

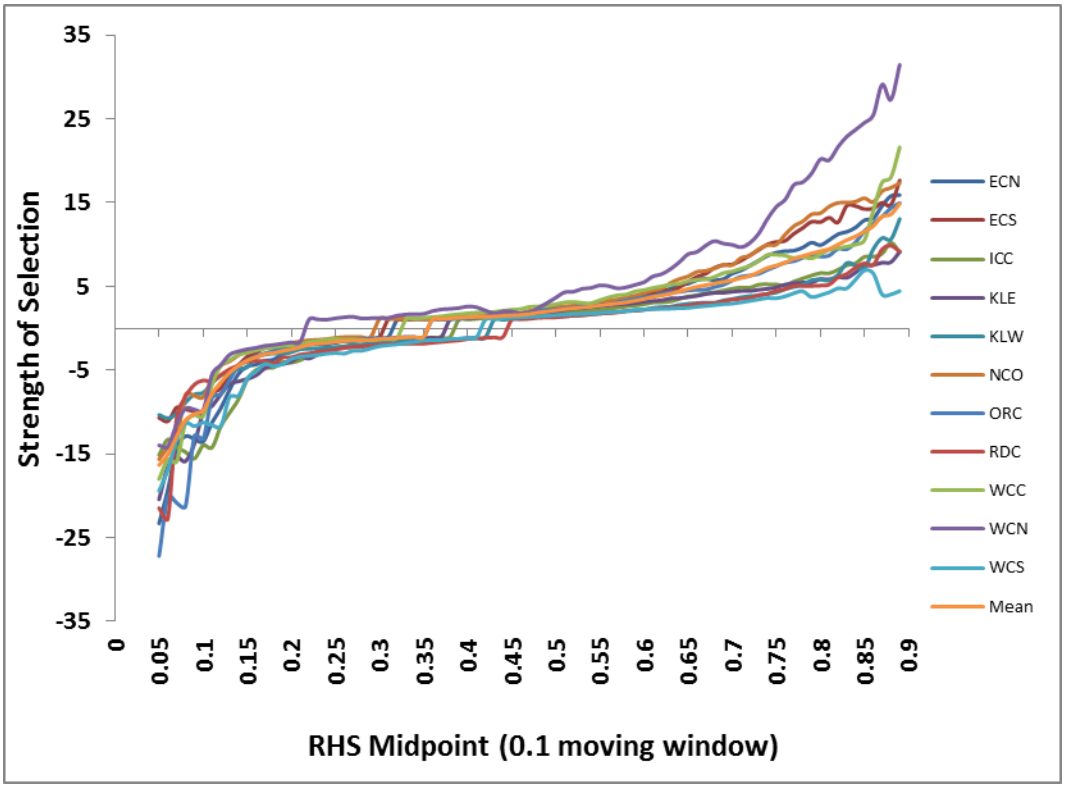
Results of Model Evaluation and Testing:

<u>Strength of selection results</u>

We plotted the observed use that areas with various RHS values receive (by nesting spotted owls in our case) relative to the abundance of such areas in each modeling region. Figure C5 shows the SOS curves for all 11 modeling regions. Although the degree of calibration varies among modeling regions, the RHS

models are generally well-calibrated, with strong selection for areas of RHS > 0.6 to 0.7, and avoidance of RHS <0.15 to 0.25.

Figure C5. Strength of Selection evaluation for all modeling regions.



Results of Model Cross-Validation

Overall, each modeling region's model proved to be fairly robust, and thus gave us confidence in the model's generality. When we evaluated the differences in the percentages of spotted owl sites classified among 10 equally-sized RHS bins between the full model (using all of the spotted owl locations – thinned by 3 km) and the cross-validated (CV) models (*i.e.*, the 25% of observations that were withheld from the developmental model, each of 10-times for each modeling region) there were generally very small differences (Table C16). The maximum percentage point difference (percentage of observations from the full model minus percentage of observations CV model) was 11.1 (see Table C16). The mean difference of the absolute values among modeling regions ranged from 1.6 (for the Klamath West) to 4.5 (for the West Cascades North). Absolute values were used for calculating means because without doing so, the positive and negative values within a modeling region will always have a mean of 0, and thus don't accurately represent overall differences between full and cross-validated models. There was an inverse (negative logarithmic) relationship between sample size of spotted owl sites and mean difference in absolute value ($r^2 = 0.537$, $P = 0.01$). Nonetheless, the magnitude of differences was generally quite low. For example, 39% of the differences were <2.0, 81% of the differences were <5.0,

and only 7% of the differences were >7.0 (absolute value in each case). These findings suggest that none of the modeling region's full models were over-fit, and that all full models have good generality.

Table C16. Results from cross-validation tests, showing absolute values of differences (% classified by full model - % classified in cross-validated model) among modeling regions

	Absolute value of differences										
Po Bin	**ECN**	**ECS**	**ICC**	**KLE**	**KLW**	**NCO**	**ORC**	**RDC**	**WCC**	**WCN**	**WCS**
0-0.099	5.2	4.8	3.9	3.0	0.9	5.2	3.3	1.9	7.9	11.1	1.7
0.1-0.199	4.4	4.6	6.1	1.1	5.0	0.2	3.3	3.1	1.9	4.2	1.7
0.2-0.299	3.3	1.0	3.1	4.6	1.4	1.1	0.2	1.4	4.0	3.4	2.6
0.3-0.399	2.8	4.5	0.9	3.7	2.8	0.5	3.0	3.5	0.9	1.3	2.6
0.4-0.499	2.8	7.9	2.5	2.4	0.0	4.5	0.7	5.2	3.7	1.3	0.8
0.5-0.599	3.1	1.0	3.6	4.4	0.8	0.1	6.2	6.1	4.4	4.5	5.5
0.6-0.699	5.2	3.1	7.0	7.3	0.3	1.4	1.9	3.3	9.9	5.3	8.1
0.7-0.799	3.5	9.7	3.4	0.6	4.0	10.2	3.4	6.8	1.7	5.8	2.9
0.8-0.899	1.5	2.5	2.1	1.0	1.1	0.2	2.0	2.2	4.0	6.8	1.2
0.9-1.0	0.3	2.4	0.4	0.3	0.1	0.8	0.4	0.5	1.0	1.1	0.1
Mean	**3.2**	**4.1**	**3.3**	**2.8**	**1.6**	**2.4**	**2.4**	**3.4**	**3.9**	**4.5**	**2.7**

Results of comparisons with independent data sets

To further evaluate the reliability of the models' predictions, we obtained independent (*i.e.* not used in model development) samples of spotted owl territory locations that represented the period 1993 to 1999 (Test96) and 2003 to 2009 (Test06) and compared their associated RHS values to corresponding values for spotted owl sites used in model development. All test sites were greater than 0.5 miles from a training site. Because the RHS models were developed using spotted owl territories from the 1996 time period, comparison with Test96 most directly addresses model accuracy. Comparison with independent spotted owl locations from 2006, however, enabled us to evaluate accuracy of the models when projected to a new time period (model transferability), and to investigate systematic shifts in RHS at spotted owl sites. These shifts may occur, for example, in areas where densities of barred owls have increased during the 1996 to 2006 period, and are displacing spotted owls from favorable habitat. If this is the case (as has been hypothesized), we might expect to see reduced use of RHS

area at 2006 spotted owl sites, relative to 1996 values **(see Methods: Spotted owl location data)**.

We obtained adequate (N ≥ 100) test samples for 2006 in four modeling regions. As data for additional modeling regions and Test96 become available, further evaluation of model accuracy should be conducted. Table C17 shows the proportions of spotted owl sites in each of five RHS "bins" for the training data (Train), and Test06. Because they allow comparison of RHS values across a gradient of relative habitat suitability, these comparisons are more informative than binary "correct classification" analyses.

Table C17. Comparison of percentage of 1996 training sites versus test samples of 2006 spotted owl locations in 5 categories of Relative Habitat Suitability

	Oregon Coast		Western Klamath		Eastern Klamath		Redwood Coast		Rangewide	
	Train	**Test**	**Train**	**Test**	**Train**	**Test**	**Train**	**Test**	**Train**	**Test**
N	247	169	358	136	375	108	392	284	2742	916
RHS bin										
0 – 0.2	7.3	7.1	8.7	2.2	6.1	4.6	4.8	3.2	6.1	4.6
0.2 – 0.4	19.0	23.1	18.2	19.8	14.1	20.4	13.8	12.7	16.5	17.8
0.4 – 0.6	35.6	35.5	38.5	46.3	38.4	39.8	42.1	44.7	36.7	41.8
0.6 – 0.8	32.8	30.2	33.5	30.8	38.7	35.2	37.2	37.7	36.7	33.8
0.8 – 1.0	5.3	4.1	1.1	0.74	2.7	0	2.0	1.8	4.0	1.2

Model evaluation summary:

All modeling regions' models were well calibrated and showed a quite similar pattern in terms of strength of selection (see Figure C5). Cross-validation results by modeling region showed that all models were relatively robust to the 25% iterative reduction in sample size (see Table C16). Lastly, comparison of model results with independent test data showed the models had good ability to predict spotted owl locations (Table C17), and performed well when projected to 2006 vegetation conditions. Overall, these evaluations suggest that our RHS models were robust and have good generality. Subsequently, we used the full dataset models.

Interpretation of model output:

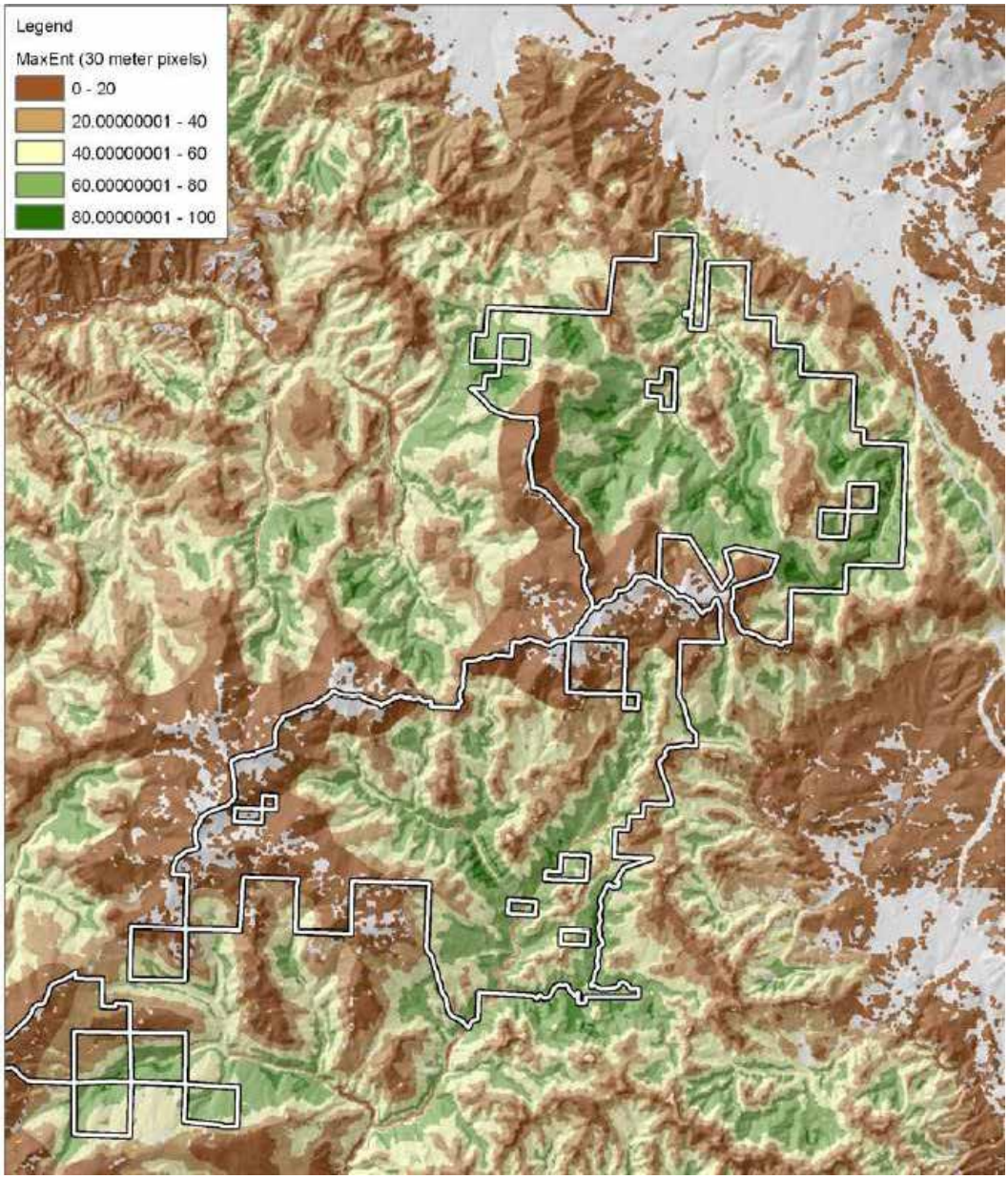
Elith *et al.* (2011) state that the MaxEnt logistic output is an attempt to estimate the probability that a species is present, given the environment (*i.e.*, the environmental conditions). For our purposes, we have taken a more conservative interpretation of the MaxEnt logistic output and interpret it to represent the relative habitat suitability (RHS) for nesting spotted owls within each modeling region. The map below (Figure C6) is the result of running each modeling region's best RHS model on each 30-m pixel within the region. That is, MaxEnt estimates a RHS value for each pixel based on the biotic and abiotic

features within the 200-ha (~800 m radius) area around it (*i.e.*, based only on the variables in the best MaxEnt model for that modeling region). It is important to understand that a high RHS value is possible for a pixel that has little inherent value (*e.g.*, there are no trees in the 30x30 m focal pixel). It may, however, be that the surrounding 200-ha has many of the attributes associated with high RHS. Similarly, a focal pixel could have many of the positive characteristics that spotted owls generally select for, but it receives a low RHS value owing to the surrounding 200-ha having few or none of the attributes associated with high RHS values.

As noted above the RHS map is designed to facilitate and enable a wide variety of processes, discussions and analyses, including section 7 consultation, implementation and evaluation of the efficacy of spotted owl conservation measures such as Recovery Action 10 and management of barred owls. This model likely has utility for a wider variety of uses and processes than we currently envision, and it can be refined by future advances in the understanding of spotted owl habitat associations.

Maps depicting the RHS model outputs for the range of the spotted owl are available at:
http://www.fws.gov/oregonfwo/Species/Data/NorthernSpottedOwl/Recovery/Library/Default.aspx#Files
Once there, click on “maps” and “AppendixCMaps.pdf” The layers can be turned on and off using the “layers” button in the upper left-hand corner. The RHS values are the base layer on this map.

Figure C6. Map depicting Relative Habitat Suitability from MaxEnt model. Higher suitability habitat conditions are indicated by darker green areas; brown colors denote lower suitability. Outline of the Mount Ashland Late-successional reserve is shown for comparison.



Modeling Process Step 2 – Develop a spotted owl conservation planning model, based on the habitat suitability model developed in Step 1, and use it to design an array of habitat conservation network scenarios.

Because the RHS maps from Step 1 consisted of finely-distributed patterns of habitat suitability across the spotted owl's geographic range, we also wanted to provide a rigorous, repeatable method for aggregating habitat value into habitat conservation networks. We used the conservation planning model "Zonation" (Moilanen and Kujala 2008) to develop a spotted owl conservation planning model which can be used to design an array of habitat conservation network scenarios. To test this model we mapped a series of alternative spotted owl conservation network scenarios based on a series of rule-sets (*e.g.*, varying land ownership categories, the inclusion of existing reserves, identifying a specific amount of "habitat value" to include). The primary output of a Zonation analysis of the landscape is a "hierarchical ranking" of conservation priority of all cells or pixels in the landscape. Zonation allows analysts to incorporate species-specific factors such as dispersal capabilities and response to habitat fragmentation into the ranking of cells, and also allows the inclusion of factors such as land ownership and status into various evaluations. It is important to recognize that the maps produced by Zonation represent user-defined scenarios that were evaluated and compared in subsequent population modeling to test this modeling process; they do not represent decisions about the size or distribution of habitat conservation areas. While Zonation uses the term "reserve" to describe the conservation areas it identifies, this term does not dictate the types of management actions that could occur in those areas.

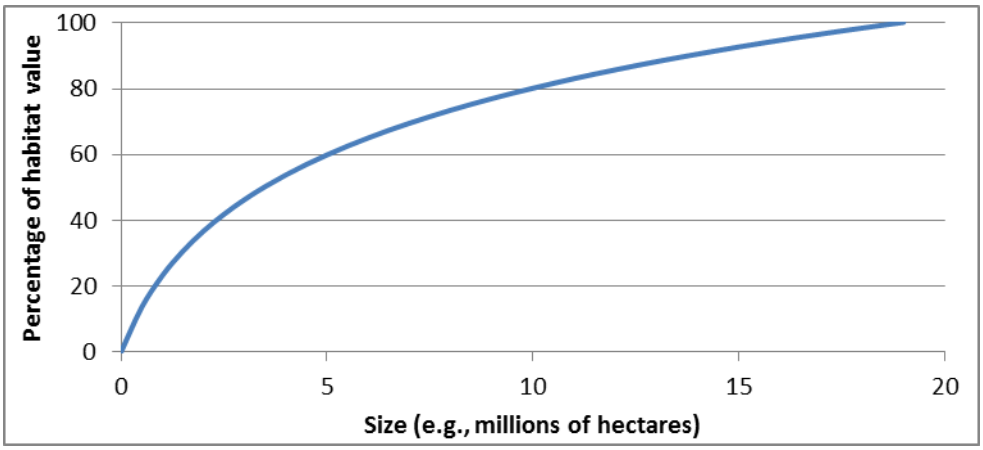
Zonation produces a hierarchical prioritization of the landscape based on the conservation value or "habitat value" of cells. A cell's habitat value is a function of its "base" value (*i.e.*, its RHS value) as well as the value of cells surrounding it. Thus, two cells of identical RHS may have different habitat value depending on how many other high, medium, and low value cells are nearby. The term habitat value therefore incorporates a larger spatial context than does RHS. Hierarchical, in this case, means that the most valuable five percent is also within the most valuable 10 percent; the top two percent is within the top five percent, and so on. Zonation uses minimization of marginal loss as the criterion to decide which cell is removed, and iteratively removes the least valuable cells from the landscape until no cells remain. The order of cell removal and its proportion of the total habitat value are recorded and can later be used to select any top fraction of cells or habitat value, the best 10 percent of cells or the top 10 percent of habitat value, for example, of the landscape.

To ensure that spotted owls and their habitat would be well-distributed throughout their range (one of the goals for recovery), Zonation analyses were conducted separately for each modeling region. This modeling region decision

also had the impact of ensuring that conservation areas would be better distributed across the range of the species.

Zonation allows analysts to identify specific areas of the landscape that represent a particular percentage of the total estimated habitat value to the species. An important attribute of the Zonation algorithm is that it attempts to produce "efficient" solutions. That is, it prioritizes cells into units that maximize the habitat value per unit area within the solution (Figure C7). For example, in one Zonation scenario, 70% of the habitat value existed on ~40% of the landscape.

Figure C7. *Hypothetical* **relationship between total size of habitat conservation system (x-axis) and percentage of habitat value "captured" (y-axis). Theoretically, the only way to capture 100% of the habitat value is to have the entire area to be considered reserve (or all areas with value >0). For this example, the entire area is ~ 19 million ha. In this example, a reserve system that is ~4 million ha "captures" ~50% of the habitat value, one that is ~9 million ha captures ~75% of the habitat value, etc.**



Because Zonation is spatially explicit, in a GIS environment the user can control several aspects of how the program evaluates the distribution of habitat value. This enables the program to emulate important aspects of the species' life history, landscape pattern of habitat, and desired attributes of a habitat conservation network.

Zonation's **Distribution Smoothing** function is a species-specific aggregation method that retains high-value areas (pixels) that are better-connected to others, resulting in a more compact solution. The user specifies the area or "smoothing kernel" within which Zonation averages or smooths habitat values, based on a two-dimensional habitat density calculation, in accordance with attributes of an organism's movement patterns or abilities, such as home range area. We compared kernel sizes corresponding to the core use area (2625 ft radius), home range (6890 ft), and median dispersal distance (17.2 miles; Forsman *et al.* 2002). The main difference in the resulting solutions from these three different settings is that the results from the kernel estimated from dispersal distance or home range were less fine-grained than the results from the kernel value estimated

from a core area. Given that we are estimating habitat conservation network scenarios at relatively large scales, the coarser-grained (home range-derived kernel values) maps provided more discrete areas as estimated networks, and thus we used the home range scale kernel size.

Zonation's **Cell Removal Method** function allows users to control the spatial pattern or "grain" of priority areas by specifying whether cell removal begins around the edges of the analysis area or at cells scattered across the analysis area. The idea behind the "Edge Removal" setting is that it is more likely to result in connectivity of higher-value areas within the more central areas of the landscape. However, because cell removal is limited to the perimeters of large landscapes, the Edge Removal option can result in large blocks containing extensive areas of unsuitable habitat such as interior valleys and high mountain peaks. The "Edge Removal with Add Edge Points" option allows the user to randomly distribute a specified number of edge points where cell removal occurs within large landscapes This setting allows more flexibility than edge removal and provides a greater chance that interior areas of poor-suitability habitat will be removed from the solution, and results in more finely-grained pattern of priority areas. The "No Edge Removal" option does not predispose Zonation to start cell removal from any particular area or region, but removes the lowest value cells in the landscape first, then the next lowest, and so on. This results in very finely-grained prioritized areas (and very long computer run times). We conducted side-by-side comparisons and found that Add Edge Points and No Edge Removal end up with nearly identical solutions (~95% overlap in identifying the top 25% habitat value areas in the landscape). To develop a series of alternative habitat conservation networks, we selected Add Edge Points, distributing 2,000 edge points into each modeling region.

Exclusion Areas are areas that were excluded from the habitat suitability base maps prior to running Zonation. Examples are areas such as high elevation alpine areas as well as generally low elevation valley areas (*e.g.*, the Willamette Valley) that are considered incapable of supporting spotted owls. Including these areas in Zonation runs would give a false impression of habitat conservation block efficiency. That is, the algorithm would be able to remove large amounts of area (high elevation and valley areas) with no impact on the loss of spotted owl habitat value. Thus, we believed these areas should be masked out from the start. The GIS layer used to represent exclusion areas is the same one (mask) developed for the NWFP Monitoring Group (Davis and Dugger, in press) and used in our MaxEnt modeling.

Selection of values for conservation value ranking:

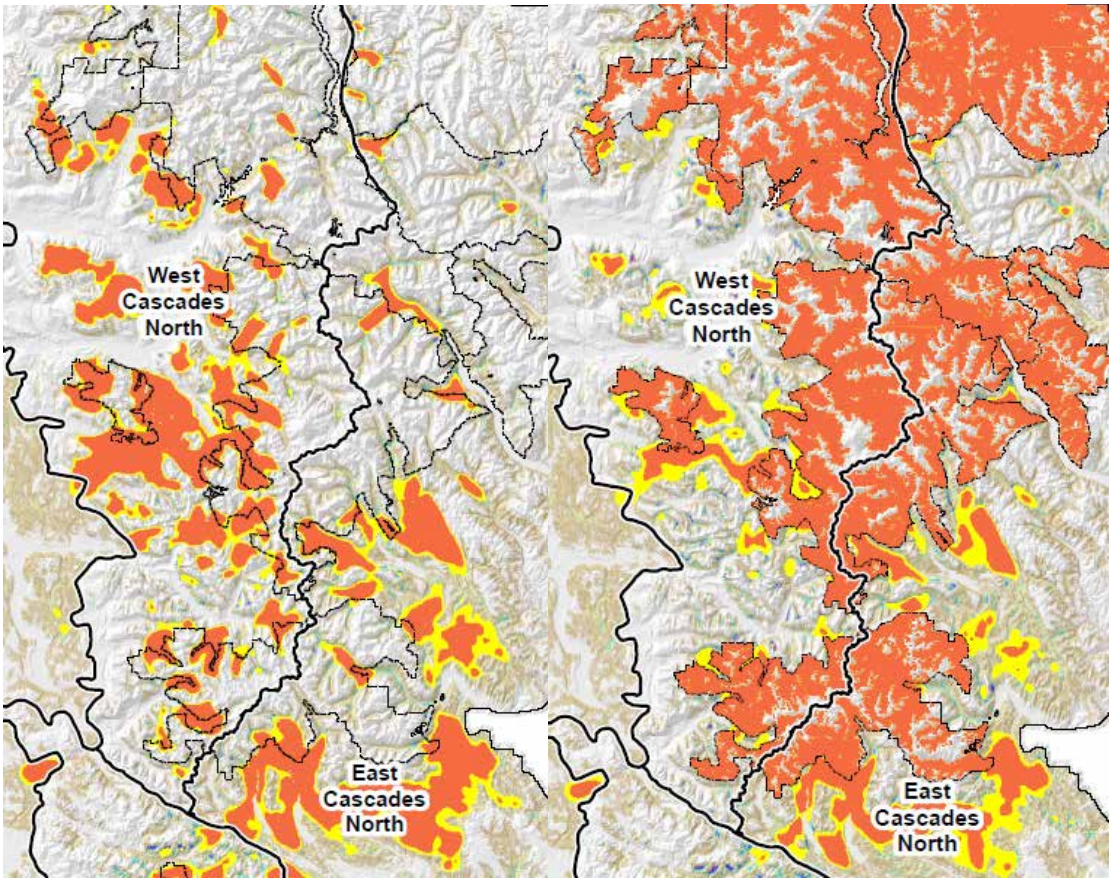
Zonation enables the user to specify the ranking values (proportion of habitat value) to display as maps of habitat conservation networks. Selection of the values for the ranking categories has a large influence on the size and distribution of habitat conservation networks. Because there is a near-infinite number of ranking values that could be selected for evaluation, we compared results across a broad gradient of habitat values (20%, 30% 40%, 50%, 60%, 70%,

and 80%), with the objective of identifying a smaller subset of reasonably diverse habitat conservation network scenarios for testing with the population model (see below). In addition, we compared habitat conservation networks from the above habitat values to the habitat values contained in existing networks such as spotted owl Critical Habitat (1992 and 2008) and the NWFP reserve network.

Hierarchical Masking allows the analyst to identify areas that must be or must not be included in the habitat conservation network. For example, existing protected areas such as Wilderness Areas and National Parks can be "forced" into the priority areas, regardless of their habitat value. Similarly, various land ownership categories can be excluded from priority areas. To accomplish this, the user identifies zones (land ownership, existing reserves, etc.) and ranks them by conservation priority (Zone 1, Zone 2, and so on). In processing, Zonation removes the lowest value cells in Zone 1 first, , and continues by removing the next lowest value cell until all cells are removed in Zone 1 before moving on to Zone 2 and any potentially subsequent zones. Because the cells in Zone 2 are assigned a higher ranking, in terms of removal order, than those in Zone 1, they are disproportionately included in the solution. This process is repeated until all zones (defined by the precedence mask) have been fully evaluated. Zonation does not re-calculate or otherwise change the habitat value of a cell according to which zone it is in. Instead, identifying zones identifies discrete areas of the landscape that are to be given higher or lower priority of consideration for reasons other than the cells' habitat value.

The basis for hierarchical masking in Zonation is to allow factors such as land status to be incorporated into the landscape prioritization. For example, forcing existing National Parks and Wilderness Areas into habitat conservation networks would recognize that these areas exist as protected areas, and thus should be included in a habitat conservation networks regardless of their value to spotted owls. However, because we used Zonation to *help identify* areas estimated to provide the most conservation value for the spotted owl, we proceeded by first conducting an evaluation based purely on habitat value (unforced), and *then* evaluated how much overlap the resulting habitat conservation networks had with existing protected areas and other land designations or ownerships. Forcing existing reserves into priority areas will likely predispose Zonation to not find optimal solutions (*i.e.*, because some non-optimal areas are forced into the solution). For example, in areas such as the northern Cascades where high-value spotted owl habitat is relatively sparsely distributed, forcing Congressionally Reserved land allocations into priority areas resulted in an extremely inefficient network design (Figure C8).

Figure C8. Comparison of Zonation 40% (yellow) and 50% (orange) solutions on all land ownerships (left) and public lands only (right). Outlines of habitat conservation network solutions in left frame correspond largely to National Park and National Forest boundaries.



Selection of Zonation scenarios – summary:

After evaluating Zonation results employing a range of values for distributional smoothing, cell removal methods, ranking values, and land status and ownership prioritization, we selected habitat conservation network scenarios comprised of 30 percent, 50 percent, and 70 percent of habitat value as reference points. These scenarios sample along a gradient from somewhat smaller than the current habitat conservation network (NWFP) to a habitat conservation network approximately twice as large as the LSR network (Table C18). We recognize that the results of population modeling may indicate other Zonation scenarios that should or could be developed and tested (feedback loop in Figure C1). *Also, it is important to recognize these scenarios are not recommendations for the specific size or location of habitat conservation blocks – they are only scenarios for the*

purpose of comparing to other scenarios to evaluate how they influence spotted owl population performance in the population simulation model.

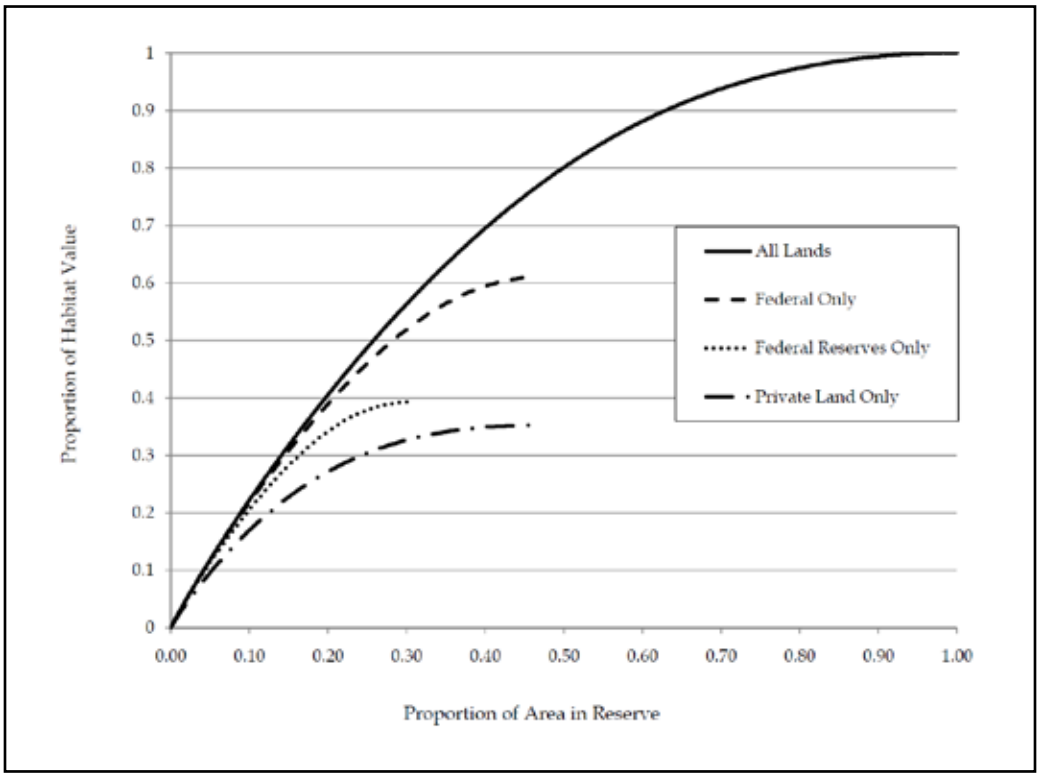
Settings and Values Used in Zonation
Distribution Smoothing: Home range area (2100 m radius)
Cell Removal Method: Add Edge points (2000 points/modeling region)
Exclusion Areas: Used NWFP non-capable habitat mask from NWFP Monitoring
Ranking Values: Used 30%, 50%, and 70% of habitat value
Hierarchical Masking: Land ownership scenarios evaluated include:

1) **No limit on inclusion** – All land ownerships were allowed to be included and existing reserves were not forced into the priority areas. This scenario was chosen to represent the potential of the entire area to provide for spotted owls.
2) **Public lands only** – Only Publicly owned lands (Federal and State) were allowed to be included in the conservation priority areas.

Maps depicting all of the initial Zonation scenarios are available at : http://www.fws.gov/oregonfwo/Species/Data/NorthernSpottedOwl/Recovery/Library/Default.aspx#Files
Once there, click on "maps" and "AppendixCMaps.pdf" The layers can be turned on and off using the "layers" button in the upper left-hand corner.

Zonation outputs can be used to compare the contributions of different land classes (ownership, reserve status, etc.) based on the area and proportion of habitat value of each land class. Figure C9 depicts the relationship between area (proportion of the spotted owl's range) that could, hypothetically, be included in a habitat conservation network and the amount of spotted owl habitat value that various habitat conservation networks would contain among four categories: 1) all lands, which represents no limits on ownerships in the habitat conservation network; 2) Federal lands only, with no priority for currently existing reserves; 3) Federal reserves only, this scenario includes only NWFP reserves (Congressional Reserves and LSRs); and 4) private lands only; no reserves on Federal lands. These depictions are for demonstrative purposes only, not recommendations. They are essentially asking what would be the conservation value to spotted owls if habitat conservation areas were restricted to various land ownership categories. For example, private lands constitute about 45 percent of the spotted owl's range and provide roughly 35 percent of the rangewide habitat value (RHS), whereas the NWFP reserve network provides 40 percent of rangewide habitat value on 30 percent of the area (Figure C9).

Figure C9. Relationship between proportion of various land ownerships/categories (no restriction, Federal lands only, Federal reserves only, or private lands only) included in a habitat conservation network and proportion of spotted owl habitat value included in the habitat conservation network.

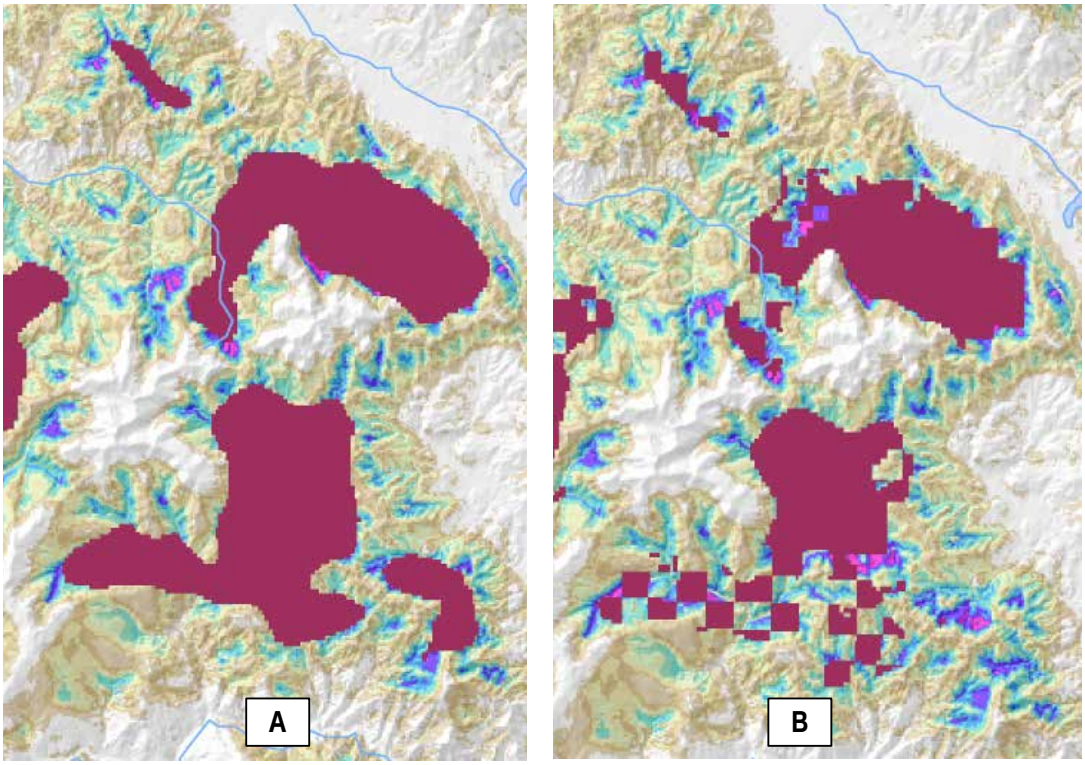


While Zonation outputs do not evaluate or predict potential spotted owl population sizes associated with different habitat conservation networks, they nonetheless permit comparison of the sizes of existing reserve or conservation networks to possible habitat conservation areas, and enable additional comparisons to be made in a GIS environment. For example, Table C18 shows a comparison of network size, percent of spotted owl training locations from the habitat modeling that falls within various habitat conservation areas, and percent of the top two Zonation habitat value ranks among 10 habitat conservation network scenarios.

Table C18. Comparison of area, percent of 1996 spotted owl sites used in model development, and percent of top 10% and 20% Zonation ranked habitat value for 10 spotted owl reserve scenarios.

Network scenario	Network scenario size (million acres)	Percent of 1996 spotted owl sites	Percent of top 10% Zonation-ranked	Percent of top 25% Zonation-ranked
NWFP	16.38	46	56.7	55.2
MOCA	11.79	33	46.3	43.8
1992 Critical Habitat	14.21	44	57.3	55.4
2008 Critical Habitat	12.77	37	49.6	47.7
Z30 All lands	13.86	50	100	100
Z50 All lands	19.27	71	100	100
Z70 All lands	26.07	87	100	100
Z30 Public lands	13.76	51	94.9	91.3
Z50 Public lands	19.32	73	95.0	93.0
Z70 Public lands	27.77	88	98.9	98.0

Figure C10. Example Zonation output map of the Mount Ashland, OR, area, depicting 30 percent of habitat value in red on all lands (A) and on Federal lands only (B).



Modeling Process Step 3 - Develop a spatially explicit spotted owl population model that reliably predicts relative responses of spotted owls to environmental conditions, and use it to test the effectiveness of habitat conservation network scenarios designed in step 2 in recovering the spotted owl. The simulations from this spotted owl population model are not meant to be estimates of what will occur in the future, but provide information on trends predicted to occur under differing habitat conservation scenarios.

The HexSim Model:

HexSim (Schumaker 2011) was designed to simulate a population's response to changing on-the-ground conditions by considering how those conditions influence an organism's survival, reproduction, and ability to move around a landscape. The modeling team developed a HexSim spotted owl scenario based on the most up-to-date demographic data available on spotted owls (Forsman *et al.*, in press), published information on spotted owl dispersal, and home range size as well as on parameters for which less empirical information was available (see below). Initially, the HexSim spotted owl model allows users to evaluate the efficacy of existing conservation strategies, under currently-estimated barred owl impacts and with currently-estimated habitat conditions, to meet recovery goals. Subsequently, the model serves as a consistent framework into which variation in spatial data layers (*e.g.*, reserve or conservation block boundaries, different assumptions about habitat conditions (RHS) inside and outside of reserves or blocks, different assumptions about RHS change on public versus private lands, and different assumptions about the impact of barred owls among modeling regions) can be introduced. Comparison of estimates of simulated spotted owl population performance estimates across the range of scenarios incorporating variation in habitat conservation network sizes, habitat trends, and barred owl influence, can inform evaluations of habitat conservation networks and other conservation measures designed to lead to spotted owl recovery.

In very general terms, we tried to design the model to answer the following questions: (1) Given current circumstances (reserves, habitat, barred owls, spotted owl demographic rates, etc.), is recovery of the spotted owl likely in the foreseeable future? (2) Given current estimates of habitat, barred owls, and spotted owl demographics, is recovery of the spotted owl likely in the foreseeable future under different habitat conservation network scenarios? (3) To what degree would management of habitat and barred owls contribute to or detract from reaching spotted owl recovery goals under a range of habitat conservation networks and management scenarios? Evaluation and ranking of the population simulation results from the model obtained across a range of habitat conditions, barred owl effects, and conservation network scenarios, and

comparison with established recovery criteria, should provide important insight into these questions. **The HexSim model is available at: www.epa.gov/hexsim.**

HexSim Overview:

HexSim is a spatially explicit, individual-based computer model designed for simulating terrestrial wildlife population dynamics and interactions. HexSim is a generic life history simulator; it is not specifically a spotted owl model. HexSim was designed to quantify the cumulative impacts to wildlife populations of multiple interacting stressors.

HexSim simulations are built around a user-defined life cycle. This life cycle is the principal mechanism driving all other model processing and data needs. Users develop the life cycle when initially setting up a simulation. The life cycle consists of a sequence of life history events that are selected from a list. This event list includes survival, reproduction, movement, resource acquisition, species interactions, and many other actions. Users can impose yearly, seasonal, daily, or other time cycles on the simulated population. Each event can work with all, or just a segment of a population, and events can be linked to static or dynamic spatial data layers. Each life cycle event has its own data requirements. Simple scenarios may use few events with minimal parameterization and little spatial data. When more complexity is warranted, HexSim allows a great deal of data and behavior to be added to its simulations.

HexSim scenarios include descriptions of one or more populations, spatial data needs, life cycle definitions, event data, and basic simulation criteria such as the number of replicates and time steps. Each population is composed of individuals, and individuals have traits that can change probabilistically, or based on age, resource availability, disturbance, competition, etc. HexSim also includes optional genetics and heritable traits (though these were not used for the spotted owl model). The use of traits allows members of the simulated population to have unique properties that change in time and space. Traits also allow populations to be segregated into classes, such as males and females, fitness categories, disease categories, etc. Combinations of trait values can be used to stratify events such as survival, reproduction, movement, etc.

Traits are a fundamental part of HexSim scenarios. Traits can be used to control most life cycle events because events can be stratified by trait combinations. For example, a movement event might be set up to operate only on a fledgling stage class. Or a survival event might assign mortalities based on the values of a trait that reflects resource acquisition. In addition, one trait's values can also be influenced by multiple other traits, which makes it possible to set up stressor interactions and complex feedback loops. Traits can also be used to capture interactions such as parasitism, competition, mutualism, breeding, etc.

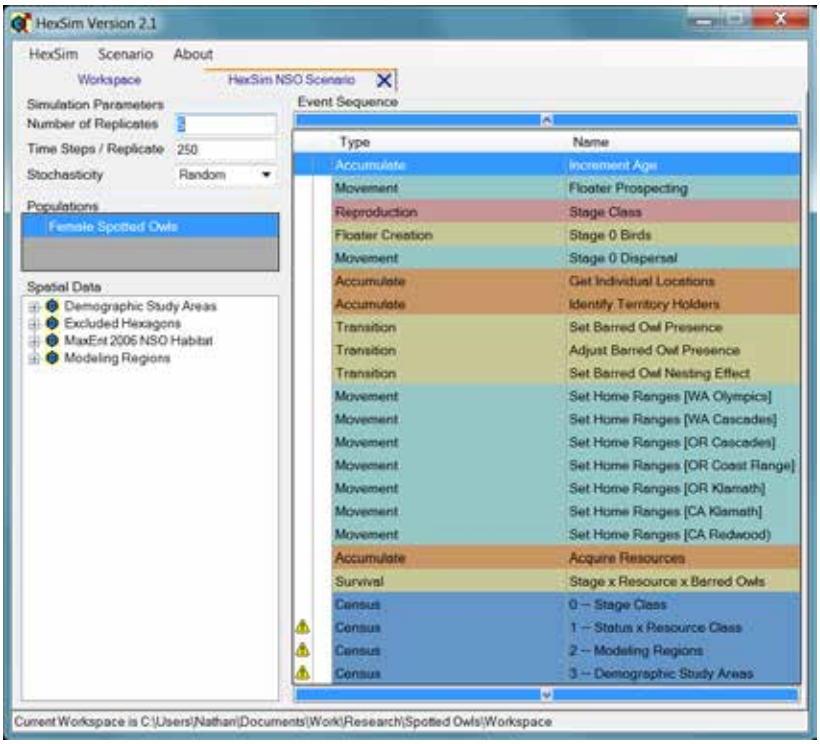
Overview of the Spotted Owl Scenario

Because females are the most influential sex in terms of population dynamics, the HexSim spotted owl scenario is a females-only model. The life cycle is simple except that the acquisition of resources by individual spotted owls is spatially stratified, and thus somewhat complex. The scenario depends on two static spatial data layers; one representing the distribution and quality of habitat, and an “exclusion layer” to prevent spotted owls from moving out into the Pacific Ocean, or into areas outside of their geographic range .

An additional layer comprised of the boundaries of both the modeling regions and demographic study areas (DSAs were used to generate HexSim reports (*i.e.*, we extracted information about spotted owls in DSAs as well as within modeling regions and for all modeling regions overall), had no effect on the simulated population. All spatial data layers are converted to grids consisting of 89- ha hexagons. To the extent possible, simulation parameter values were estimated based on published empirical data.

The HexSim simulations began with 10,000 spotted owls being virtually introduced into the study landscape. The initial population's ages were randomly distributed, and they were placed preferentially into areas of high quality habitat. Once initialization was complete, individual spotted owls were subjected to the event cycle shown in Figure C11. The year begins with each individual becoming a year older. Next, floaters (spotted owls without a territory) prospect for a territory. This is followed by reproduction and fledgling dispersal. Dispersing fledglings do not prospect for a territory.

Figure C11. HexSim event cycle for spotted owls



After dispersal, a determination is made regarding whether territorial spotted owls are exposed to a barred owl. This determination is made once for each territorial spotted owl, and the probability that a spotted owl is exposed to a barred owl varies by modeling region and is based on data from the DSAs. Two transition events accomplish this task. Exposure to a barred owl can impact spotted owl nesting rates. This is handled by a third transition event.

The region-specific probabilities for spotted owl exposure to barred owls were based on the proportion of spotted owl territories where barred owls were detected each year on the 11 DSAs (see Appendix B; Forsman *et al.*, in press). In the model, spotted owl *survival rates* are negatively affected by the presence of barred owls (see Table C22). Due to a lack of empirical information on the effects of barred owls on spotted owl *nesting rates*, this impact was set to zero. This likely represents an underestimate of the true effects of barred owls on spotted owls.

Next, each spotted owl establishes a home range. The simulated spotted owls have small defended territories, but large overlapping home ranges. Home range size varies with modeling region. The spotted owls extract resources from their home ranges, and thus they experience competition for resources from conspecifics. Finally, resource acquisition and survival are simulated. Survival varies based on stage class, resource acquisition class, and exposure to barred owls.

Home range sizes were set to the mean of the available regional-specific estimates (see summary in Schilling 2009). Spotted owl survival rates were based on study area-specific estimates from Forsman *et al*. (in press), with adjustment for the impact of barred owls across all study areas as calculated from the survival meta-analysis model containing an additive barred owl effect, also from Forsman *et al.* (in press).

The Population Parameters

Three distinct component groups were involved in the specification of the HexSim spotted owl population. These involved a set of basic properties, the definition of several different population traits, and finally the establishment of rules for the spotted owl's use of space and resource needs. The basic properties were used to establish an initial population size of 10,000 spotted owls, and to define an exclusion layer. Individuals were initially placed into the best hexagons in the simulation landscape, but only one spotted owl was allowed per hexagon.

Seven traits were created as part of the spotted owl population definition. These traits track stage class, location (modeling region and possibly DSA), resource class, territory status (territorial vs. floater), exposure to barred owls, and barred owl impacts on spotted owl nesting. Table C19 shows each possible trait value.

Table C19. Spotted owl scenario traits and value categories

Trait	Values
Stage Class	Stage 0
	Stage 1
	Stage 2
	Stage 3
Resource Class	Low
	Medium
	High
Territory Status	Floater
	Territorial
Barred Owl Presence	Pending
	Absent
	Present
Barred Owl Nesting Effect	Normal
	Halted

Trait	Values
Modeling Region	North Coast Olympics
	Oregon Coast
	East Cascades South
	East Cascades North
	West Cascades North
	West Cascades Central
	West Cascades South
	Klamath East
	Klamath West
	Inner-California Coast Range
	Redwood Coast

Trait	Values
DSA	Cle Elum
	Coast Ranges
	HJ Andrews
	Klamath
	Olympic
	Rainier
	South Cascades
	Tyee
	Warm Springs
	Wenatchee
	Hoopa
	Marin
	NW California
	Simpson

The simulated spotted owls produced each year begin life at age zero, and stage class zero. Each year they transition into the next stage class. At age 3 they reach stage class three, which is the terminal stage class. The spotted owls always belong to one of three resource classes, depending on the amount of resources they are able to acquire from their home range. Resources are a function of the mean RHS of hexagons, derived from the MaxEnt models (see above). Spotted owls that acquire 2/3 or more of their resource target are placed in the high resource class. Those that attain less than 1/3 of their resource target are placed into the low resource class. All other spotted owls are placed into the medium

resource class. Resource targets vary by modeling region, and are described below.

The territory status trait is used to record whether individual spotted owls own a territory, or are floaters. The barred owl presence trait categorizes individual spotted owls as being exposed, or unexposed, to a barred owl. This decision is made once for each territorial spotted owl. The barred owl nesting effect trait is used to assign a probability that exposure to a barred owl will cause a spotted owl to avoid nesting. This evaluation is repeated every year for every spotted owl.

The modeling region and demographic study area traits are used to track individual spotted owl locations. The 11 modeling regions are space-filling and non-overlapping. Each individual spotted owl occupies one modeling region at any one time. If a spotted owl territory spanned multiple modeling regions, it was assigned to the region in which the majority of its territory hexagons fell. The demographic study areas (DSAs) take up just a fraction of the landscape. So at any moment most spotted owls will not be in a DSA. Resource targets (explained below) and home range size vary by modeling region.

The population parameters also control individual's use of space. The simulated spotted owls had territory sizes of no more than three 214-acre hexagons. This territory size represents a reasonable approximation of a spotted owl core area (see discussion of spatial scale above). Hexagons had to have at least a score of 35 (out of 90 possible) to be usable in forming a territory. We decided on a minimum score of 35 after evaluating the scores of hexagons overlaid on 3,790 spotted owl nest sites. We evaluated the score for the focal hexagon (the one in which the nest resided), the second, and third closest hexagons, as well as the mean scores of the first, second, and third hexagons. More than 75% of the nest sites were in hexagons with scores >35. Similarly, 73% of the spotted owl sites had a mean score >35 for the focal, second, and third closest hexagons. Although other scores might be reasonable, we reasoned that increasing the score would unreasonably inhibit settlement on suitable areas, whereas decreasing the score would result in unrealistic densities in areas with relatively poorer quality habitat. Territory size had little significance for the simulated population dynamics, as the spotted owls derive resources from their home ranges. The territories served as a core area around which home ranges could be constructed. Territories, in the HexSim simulations, were exclusively used areas, whereas the remainder of the home range area could overlap with that of neighboring spotted owls.

Each simulated spotted owl has a resource target, which controlled how much resource it must have access to in order to be placed into the highest resource class. The resource targets vary by modeling region. Spotted owls that acquire 2/3 or more of their resource target are placed into the high resource acquisition class. Those that attain less than 1/3 of their resource acquisition target are placed into the low resource acquisition class. All other spotted owls end up in

the medium resource acquisition class. The resource targets are listed in Table C20.

Table C20. Estimated resource targets based on RHS values at 3,790 spotted owl locations

Modeling Region	Home Range Size (in hexagons)	Resource Target
North Coast Olympics	128	1250
East Cascades North	84	1000
West Cascades North	84	1250
West Cascades Central	84	1250
Oregon Coast	48	375
West Cascades South	46	375
Inner CA Coast Range	37	375
East Cascades South	35	750
Klamath East	35	375
Klamath West	35	375
Redwood Coast	14	250

The Event Sequence

There are 23 events in the HexSim spotted owl scenario. Not all of these events modify the population, and some have similar or related functions. These events are described in turn below. Each event is listed by type (*e.g.*, movement) and specific name (in square brackets).

Accumulate [Increment Age]

This event makes each individual one year older. As a result, stage 0 individuals will move into stage 1, stage 1 individuals will move into stage 2, and stage 2 individuals will move into stage 3.

Movement [Floater Prospecting]

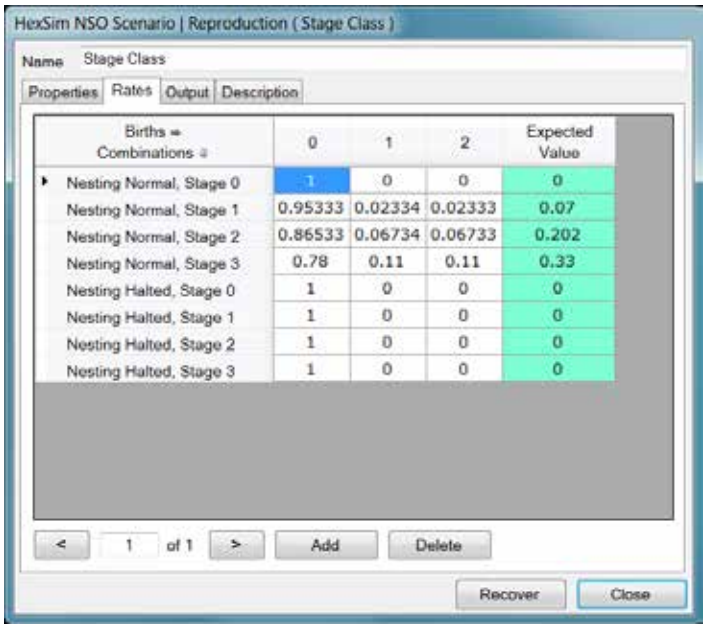
HexSim's movement event controls dispersal and prospecting behavior. But any one event may do either or both. This event only performs prospecting, but it does so for all spotted owls that are floaters (*i.e.*, those who do not own a territory). Individual floaters are allowed to search an area of up to 500 86.6 - hectare hexagons in search of a vacant area from which a territory could be constructed. The search strategy is imperfectly informed by resource quality.

That is, spotted owls tended to construct home ranges from high quality hexagons, but they did not select the best sites with certainty.

Reproduction [Stage Class]

HexSim's reproduction module is parameterized by assigning probabilities to each possible clutch size. Reproduction is also stratified by traits. In this case, the maximum clutch size was set to 2, and reproduction rates were varied by stage class, and based on the Barred Owl Nesting Effect trait values. The reproductive rates used in the event are shown in Figure C12. The unperturbed (by barred owls) reproductive rates were obtained from Table 3 of Forsman *et al.* (in press).

Figure C12. Estimated spotted owl reproductive rates by stage class



Births = Combinations	0	1	2	Expected Value
Nesting Normal, Stage 0	1	0	0	0
Nesting Normal, Stage 1	0.95333	0.02334	0.02333	0.07
Nesting Normal, Stage 2	0.86533	0.06734	0.06733	0.202
Nesting Normal, Stage 3	0.78	0.11	0.11	0.33
Nesting Halted, Stage 0	1	0	0	0
Nesting Halted, Stage 1	1	0	0	0
Nesting Halted, Stage 2	1	0	0	0
Nesting Halted, Stage 3	1	0	0	0

The column headings in Figure C12 correspond to clutch sizes. The rows contain all of the permutations of the two trait values. The right-most column shows the expected values, which in a females-only model, equal fecundities. Individuals whose nesting has been halted by a barred owl are assigned a 100% probability of having a clutch size of zero. The same is true for stage class 0 individuals. Otherwise, the probabilities of having clutches of size 1 and 2 were set as equal as possible, to whatever value was necessary to produce the fecundity values reported in Forsman *et al.* (in press). Finally, the probability of having a clutch of size zero was set so that each row summed to exactly 1.0.

Floater Creation [Stage 0 Birds]

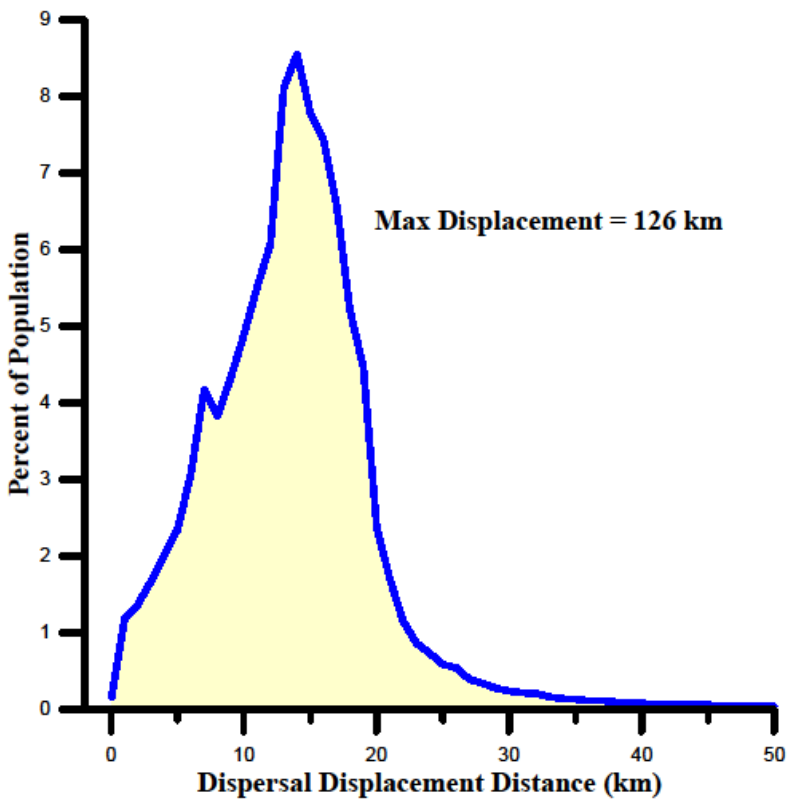
In HexSim, recruits become a co-owner of their mother's territory. They will not disperse from their natal territory unless they are forced to by a floater

creation event. This floater creation event removes all stage 0 birds from their natal groups. These animals disperse in the next event.

Movement [Stage 0 Dispersal]

HexSim's movement event controls dispersal and prospecting behavior. Any one movement event may do either or both. This event strictly performs dispersal for stage class 0 spotted owls. The dispersing birds move with moderate auto-correlation until they encounter enough resource that a territory may be constructed (see above). Territory construction does not actually take place at this time. The dispersers are limited to moving 250 km total distance. The birds have a slight repulsion to poor-quality areas of the landscape, but are not prevented from moving into zero-valued hexagons. Figure C13 shows an example of the distribution of simulated dispersal displacement distances produced by this movement event. These data were gathered from five replicate simulations, for years 100-250. The total number of dispersal events in this period was approximately 852,000. The shape of this frequency distribution will change if either the rules for stopping (3 territory-quality hexagons encountered in succession) or the degree of autocorrelation (50%) are modified.

Figure C13. Distribution of 852,000 simulated Year 1 dispersal distances



Accumulate [Get Individual Locations]

This event records which modeling region each spotted owl is in. If an individual falls within a demographic study area then this event will captures that information, as well.

Accumulate [Identify Territory Holders]

This event updates a trait that segregates into two classes: floaters and territory-holders.

Transition [Set Barred Owl Presence]

This transition event assigns values to the Barred Owl Presence trait. Each modeling region was assigned a separate barred owl encounter probability, based on field data illustrating the proportion of spotted owl territories on DSAs where a barred owl was documented each year (Appendix B; Forsman *et al.*, in press). Using these probabilities, this event places each territorial spotted owl into one of two classes. The classes indicate whether the spotted owl is exposed to a barred owl or not. Once this determination is made for a specific spotted owl, it is not changed until that spotted owl dies or otherwise leaves the territory. The probabilities that were used are shown in Table C21.

Table C21. Barred owl encounter probabilities estimated from Forsman *et al.* (in press)

Region	Encounter Probability
North Coast Olympics	0.505
East Cascades North	0.296
West Cascades North	0.320
West Cascades Central	0.320
Oregon Coast	0.710
West Cascades South	0.364
Inner CA Coast Range	0.213
East Cascades South	0.180
Klamath East	0.245
Klamath West	0.315
Redwood Coast	0.205

Transition [Adjust Barred Owl Presence]

This transition event simply removes the barred owl presence designation from floater spotted owls. This way, if a spotted owl was to give up its territory and leave, it would not retain its barred owl presence / absence designation. In the present scenario territorial spotted owls have perfect site fidelity, so this event has no impact.

Transition [Set Barred Owl Nesting Effect]

This transition event uses the barred owl presence trait to set the value of a barred owl nesting effect trait. This allows spotted owls that are exposed to a barred owl to be placed into a non-nesting category with some probability. As this probability increases from zero, barred owls have an increasingly strong influence over spotted owl nesting rates, and hence reproductive output. In these simulations, the barred owl effect on spotted owl nesting was set to zero.

Movement [Set Home Ranges]

Eight different movement events are used to set home range sizes differently based on modeling region. These movement events only establish home ranges for territorial spotted owls. The home range sizes used are listed in Table C22. Spotted owls acquire resources from their home ranges, and the home ranges for different birds may overlap; territories however, cannot overlap. This results in competition among spotted owls for resources. Spotted owl home ranges were always contiguous, but their shapes were not constrained. The home range sizes used were developed from the published results of many field studies, and were compiled by the modeling team.

Table C22. Spotted owl home range sizes used in population modeling.

Region	Home Range Size (in hexagons)
North Coast Olympics	128
East Cascades North	84
West Cascades North	84
West Cascades Central	84
Oregon Coast	48
West Cascades South	46
Inner CA Coast Range	37
East Cascades South	35
Klamath East	35
Klamath West	35
Redwood Coast	14

Accumulate [Acquire Resources]

This "accumulate event" assigns individual spotted owls to a resource class, based on how much resource they acquire from their home ranges. Habitat quality and quantity, plus competition with conspecifics will dictate what resource class individual spotted owls end up in.

Survival [Stage x Resource x Barred Owls]

The survival event is stratified by stage class, resource class, and exposure to barred owls (which is binary). The survival rates that were used are shown in Table C23. The derivation of these values is discussed in a separate section below.

Census [x 4]

Four census events are used to track the number of spotted owls by stage class, resource class, modeling region, and demographic study area.

Table C23. Estimated survival rates of spotted owl based on stage class, resource class, and barred owl effect

Without Barred Owls			With Barred Owls		
Stage Class	**Resource Class**	**Survival Rate**	**Stage Class**	**Resource Class**	**Survival Rate**
Stage 0	Low	0.366	Stage 0	Low	0.28
	Medium	0.499		Medium	0.413
	High	0.632		High	0.546
Stage 1	Low	0.544	Stage 1	Low	0.458
	Medium	0.718		Medium	0.632
	High	0.795		High	0.709
Stage 2	Low	0.676	Stage 2	Low	0.590
	Medium	0.811		Medium	0.725
	High	0.866		High	0.780
Stage 3	Low	0.819	Stage 3	Low	0.733
	Medium	0.849		Medium	0.763
	High	0.865		High	0.779

Spatial Data

The Baseline HexSim spotted owl scenario uses four different map files. All four maps are static (they do not change with time), and each is made up from 538,395 hexagons arranged in 1430 rows and 377 columns. Individual hexagons are 1000 meters in diameter, and 86.6 hectares in area. The spatial data were developed by sampling raster imagery, using a tool that is built into the HexSim model. The sampling process involves intersecting a grid of hexagonal cells with a raster image, and then computing a per-hexagon mean from a series of weights assigned to the land cover classes present in the raster data.

The habitat map (*MaxEnt 2006 NSO Habitat)* captures spotted owl resource quality, and was derived from RHS values developed using MaxEnt in Step 1 (see above). In HexSim, each land cover class was assigned a weight equal to its category ID. The category IDs ranged between zero and 97. Thus when the HexSim resource quality map was constructed from this raster file, the best possible hexagon score was 97.00; this upper limit was never realized because each hexagon's value represented an average of the pixels underneath it. The hexagons in the HexSim resource quality map vary between 0.00 and 90.37.

A map delineating the study area (*Excluded Hexagons)* was binary, with ones being assigned to each hexagon within the range of the spotted owl, and zeros elsewhere. Simulated spotted owls were not allowed to move into hexagons that were zero-valued in this map. This map included boundaries to the study area, such as the Pacific Ocean and other areas outside of spotted owl's range, or outside our area of inquiry (*e.g.*, the spotted owl's range in British Columbia).

The final two maps depict the locations of the modeling regions and DSAs. The map called *Modeling Regions* breaks the range of the spotted owl up into 11 different regions. This map was used to identify which region individual spotted owls occupied, because each modeling region had different resource requirements and home range sizes. Similarly, a map called D*emographic Study Areas* indicates the locations of 14 different DSAs.

Survival Rates

The survival event is stratified by stage class, resource class, and exposure to barred owls. To begin with, 9 survival rates were derived from Table 12 in Forsman *et al.* (in press). These rates corresponded to the three oldest stage classes x 3 resource classes. Forsman *et al.* (in press) provided stage class-specific survival estimates for each of 11 DSAs. For each study area and stage class, mean apparent survival values for males and females were provided. We computed the mean of each pair and identified the smallest and largest of these mean values. For any given stage class, the smallest mean value was assigned to individuals in the low resource class. Likewise, the largest stage-specific mean value was assigned to individuals in the high resource class. The stage-specific survival rates for individuals in the medium resource class were set equal to the mean taken over all of the survival estimates present in Table 12 of Forsman *et. al* (in press) for that stage class. Through this process survival rates were obtained for stage 1-3 spotted owls in all three resource classes.

Stage class 0 survival estimates were taken from Franklin *et al*. (1999: 27-28). This is the final report titled "Range-wide status and trends in northern spotted owl populations" that was written after a major workshop held in Corvallis, Oregon, in 1999 to estimate demographic rates of the subspecies. The estimates of juvenile survival rates for three study areas from banding studies were adjusted to compensate for emigration rates, based on radio telemetry studies conducted by Eric Forsman (unpublished data). Mean, minimum and maximum juvenile survival rates were taken from this reference and used in the model. The mean value for Stage class zero was set to the midpoint between the minimum and maximum value.

Finally, survival rates were varied based on the presence or absence of barred owls, and the magnitude of their effect was based on the best meta-analysis model for survival with an additive barred owl covariate across all DSAs from Forsman *et al.* (in press). These values were stratified by both stage class and resource class.

Evaluation of Model Calibration

The HexSim model simulated a females-only population of spotted owls throughout their range. The principal metric used to evaluate the model was the simulated population size. The numbers of female spotted owls were tracked range-wide, per modeling region, and also per DSA. The model's performance was assessed by comparing all three measures of simulated population size to field data. We compared simulation year 50 HexSim estimates to field data for 8 DSAs. For this comparison, we used the HexSim simulations during which barred owl impacts were inserted during year (or time-step) 40. After barred owl impacts were incorporated at time-step 40, they remained constant for the remaining 210 time-steps. For these simulations we did not attempt to back-cast barred owl "invasion" dynamics. Our "scenario", therefore, predisposed barred owl impacts to occur all at once, not incremented. We determined by inspection that simulation year 50 most closely represented the present day.

HexSim simulations are stochastic, and to quantify population size, the mean was taken from 5 replicate simulations. Each simulation was 250 time-steps (years) in duration. This does not suggest that spotted owl population sizes were forecasted 250 years into the future. Doing so would at minimum require performing the simulations with a series of maps illustrating habitat changes through time. In contrast, these initial simulations were performed with static data from year 0 to year 40, then (if changes were introduced) changes in barred owl or RHS were introduced and remained static until year 250. The length of the simulations (250 years) simply allowed a steady-state population size and trend to be estimated.

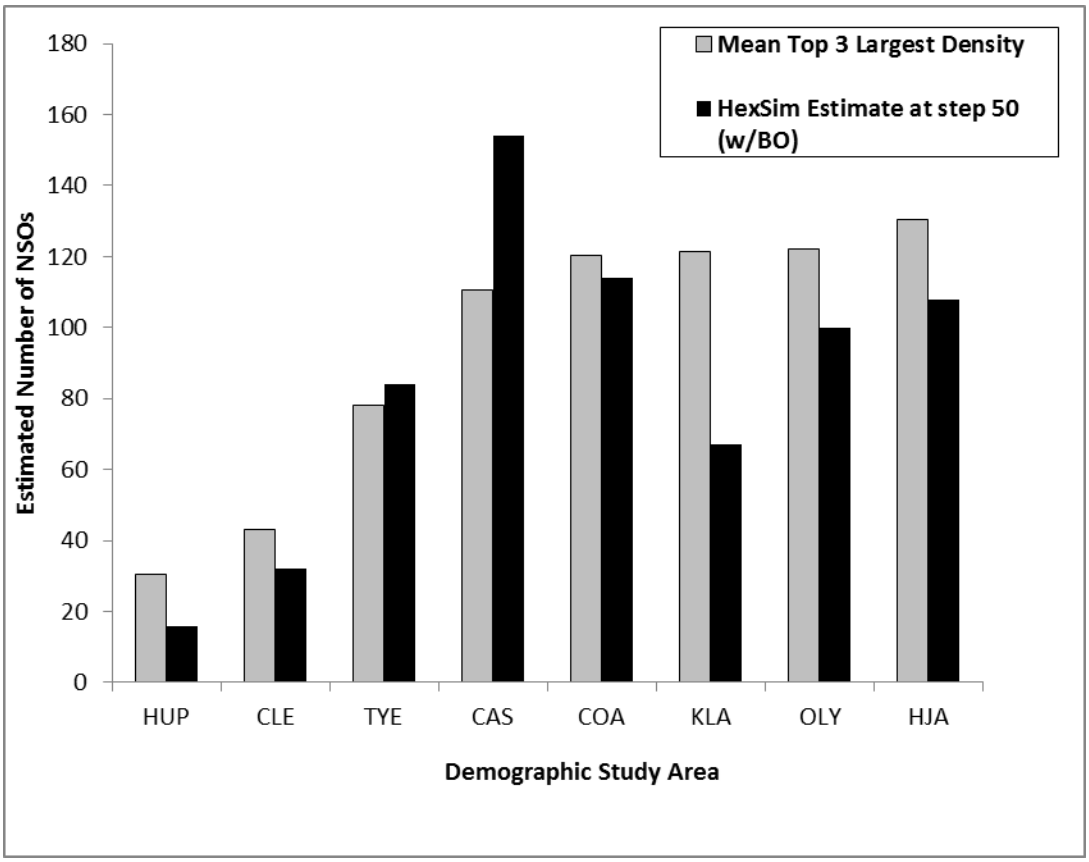
Most, but not all DSAs had data that could be used to approximate density of female spotted owls. Additionally, not all DSAs functioned as "density study areas", and they did not always sample spotted owls identically, nor present data consistently (among DSAs at least). Nonetheless, most DSA annual reports contained tables of historic data which revealed trends. For calibration purposes data from the following DSAs were used: Cle-Elum, Olympic, Oregon Coast, HJ Andrews, Tyee, Klamath, Cascades, and Hoopa. Several calibration iterations were performed by varying resource requirements one modeling region at a time.

Discrepancies in the fit between simulated and observed population size were addressed by varying the resource targets (described above). The resource targets were specified on a modeling-region basis, and they indicated how much resource an individual spotted owl living in a specific region would attempt to acquire. The resource targets were a proxy for resource availability, which varied from region to region and was not fully captured in the RHS maps. As the

resource targets increased, individual spotted owl's needs for resources increased. An inability to acquire sufficient resources could cause spotted owls to drop into the lower resource acquisition classes, which would then lower their survival rates.

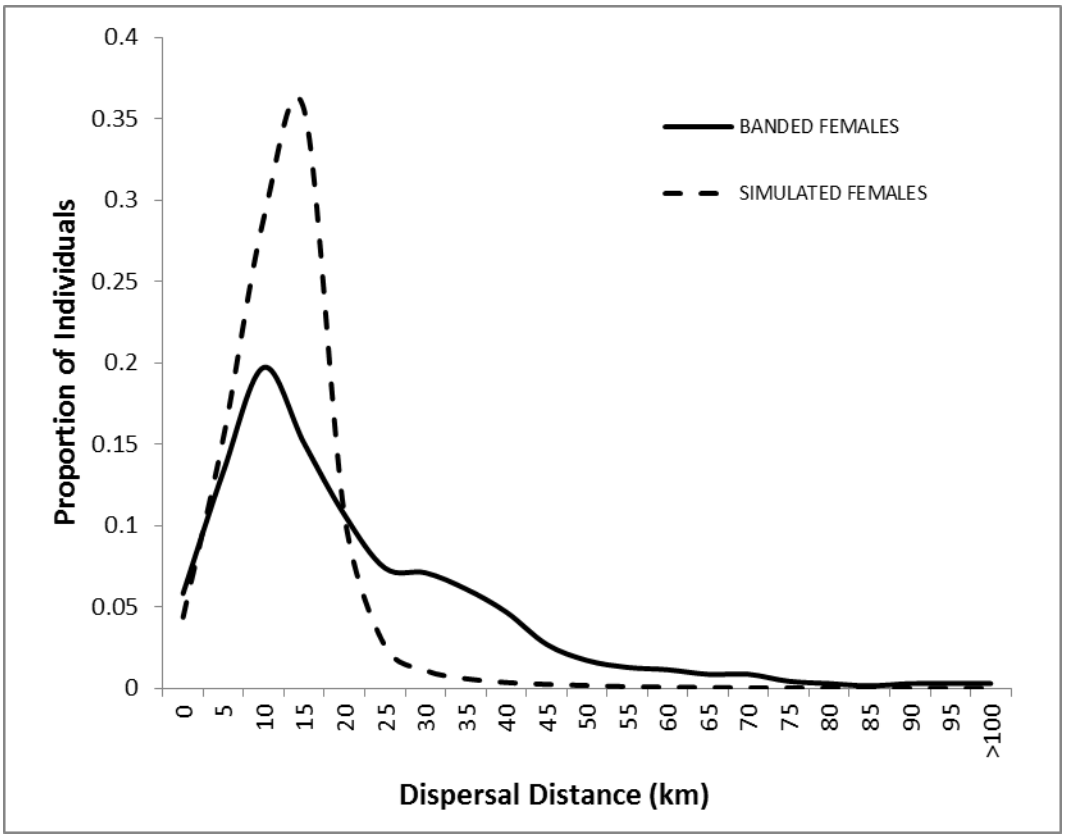
The Baseline HexSim simulations, in which barred owl impacts were introduced at time-step 40, then remained static, produced an estimated total female spotted owl population size within the eight DSAs of 675. From field sampling, the total estimated female spotted owls in those DSAs based on the largest number recorded between 1996 and 2006 was 778. The average of the three highest density years from the annual reports (using only data from 1996-2006) for total estimated spotted owl females was 756. The mean of the highest three years (1996-2006) was selected instead of the highest single year in order to reduce the chance that a single year was uncharacteristic of the DSA (Figure C14). Differences in number of female spotted owls on the eight DSAs between those estimated from field sampling and those estimated from our HexSim runs ranged from 5% to 47%, with a mean absolute percentage difference of 26%. Subsequent changes to HexSim did not eliminate these differences.

Figure C14. Model calibration: Comparison of simulated spotted owl population size (time step 50) to estimates based on field sampling in eight Demographic Study Areas.



Dispersal is a critical process through which landscape structure impacts spotted owl population size and meta-population structure, and is a primary concern in habitat conservation network design (Murphy and Noon 1992). Of particular importance is natal dispersal; the movements of juvenile spotted owls between their natal site and the site where they eventually establish breeding territories. We evaluated the performance of HexSim relative to natal dispersal by comparing graphs of simulated versus observed natal dispersal displacement distances (Figure C15). HexSim generates reports of annual dispersal events by non-territorial (juvenile and floater) spotted owls. The dispersal behavior of the simulated spotted owls was affected principally by landscape structure, the dispersal stopping criteria, and the amount of autocorrelation (both discussed above). Observed natal dispersal distances were estimated from movements of both banded and radio-marked spotted owls (Forsman *et al.* 2002).

Figure C15. Model calibration: Comparison of natal dispersal distances of banded female spotted owls (N= from Forsman *et al.* 2002) to Year 1 movements of HexSim simulated females (N=850,000).



Because our HexSim spotted owl scenario consists solely of females, we limited the comparison to banded female spotted owls. The distributions of natal dispersal distances for 328 banded female spotted owls were generally similar to 850,000 dispersal events recorded during a 250 time-step (years) HexSim simulation. The majority of both observed and simulated dispersal distances

were between one and 25 km, however, a much smaller proportion of simulated dispersal distances were greater than 25 km. This disparity may be due to differences in the time span encompassed within each data set; distances from Forsman *et al.* (2002) consist of distances made over a period of 1 to 4 years whereas simulated distances were available only for dispersal movement events made during the first year of life (Year 1). This comparison could be improved by linking the annual dispersal movement events of simulated spotted owls in HexSim and reporting final natal dispersal distances as in Forsman *et al.* (2002).

Uncertainties and Limitations

An important goal of the spatial population modeling effort is to provide a tool to evaluate and compare the suitability of suites of habitat conservation network scenarios. Each scenario represents a unique ensemble of conditions that could affect future spotted owl population size and trends. The overall amounts of spotted owl habitat, the arrangement of habitat conservation networks, and barred owl influences will vary from scenario to scenario.

Several conclusions about each scenario could be drawn from the HexSim spotted owl simulations. Very specific results, such as estimates of absolute population size, will be the most sensitive to parameter uncertainties. Less specific conclusions, such as the relative differences between scenarios, will be increasingly robust. The HexSim simulations provide, at a minimum, a repeatable methodology for qualitatively ranking the efficacy of the habitat conservation scenarios. This analysis might also extend further, to include a quantification of individual reserve or block carrying capacities, and attendant probabilities of extinction. The conclusions that are drawn from a simulation model must balance concern over uncertainties with the desire to preserve a threatened species.

The HexSim spotted owl simulation model resulted from an attempt to construct the simplest model that could do a credible job of ranking habitat conservation network scenarios. HexSim makes adding realism relatively simple. But more life history detail does not automatically translate into more accurate forecasts. Realism comes at a cost since complex models have larger numbers of parameters, and thus greater data requirements.

There are many details that could be added to the existing HexSim simulation model. Examples include environmental stochasticity, the explicit modeling of spotted owl males (including mate-finding and pairing) and barred owl populations, genetics, disturbance regimes such as fire, etc. Some of these "enhancements" might provide more accurate forecasts of future spotted owl population sizes and probabilities of extinction, and decisions whether to incorporate some of them can be made in the future by model users depending on their specific needs. These enhancements, however, are not necessary in order to reliably rank habitat conservation network scenarios based on their likelihood of facilitating recovery of the spotted owl.

The modeling team considered several enhancements that could be added to the current HexSim spotted owl model. Some enhancements that might be made to the HexSim model are listed below.

Environmental Stochasticity

Incorporation of environmental stochasticity into HexSim scenarios will be necessary when estimates of population size or extinction probability need to be made. However, the addition of environmental stochasticity is unlikely to change the order in which habitat conservation network scenarios rank (*i.e.*, from least to most likely to recover the spotted owl). Developing a modeling process to determine the rank-ordering of scenarios was the modeling team's primary goal, and environmental stochasticity was left out of these simulations in order to limit the computational burden associated with that analysis. Environmental stochasticity should be added to the HexSim model before it is used to estimate population sizes or extinction rates. At that time, the more variable model could be used to test a subset of the rank-ordering results obtained without environmental stochasticity. Recent research into the effects of variability in climate on spotted owl demographic rates (Glenn *et al.* 2010) suggested adding realistic variation in annual temperature and precipitation would provide an important element of environmental stochasticity into HexSim simulations.

Effect of habitat quality on reproductive rates

The HexSim spotted owl model links habitat quality to survival rates through resource acquisition. Individual spotted owls acquire resources from their simulated home ranges, and better quality home ranges provide greater resources. But home ranges overlap, and competition between spotted owls will lower resource availability. Resource acquisition, because it links landscape structure and intra-specific competition, is a more realistic driver of survival rates than habitat quality would be on its own. Resource acquisition could easily influence reproduction in exactly the same way that it influences survival. Unfortunately, the most recent meta-analysis (Forsman *et al.*, in press) was inconclusive regarding the role that habitat quality played in determining reproductive rates. For this reason, the modeling team elected to not vary spotted owl reproductive rates as a function of resource acquisition.

Effect of barred owls on reproductive rates

The HexSim spotted owl model includes the machinery necessary for barred owl influences to include a lowering of spotted owl reproductive rates. This is done by setting a probability that a spotted owl in the presence of a barred owl will nest. Each year, every affected territorial spotted owl will make an independent nesting decision, based on this probability. However, in the current model, the probability that a spotted owl in the presence of a barred owl will forgo nesting entirely is set to zero.

Modeling team members determined that range-wide empirical estimates were not sufficient to assign region-by-region probabilities for barred owl impacts on spotted owl reproduction. Such impacts could come in several forms. For example, the presence of a barred owl could cause a spotted owl to abandon its territory, to keep the territory but forgo nesting (or calling for a mate), or a barred owl could lower effective spotted owl reproductive rates by interfering with nest-tending or preying on spotted owl offspring.

In order to simulate territory abandonment, it would be necessary to explicitly model barred owl locations across the landscape. But sufficient data on barred owl locations and habitat associations were not available range-wide to permit doing more than setting region-by-region probabilities of barred owl occurrence. Simulating barred owl predation on spotted owl offspring runs the risk of double-counting this impact, since barred owl presence does lower survival rates in the HexSim spotted owl model. As described above, the model is able to simulate a lowering of spotted owl nesting rates (when in the presence of a barred owl). But sufficient data was not available range-wide to do more than speculate on the associated parameter values.

Interaction between habitat and barred owl effect

By incorporating the barred owl into the spotted owl scenario as a dynamic spatially explicit stressor, the influence of habitat on barred owl presence and barred owls effects to spotted owl occupancy (extinction rates), recruitment and survival could be more realistically simulated. While there is new information suggesting that habitat and barred owl effects may interact, the data necessary to develop reliable models of barred owl habitat suitability are not available. For this reason, the modeling team elected not to attempt this. Moreover, outcomes of modeling region-specific simulations suggest that the current barred owl parameterization is realistic; low to intermediate barred owl encounter probabilities act to depress spotted owl populations but do not result in extinction.

Sensitivity Analyses

When the HexSim spotted owl model is used to make estimates of population size, or probabilities of extinction, it will be necessary to also conduct a sensitivity analysis. The modeling team has conducted some work on a traditional sensitivity analysis. Whereas a traditional sensitivity analysis is focused on making small changes to individual parameter values, it would be instructive to complement this work with an assessment of the consequences of varying elements of the model structure itself. Examples of model design elements that might be varied include the lack of direct effects of resource acquisition on reproductive rates, the number of resource acquisition levels being simulated, and some of the behavioral features associated with dispersal and prospecting.

The most important parameters in any model of the spotted owl are going to be the survival and reproductive rates. The rates used in the HexSim survival and reproduction events have been derived from the most recent compendium of spotted owl field data (Forsman *et al.*, in press). Still, some uncertainty is introduced when these survival data are used to assign rates to spotted owls in three different resource acquisition classes, as that process involves extrapolation. We therefore elected not to use a larger number of resource acquisition classes. Likewise, the impact of barred owls on spotted owl reproduction is not perfectly understood, and certainly varies from region to region (as we represent in the HexSim scenarios).

One element of realism that the modeling team deemed necessary for this analysis was ensuring that the simulated spotted owls' home ranges and resource requirements varied by modeling region. The variation in home range size is supported by much published information (see review in Schilling 2009). The variation in resource requirements was used to account for regional differences in resource quality that were not captured in the MaxEnt resource map. In areas where the resource quality was known to be lower, spotted owls were assigned a higher resource requirement. The resource requirements were used as a fitting parameter that made it possible to adjust regional population sizes independently.

The HexSim spotted owl model described here is simple, but not overly so. It is likely the most realistic spatially-explicit individual-based spotted owl simulation that has been developed to-date. Its design and complexity mirror what is being asked of it. Additional complexity may be added at a future time as needed to meet the goals that accompany other planning exercises.

Testing Modeling Process Applications – Using the HexSim Spotted Owl Scenario model to compare the demographic effectiveness of various habitat conservation network scenarios and other recovery strategies:

For the Revised Recovery Plan, the modeling team's objective was to develop and test a modeling framework (Steps 1-3) that would support a wide variety of recovery actions, including evaluation of habitat conservation network scenarios. To facilitate the implementation of recovery actions contained in the Revised Recovery Plan, the modeling team established a process for developing scenarios and conducted preliminary population simulations to compare a sample of habitat conservation network scenarios in order to test the modeling framework's reliability. The results from these preliminary comparisons were necessary in order to obtain feedback on the overall framework and provided the basis for revisions to the HexSim model. This objective was completed as part of the recovery planning process. The following evaluation consists of the actual comparison of simulated spotted owl population responses among many alternative scenarios representing various recovery strategies and habitat conservation networks.

Development of Scenarios for Evaluation and Comparison in HexSim

An important use of the modeling framework is to simulate spotted owl population performance relative to three primary sources of variation: size (area) and distribution of habitat conservation networks; trends in habitat conditions inside and outside of the habitat conservation networks; and trends in the influence of barred owls. Considering the many possible variations in network designs, land ownership limitations, future habitat trends, and barred owl effects that could be evaluated, it is clear the number of scenarios needed to evaluate all of the possibilities could increase rapidly and become unfeasible. Instead, the modeling team developed an iterative process for evaluation of scenarios; establishing broad sideboards in earlier comparisons, then testing the models' sensitivity to habitat conditions and barred owl effects. The HexSim spotted owl model can also be used to evaluate the response of spotted owl populations to future climate scenarios.

To test the modeling framework's ability to evaluate the influence of habitat conservation network size (area) and spatial distribution on spotted owl population performance, we analyzed a subset of 10 habitat conservation network scenarios from Step 2 representing a wide range of sizes (proportions of "habitat value"), as well as existing habitat conservation networks (Table C24).

Table C24. Initial set of habitat conservation networks evaluated in population modeling Rounds 1-3.

Network **scenario**	**Code**
Northwest Forest Plan Reserve Network	**NWFP**
Managed Owl Conservation Areas	**MOCA**
1992 Critical Habitat	**1992CH**
2008 Critical Habitat	**2008CH**
30% Zonation (All Lands Available)	**Z30all**
50% Zonation (All Lands Available)	**Z50all**
70% Zonation (All Lands Available)	**Z70all**
30% Zonation (Public Lands Only)	**Z30pub**
50% Zonation (Public Lands Only)	**Z50pub**
70% Zonation (Public Lands Only)	**Z70pub**

Maps depicting each of the network scenarios listed above are available at: http://www.fws.gov/oregonfwo/Species/Data/NorthernSpottedOwl/Recovery/Library/Default.aspx#Files
Once there, click on "maps" and "AppendixCMaps.pdf" The layers can be turned on and off using the "layers" button in the upper left-hand corner.

The habitat conservation networks listed in Table C24 form the basis for a series of comparisons in the population modeling environment (called Rounds) wherein different environmental conditions such as barred owl effects and habitat conditions are manipulated both spatially and temporally (scenarios).

Each habitat conservation network that is subjected to different conditions is termed a habitat conservation network scenario. Rounds simply articulate the specific modifications that are made. The following paragraphs provide descriptions of the scenarios developed by the modeling team, and the results of HexSim runs for the scenarios in Rounds 1-3.

Interpreting HexSim results:

Each HexSim simulation run provides estimates of population size at any chosen time period as well as population trend over any range of time steps. Estimates are reported at both range-wide and regional scales. It is important to recognize that the results are intended to allow comparison of *relative population performance* among alternative habitat conservation network scenarios, not predictions of actual population size or trend in the future.

When a HexSim simulation starts, the number of individuals, age class distribution, spatial arrangement of territories, and other population attributes will have values that reflect the model's initial conditions. It takes many years for these artifacts to subside, and thus for the population's stable-state dynamics to become evident. Simulations were started with 10,000 female spotted owls, thus this initial period of transitory dynamics involved a period of rapid (apparent) population decline for the first 25 or 30 time-steps; typically subsiding by approximately time step 50. It is important not to confuse this decline with an observed or predicted loss in spotted owl numbers that has resulted from changing environmental conditions. We could have chosen to begin simulations with many fewer spotted owls than are known to currently exist in the landscape (say 250), and waited many time-steps for them to increase and reach some sort of equilibrium with their simulated landscape. That would have resulted in a rapid (apparent) population *increase*, but again would simply be the transitory dynamics involved with the starting population conditions. The point is that the first 25-30 time steps are not meant to be interpreted, but can be thought of as a "burn-in" period for the simulation whereby the simulated spotted owls equilibrate with the simulated environment.

Round 1: Baseline (2006) conditions

This was the simple "Baseline" scenario that was used to evaluate parameterization of the HexSim spotted owl scenario. This scenario assumes no change in habitat quality through time (2006 RHS map); therefore the 10 habitat conservation networks listed above are not compared (because nothing different happens inside and outside of habitat blocks in this scenario). Also, barred owl effects remain constant over time (either at zero or constant at their currently-estimated impacts, beginning at time step 40).

Figures C16 through C18 highlight differences in the relative influence of barred owls among modeling regions. Rangewide, barred owls act to depress spotted owl populations to roughly 50 percent of potential population size without barred owls (Figure C16). However, spotted owl populations in modeling

regions with high barred owl encounter rates such as the Oregon Coast Ranges (P_{BO} = 0.710; figure C17) decline rapidly in comparison to modeling regions with low to intermediate barred owl encounter rates such as the Western Klamath (P_{BO} = 0.315; figure C18).

Figure C16. Results of HexSim Round 1 model runs with five replicates each for "Without STVA" (barred owl) impacts and "With STVA" impacts for the spotted owl's entire geographic range in the U.S. The apparent within-year variation that appears in the figure is a function of an "even-odd" year effect on reproduction that was included in this version of the HexSim model.

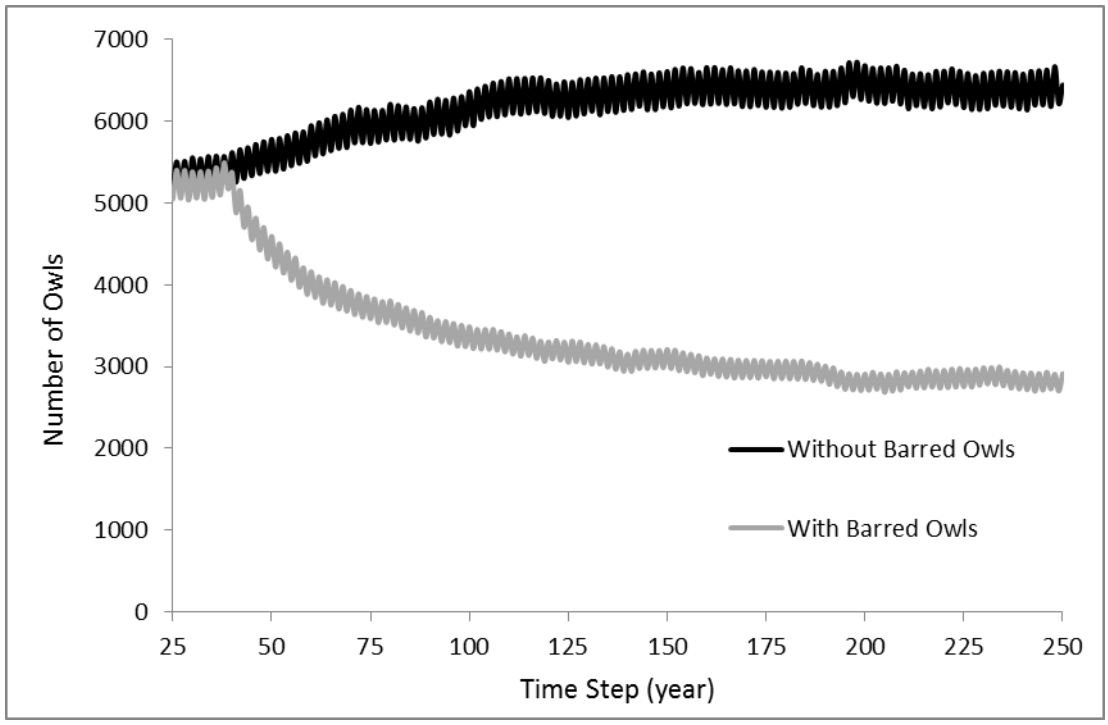


Figure C17. Simulated Round 1 spotted owl population sizes in the Oregon Coast Ranges modeling region showing 1) current barred owl influence and 2) barred owl influence removed.

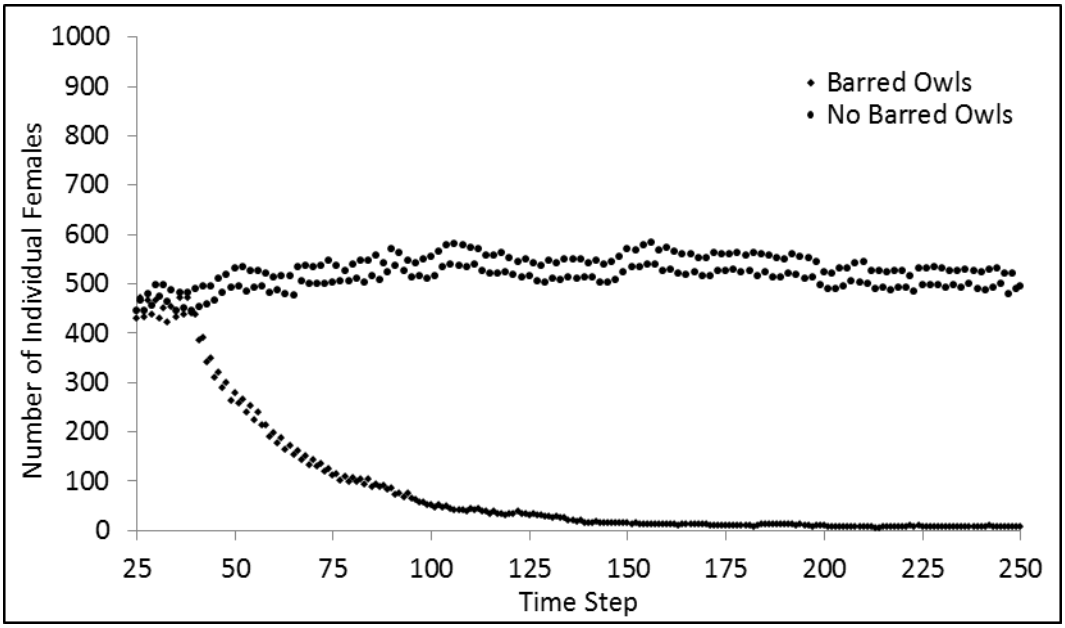
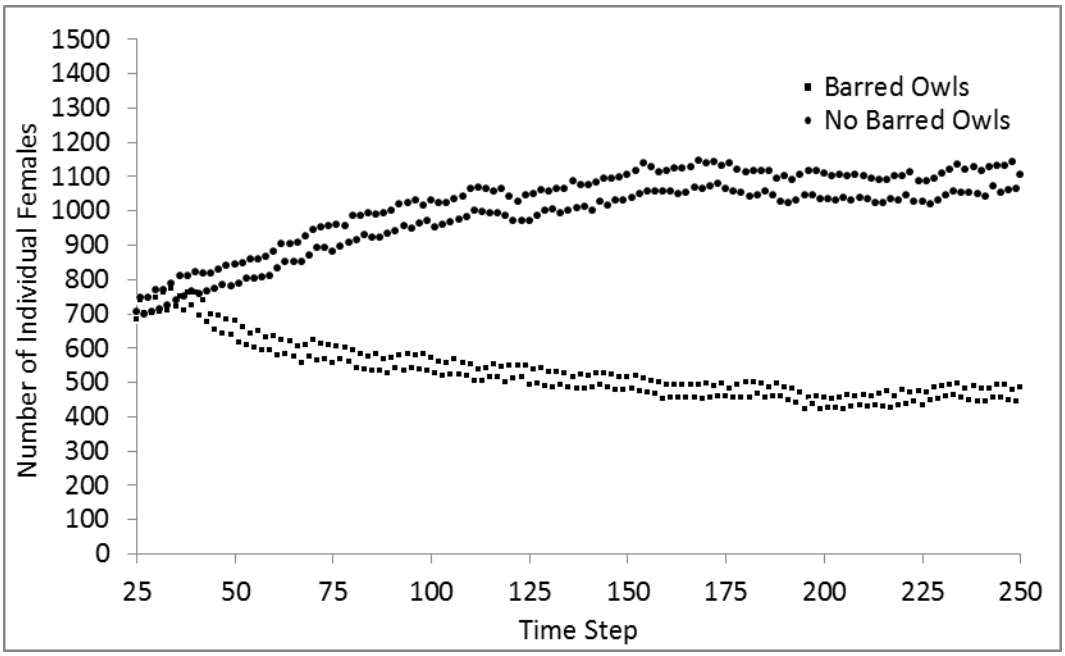


Figure C18. Simulated Round 1 spotted owl population sizes in the Western Klamath modeling region showing 1) current barred owl influence, and 2) barred owl influence removed.



Round 2: Simulating a high degree of reliance on habitat conservation networks

Because the primary objective in this evaluation is to compare estimated spotted owl population performance across a range of habitat conservation network, the goal of Round 2 was to "isolate" the habitat conservation networks by devaluing non-network habitat suitability and holding habitat in networks at its 2006 estimated level throughout the simulation. In this scenario, we reduced relative habitat suitability (RHS) *outside* of habitat conservation networks to 34 (RHS=0.34); *just below* that needed for territory establishment; RHS within networks remained unchanged. The influence of barred owls was held to the currently-estimated encounter rates calculated from Forsman *et al.* (in press); the barred owl influence was slotted in at year 40. We repeated Round 2 with *No barred owl effect*, to evaluate the relative contribution of habitat and barred owl effects on simulated spotted owl population performance. The results of the Round 2 simulations allow for an evaluation of the relative influence of habitat conservation network size and distribution (relying primarily on public versus both public and private lands) and barred owls on spotted owl population performance – when the habitat conservation network provides nearly all nesting and roosting habitat.

Round 3: Simulating RA10 - retention of high-quality habitat outside of habitat blocks

The goal of Round 3 was to evaluate the relative contribution of habitat conditions *outside* of habitat conservation networks to spotted owl populations; Scenarios R3S1 through R3S10 are intended to emulate the management approach of maintaining occupied spotted owl territories outside of network areas . RHS within habitat conservation networks was held constant, and areas of high RHS (>50) *outside* of networks (on public lands) were retained through time. Areas of RHS between 35 and 49 (outside of networks) were decremented to RHS 34. Scenarios R3S11 through R3S20 were similar but apply to *all* non-network lands (public and private). We repeated Round 3 with *No barred owl effect*, to evaluate the relative contribution of habitat and barred owl effects on simulated spotted owl population performance.

Figures C19 and C20 provide examples of different metrics that can be used to compare estimated spotted owl population outcomes among habitat conservation network scenarios, in this case Rounds 2 and 3 described above. Initial results using a wide range of population metrics can provide insights for meeting the recovery criteria established in the Revised Recovery Plan. Comparison of these estimates of spotted owl population performance across the range of scenarios can inform evaluation of habitat conservation networks designed to lead to spotted owl recovery.

Figure C19 provides results for the entire range of the spotted owl, but as described in Round 1 and evidenced in Figure C20, it is important to recognize that population outcomes may differ markedly among modeling regions.

Figure C19. Comparison of percent population change (rangewide) between year 25 and year 250 under the scenarios in Rounds 2 and 3, with and without barred owl influence. MOCAs and Critical Habitat were not compared for Round 3.

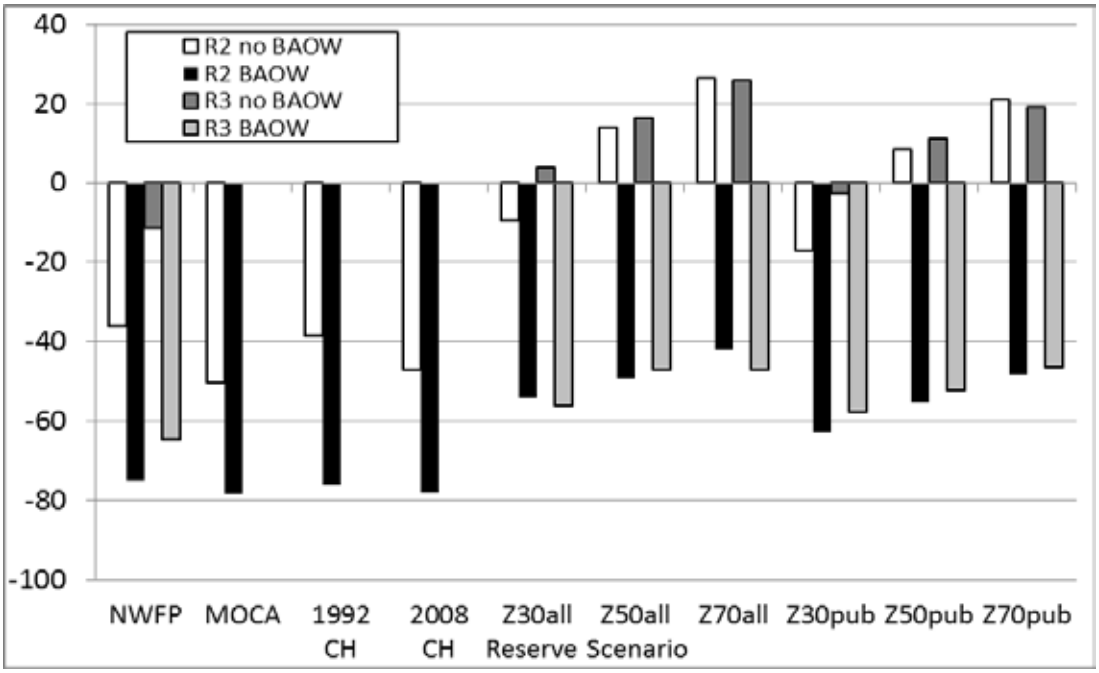
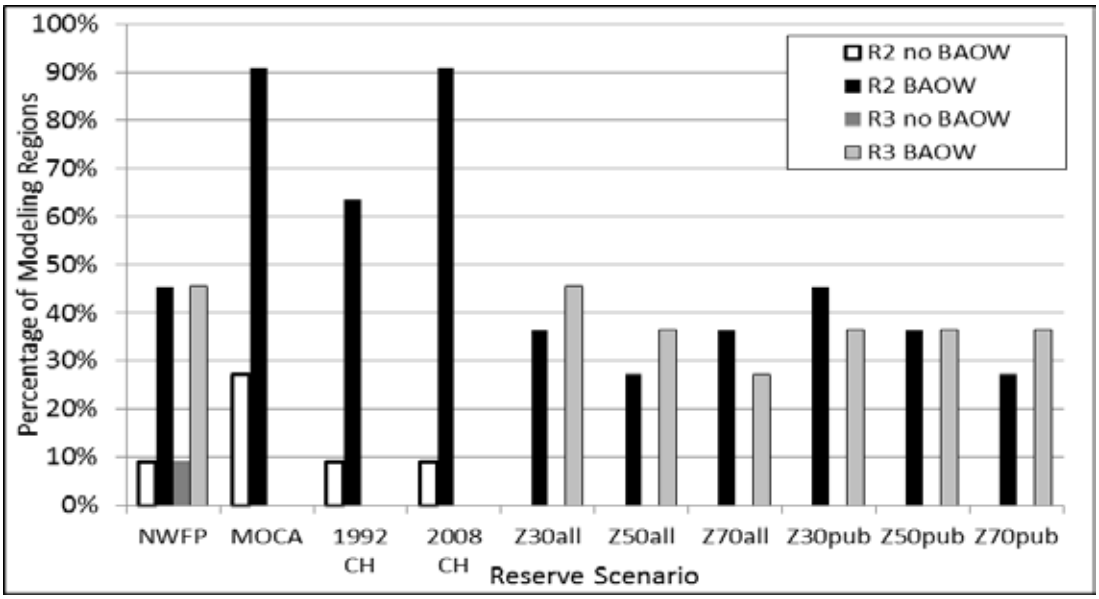


Figure C20. Percentage of modeling regions whose simulated populations declined by more than 75% between years 25 and 250 (indication of extinction risk) under the scenarios in Rounds 2 and 3, with and without barred owl influence.



The interaction of network size with other conservation measures is highlighted in Figures C19 and C20. In Round 3 (simulated RA10 - retention of likely occupied, high-quality habitat with RHS>50 in non-network areas), the amount of habitat "retained" is inversely proportional to the size of area within habitat conservation networks Subsequently, RA 10's benefit to simulated spotted owl populations is relatively less for larger habitat conservation network scenarios such as Z50 and Z70.

Conclusions:

The analysis presented in this appendix is intended to demonstrate how the three-part modeling framework can be used to evaluate spotted owl population response to a variety of environmental conditions such as habitat variation and barred owls. Although this initial analysis is intended to evaluate the modeling framework, it provides insight into factors influencing spotted owl populations and conservation planning for recovery of the spotted owl.

HexSim population simulations can be completed for the entire range of the spotted owl as well as for subsets of the species' range, such as individual modeling regions or DSAs. This capability enables evaluation of varying environmental conditions and subsequent population effects occurring in different parts of the species' range. For example, the relative effect of barred owls on spotted owl survival and subsequent population size varies among modeling regions, in accordance with different barred owl encounter rates (Table C25). Comparison of the relative differences between simulated spotted owl populations without barred owls and those resulting from different barred owl encounter rates among modeling regions (Figures C17 and C18) suggests there may be barred owl population levels (encounter rates) below which spotted owl populations remain stable (albeit at lower population sizes). Further evaluation of these relationships may inform planning of barred owl management scenarios.

Table C25. Barred owl encounter probabilities estimated from Forsman *et al.* (in press)

Region	Encounter Probability
North Coast Olympics	0.505
East Cascades North	0.296
West Cascades North	0.320
West Cascades Central	0.320
Oregon Coast	0.710
West Cascades South	0.364
Inner CA Coast Range	0.213
East Cascades South	0.180
Klamath East	0.245
Klamath West	0.315
Redwood Coast	0.205

As shown in Figure C1, the modeling framework contains feedback loops that facilitate an iterative process, with each iteration informed by the results of previous scenarios and simulated population outcomes. This process enables an adaptive approach to developing and testing conservation measures. As new

information from monitoring or other research becomes available, its influence on spotted owl conservation can be incorporated into subsequent evaluations in a consistent manner.

In sum, it was our goal to develop a modeling framework that can be applied by interested parties to make better informed decisions concerning spotted owl management and recovery. The analyses described in this appendix represent a small subset of possible scenarios and are presented to test the framework and to give potential users of this approach some preliminary exposure to the models' potential utility. Future conservation planning for spotted owls will require development and evaluation of additional scenarios that are relevant to the management questions of particular interest to various stakeholders. These future planning efforts will likely address temporal factors such as changing barred owl populations, climate change, and future habitat change. They might also apply to private land managers who are evaluating different options within a Habitat Conservation Planning scenario, or Federal land managers who are considering recommendations for amending long term forest management plans. Whatever the use to which this framework is applied, our goal was to provide managers with tools that will ultimately result in better informed decisions for spotted owl conservation.

Literature Cited

Akaike, H. 1974. A new look at statistical model identification. IEEE Transactions on Automatic Control. AU-19:716-722.

Anthony, R.G., E.D. Forsman, A.B. Franklin, D.R. Anderson, K.P. Burnham, G.C. White, C.J. Schwarz, J. Nichols, J.E. Hines, G.S. Olson, S.H. Ackers, S. Andrews, B.L. Biswell, P.C. Carlson, L.V. Diller, K.M. Dugger, K.E. Fehring, T.L. Fleming, R.P. Gerhardt, S.A. Gremel, R.J. Gutiérrez, P.J. Happe, D.R. Herter, J.M. Higley, R.B. Horn, L.L. Irwin, P.J. Loschl, J.A. Reid, and S.G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monograph No. 163.

Barrows, C. and K. Barrows. 1978. Roost characteristics and behavioral thermoregulation in the spotted owl. Western Birds 9:1-8.

Bingham, B.B. and B.R. Noon. 1997. Mitigation of habitat "take": Application to habitat conservation planning. Cons. Biol. 11(1): 127-139.

Blakesley, J.A., A.B. Franklin, and R.J. Gutierrez. 1992. Spotted owl roost and nest site selection in northwestern California. J. Wildl. Manage. 56(2):388-392.

Blakesley, J. 2004. Habitat Associations. Chapter 5 *in* S. P. Courtney, J. A. Blakesley, R. E. Bigley, M. L. Cody, J. P. Dumbacher, R. C. Fleischer, A. B. Franklin, J. F. Franklin, R. J. Gutiérrez, J. M. Marzluff, L. Sztukowski. Scientific evaluation of the status of the northern spotted owl.

Carey, A.B., S.P. Horton, and B.L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. Ecological Monographs 62(2):223–250.

Carroll, C. and D.S. Johnson. 2008. The importance of being spatial (and reserved): assessing northern spotted owl habitat relationships with hierarchical Bayesian models. Conservation Biology 22:1026–1036.

Carroll, C. 2010. Role of climatic niche models in focal-species-based conservation planning: Assessing potential effects of climate change on northern spotted owls in the Pacific Northwest, USA. Biol. Cons. Xxxxxxxx

Carroll, C., J.R. Dunk, and A. Moilanen. 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest. Global Change Biology 16:891-904.

Clark, D.A. 2008. Demography and Habitat Selection of Northern Spotted Owls in Post-Fire Landscapes of Southwestern Oregon. Thesis, Oregon State University. Corvallis, Oregon. 202 pp.

Davis, R. and J. Lint. 2005. Habitat status and trends. Pages 21–82 in J. Lint, technical coordinator. Northwest Forest Plan—the first 10 years (1994–2003): status and trends of northern spotted owl populations and habitat. General Technical Report PNW-GTR-648, Pacific Northwest Research Station, U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Davis, R.J., tech. coord. Northwest Forest Plan—Status and Trend of Northern Spotted Owl Populations and Habitats from 1994 to 2008. Gen. Tech. Rep. PNW- GTR-###. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station:##-##.

Dugger, K.M., F. Wagner, R.G. Anthony, and G.S. Olson. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. Condor 107:863–878.

Dunk, J.R., W.J. Zielinski, and H. Priestler. 2004. Predicting the occurrence of rare mollusks in northern California forests. Ecological Applications 14(3): 713-729.

Elith *et al.* 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2):129-151.

Elith, J., S.J. Phillips, T. Hastie, M. Dudik, Y.E. Chee, and C.J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and distribution 17:43-57.

Elith, J. and J.R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review Ecology Evolution Systematics. 40:677-697.

Forsman, E.D., R.G. Anthony, K.M. Dugger, E.M. Glenn, A.B. Franklin, G.C. White, C.J. Schwarz, K.P. Burnham, D.R. Anderson, J.D. Nichols, J.E. Hines, J.B. Lint, R.J. Davis, S.H. Ackers, L.S. Andrews, B.L. Biswell, P.C. Carlson, L.V. Diller, S.A. Gremel, D.R. Herter, J.M. Higley, R.B. Horn, J.A. Reid, J. Rockweit, J. Schaberl, T.J. Snetsinger, and S.G. Sovern. In press. Population demography of northern spotted owls: 1985–2008. Studies in Avian Biology. Cooper Ornithological Society.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR. 452pp.

Franklin, A.B., D.R. Anderson, R.J. Gutiérrez, and K.P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Ganey, J.L., R.P. Balda, and R.M. King. 1993. Metabolic rate and evaporative water loss
of Mexican spotted and great horned owls. Wilson Bulletin 105(4):645-656.

Glenn, E.M. 2009. Local weather, regional climate, and population dynamics of northern spotted owls in Washington and Oregon. Dissertation, Oregon State University, Corvallis.

Glenn, E.M., R.G. Anthony, and E.D. Forsman. 2010. Population trends in northern spotted owls: Associations with climate in the Pacific Northwest. Biol. Cons. 143:2543-2552.

Gremel, S. 2005. Factors controlling distribution and demography of northern spotted owls in a reserved landscape. Thesis, University of Washington, Seattle.

Gutiérrez, R.J., A.B. Franklin, and W.S. LaHaye. 1995. Spotted owl (*Strix occidentalis*) in A. Poole and F. Gill (editors), The birds of North America, No. 179. The Academy of Natural Sciences and The American Ornithologists' Union, Washington, D.C.

Gutiérrez, R. J., M. Cody, S. Courtney, and A.B. Franklin. 2007. The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. Biological Invasions 9:181–196.

Heinrichs, J.H., D.H. Bender, D.L. Gummer, and N.H. Schumaker. 2010. Assessing critical habitat: evaluating the relative contributions of habitats to population persistence. Biological Conservation 143:2229-2237.

Hemstrom, M, T. Spies, C. Palmer, R. Keister, J. Teply, P. McDonald and R. Warbington. 1998. Late-successional and old-growth forest effectiveness monitoring plan for the Northwest Forest Plan. Gen. Tech. Rep. PNW-GTR-438. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 37 p.

Hessburg, P. F., Salter, R. B., Richmond, M. B., Smith, B. G. 2000. Ecological Subregions of the Interior Columbia Basin, USA. Applied Vegetation Science. 3(2): 163-180.

Hershey, K.T., E.C. Meslow, and F.L. Ramsey. 1998. Characterisics of forests at spotted owl nest sites in the Pacific Northwest. J. wildl. Manage 62(4):1398-1410.

Hirzel, A.H., G. LeLay, V. Helfer, C. Randin and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presence. Ecological Modelling. 199:142-152.

Hunter, J.E., R.J. Gutierrez, and A.B. Franklin. 1995. Habitat configuration around spotted owl nest sites in northwestern California. Condor 97:684-693.

Johnson, D. H. 2001. Validating and evaluating models. Pages 105–119 in T. M. Shenk and A. B. Franklin (editors), Modeling in natural resource management. Island Press, Covelo, California

Kennedy, R.E.; Yang, Z.; Cohen, W.B. 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr - temporal segmentation algorithms. Remote Sensing of Environment. 114(12): 2897-2910.

Kennedy, R.E.; Cohen, W.B.; Schroeder, T.A. 2007. Trajectory-based change detection for automated characterization of forest disturbance dynamics. Remote Sensing of Environment. 110: 370-386.

Kuchler, A.W. 1977. The map of the natural vegetation of California. Pages 909-938 In M.G. Barbour and J. Major, editors, Terrestrial vegetation of California. Wiley-Interscience, reprinted by the California Native plant Society 1988, Sacramento, CA.

LaHaye, W.S. and R.J. Gutiérrez. 1999. Nest sites and nesting habitat of the northern spotted owl in northwestern California. Condor 101:324-330.

Lint, J.; Noon, B.; Anthony, R.; Forsman, E.; Raphael, M.; Collopy, M.; Starkey, E. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. Gen. Tech. Rep. PNW-GTR-440. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 43 p.

Livezey, K.B., R.M. Engeman, D.F. Rock, and D.A. Yasuda. 2007. Considering control of invasive barred owls to benefit California spotted owls: Possible justification and draft methods. Pages 72-81 In Witmer, G.W., W.C. Pitt, and K.A. Fegerstone, Editors, Managing Vertebrate Invasive Species: Proceedings of an International Symposium. USDA APHIS/WS, National Wildlife Research Center, Fort Collins, CO. 2007.

McNab, H.W. and P.E. Avers. 1994. Ecological subregions of the United States: Section descriptions. Publication WO-WSA-5. USDA Forest Service, Washington, D.C.

Meyer, J.S., L.L. Irwin, and M.S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs 139:1–51.

Moilanen A, H. Kujala. 2008. Zonation: software for spatial conservation prioritization. User Manual v2.0. Metapopulation Research Group, University of Helsinki, FI. Available at <http://www.helsinki.fi/bioscience/consplan/software/Zonation/index.html>. Accessed 3 March 2011.

Murphy, D.D. and B. R. Noon. 1992. Integrating scientific methods with habitat conservation planning: reserve design for northern spotted owls. Ecological Applications 2: 3-17.

Noon, B.R. and A.B. Franklin. 2002. Scientific research and the spotted owl (Strix occidentalis): Opportunities for major contributions to avian population ecology. Auk 119(2):311-320.

Ohmann, J.L. and M.J. Gregory. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. Canadian Journal of Forest Research. 32: 725-741.

Olson, G.S., E.M. Glenn, R.G. Anthony, E.D. Forsman, J.A. Reid, P.J. Loschl, and W.J. Ripple. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. Journal of Wildlife Management 68:1039–1053.

Pearce, J. and S. Ferrier (2000). Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Pearson, R.R. and K.B. Livezey. 2003. Distribution, numbers, and site characteristics of spotted owls and barred owls in the Cascade Mountains of Washington. Journal of Raptor Research 37:265–276.

Phillips, S.J., R.P. Anderson, and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190:231–259.

Phillips, S.J., M. Dudik, J. Elith, C.H. Graham, C.H., A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19(1):181-197.

Phillips S.J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175.

S. J. Phillips, and J. Elith. 2010. POC plots: calibrating species distribution models with presence-only data. Ecology 91:2476-2484.

Raphael M.G., K. S. McKelvey, B. M. Galleher. 1998. Using geographic information systems and spatially explicit population models for avian conservation: a case study. Pages 65-74 *In* Marzluff JM, Sallabanks R, eds. Avian conservation: research and management. Island Press, Washington.

Reed, J.M., H.R. Akcakaya, M. Burgman, D. Bender, S.R. Beissinger and J.M. Scott. 2006. Critical habitat. Pages 164-177 in Scott, J.M., D.D. Goble and

F.W. Davis, editors, The Endangered Species Act at thirty. Island Press, Washington, D.C.

Rosenberg, D.K. and K.S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. J. Wildl. Manage. 63(3): 1028-1038.

Schilling, J.W. 2009. Demography, home range, and habitat selection of northern spotted owls in the Ashland Watershed. M.Sc. Thesis, Oregon State University, Corvallis, OR. 129 pp.

Solis, D.M., and R.J. Gutiérrez. 1990. Summer habitat ecology of northern spotted owls in northwestern California. Condor 92:739–748.

Stalberg, D., K.E. Fehring, L.Y. Pomara, N. Nur, D.B. Adams, D. Hatch, G.R. Geupel and S. Allen. 2009. Modeling nest-site occurrence for the northern spotted owl at its southern limit in central California. Landscape and Urban Planning. 90:76-85.

Swindle, K.A., W.J. Ripple, E.C. Meslow, and D. Schafer. 1999. Old forest distribution around spotted owl nests in the central Cascade Mountains, Oregon. Journal of Wildlife Management 63:1212–1221.

Thome, D. M., C. J. Zabel, and L. V. Diller. 1999. Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. Journal of Wildlife Management 63(1):44-59.

USFWS (U.S. Fish and Wildlife Service). 1992b. Draft final recovery plan for the northern spotted owl. U.S. Fish and Wildlife Service, Portland, Oregon.

Warren, D.L. and S.N. Seifert. 2011. Environmental niche modeling in MaxEnt: The importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21:335–342.

Wisz, M.S., R.J. Hijmans, J. Lis, A.T. Peterson, C.H. Graham, A. Guisan. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763-773.

Zabel, C. J., J.R. Dunk, H.B. Stauffer, L.M. Roberts, B.S. Mulder, and A. Wright. 2003. Northern spotted owl habitat models for research and management application in California (USA). Ecological Applications 13:1027–1040.