Assessing risks to spotted owls from forest thinning in fire-adapted forests of the western United States

Danny C. Lee a,*, Larry L. Irwin b

a USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, CA 95521, USA
b National Council for Stream and Air Improvement, P.O. Box 68, Stevensville, MT 59870, USA

Abstract

Concern for viable spotted owl (Strix occidentalis) populations has played prominently in the management of western forests in the United States. Historically, much of the debate has focused on the impacts of commercial timber harvest. Increasingly, the conflict is shifting to the habitat needs of owls versus the need for active management of fire-adapted forest ecosystems to reduce the occurrence of uncharacteristic wildland fire that threatens multiple resource values. While some authors have called for active fuels management within the range of spotted owls, concerns remain over potential effects of less intensive, but more extensive, fuel reduction activities (i.e., thinning and prescribed burning). Reconciling fire and fuels management with owl conservation requires rigorous analysis of both the short- and long-terms risks of action versus no action. We use published literature and data from the southern Sierra Nevada to examine the potential effects of landscape-level reductions in canopy cover (CC) on owl occupancy and reproduction. Using a combination of population data, canopy cover measurements, and forest simulation models, we show that modest fuels treatments in the Sierra Nevada would not be expected to reduce canopy cover sufficiently to have measurable effects on owl reproduction. Sixty-year simulations predict that mechanical thinning or mechanical thinning plus fuel-break construction treatments in combination with either no fire or mixed-lethal fire scenarios will not degrade canopy conditions in productive owl territories, nor impede improvement of non-productive territories. In contrast, lethal fire simulations produced a pronounced and lasting negative effect. Our analysis supports the hypothesis that habitat needs for owl reproduction can be incorporated in developing effective fire and fuels management strategies that lessen the chances of uncharacteristic wildfire. Projections of future population trends are tempered by the knowledge that non-habitat factors such as variations in weather profoundly affect population dynamics.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Spotted owl; Strix occidentalis; Wildland fire; Canopy cover; Forest thinning; Risk assessment

1. Introduction

Concerns for the viability of spotted owls (Strix occidentalis) profoundly influence forest management in the western United States. Conservation
planning for all three subspecies – the northern spotted owl (S. o. caurina), the California spotted owl (S. o. occidentalis), and the Mexican spotted owl (S. o. lucida) – has motivated changes in forest policy from the temperate rain forests of the Olympic peninsula to the dry forests and canyons of the American Southwest. The conflict is rooted in the spotted owl’s association with late-seral or old-growth forest conditions (Gutierrez, 1996; Noon and McKelvey, 1996). Concern for the owls increased as western forests changed from more than a century of logging, land use conversion, and wildland fire suppression. In the 1980s the spotted owl became a cause célèbre for protection of remaining old-growth forests and ushered in an era of intense public scrutiny and scientific investigation (Simberloff, 1987; Noon and Murphy, 1997; Noon and Franklin, 2002). Listing of the northern and Mexican subspecies under the Federal Endangered Species Act, the recent petitioning of the California subspecies, and various state regulations ensure the owl’s prominence in forest planning.

In the publicly owned forests managed by the USDA Forest Service and USDI Bureau of Land Management, forest management objectives have perceptibly shifted, leading to restrictions in timber harvest in the Pacific Northwest and Sierra Nevada. Yet, the large and uncharacteristically severe wildfires of recent years remind us that timber harvest is not the only agent of change in forests. An increasing body of scientific literature argues that decades of fire suppression and outdated timber harvest practices have fundamentally changed composition and structure in many inland forests, particularly the drier and lower-elevation forests below the true fir (Abies spp.) zone (Agee, 1993, 1998; Skinner and Chang, 1996; Hessburg and Agee, 2003; Perry et al., 2004). The resulting build-up of both live and dead fuels has increased the probability of stand-replacing fire in fire-adapted ecosystems that historically experienced more frequent, less intense wildfire (Agee and Edmonds, 1992; Covington et al., 1994). Relatively open forests once dominated by shade-intolerant, fire-resistant tree species are now densely packed with fires, incense cedar (Calocedrus decurrens), tanoak (Lithocarpus densiflorus), and other shade-tolerant species. The changes are not universal, but there is general agreement that many areas of the pine (Pinus spp.) and mixed conifer forests of the Southwest, eastern Cascades, and interior California are at a level of risk to high-intensity fire that is unprecedented in post-European settlement.

Unfortunately, this zone of high-risk forests includes much of the eastern range of the spotted owl. Efforts to reduce wildland fire risks raise the question of whether active forest management towards such ends is compatible with conserving owls. The topic is not new. In the Sierra Nevada, Verner et al. (1992) predicted increases in “stand-destroying” fires that will accelerate the loss of old-growth attributes, including remnant old trees that are vital to owl nesting success. Weatherspoon et al. (1992) suggested that severe wildfire may represent the greatest threat to current owl habitat in Sierran mixed-conifer forests, and recommended, “aggressive, environmentally sound fuels management programs to reduce wildfire hazard in and around owl habitat.” Buchanan et al. (1995) suggested that active management is required to reduce risk of large-scale habitat loss to wildfires in the eastern Washington Cascades. In a recent commentary on national forest fire policy, Franklin and Agee (2003) pointed to the Sierra Nevada mixed conifer forests as areas “likely to experience uncharacteristic stand-replacing fires without active fuels treatments and prescribed burning programs, with the resulting loss of critical watershed and habitat for the California spotted owl and other endangered wildlife.” Recent large, intense fires within the range of the spotted owl from northern Washington to New Mexico support the view that forest conditions in some locations are primed for wildland fires that could render owl habitat unsuitable for decades (Irwin and Thomas, 2002).

Direct empirical evidence regarding the effect of fire on owls is scant. A recent, qualitative review of the short-term effects of wildland fire on important demographic parameters identified 11 territories that experienced wildland fire from among >300 study territories, 8 of which had information on fire severity (Bond et al., 2002). Bond et al. (2002) concluded that relatively large wildland fires that burned >80% of each of these 11 territories, primarily at low to moderate severity, apparently had little short-term (1 year) effect on individual survival, site fidelity, mate fidelity, and reproductive success of spotted owls.
Bond et al. (2002) suggested, “prescribed burning could be an effective tool in reducing current fire risk and restoring forest to natural conditions with minimal short-term impacts to owls,” but were careful to note that further empirical testing is needed before embarking on wide-scale prescribed burning in owl territories.

Proposals to reduce wildland fire risks in occupied owl habitat are often resisted because of concerns for short-term habitat loss for a species of special concern. Regulatory agencies such as the USDI Fish and Wildlife Service often adopt a short-term, risk-averse position (Irwin and Thomas, 2002), in which active management is seen as possible “take” of the species. Comments received by the USDA Forest Service during the Sierra Nevada Forest Plan Amendment process suggest concern over the intensity of treatments in key areas such as protected activity centers for owls and the extensive scope of proposed fuels management activities (USDA, 2004, vol. 2). To be effective, a fuels management program must be extensive and inclusive (Agee et al., 2000), which raises the potential for broad-scale application of treatments to have negative cumulative impacts. Clearly, there is no consensus among the public or scientific community on this topic, and empirical data to evaluate cumulative effects of broad-scale efforts to reduce fuels are lacking.

Questions of short-term versus long-term risks, intensity of treatments, and cumulative effects lend themselves to scientific scrutiny. Indeed, the remarkable literature on spotted owls and the forests that they inhabit make them ideal candidates for rigorous analysis (see Noon and Franklin, 2002, and references therein). The immediacy of the fire threat creates an urgency to act even as key uncertainties remain. Models are needed that will permit quantitative exploration of potential risks. Here, we demonstrate an analytical approach that uses available data and tools to explore key questions related to the tradeoffs among short- and long-term risks of managing wildland fire, fuels, and owls. Our analysis focuses on the relationship between forest structure and reproductive success at the scale of the nesting territory, and models potential vegetation changes at the stand and landscape levels. The interrelated nature of these questions highlights the need for comprehensive, place-based assessments.

1.1. Forest structure and life history traits

Demographic modeling of spotted owls suggests that long-term persistence may be most sensitive to the level of adult survival (Noon and Biles, 1990). Empirical studies of adult survival have shown relatively high rates (>0.8) that do not exhibit large spatial or temporal variability, limiting the ability to demonstrate a measurable effect of habitat. This is not equivalent to saying an effect is not present. Spotted owl demographic studies are observational in nature; all owls are free to select where they spend time nesting, roosting, or foraging. Multiple studies consistently show that owls spend a disproportionate amount of time in areas with relatively dense canopy and older trees, and nests are found disproportionately in older stands (Verner et al., 1992). Preference use by owls has led some researchers to categorize areas into broad classes of nesting, foraging, or non-use habitat based primarily on vegetation characteristics. Franklin et al. (2000) demonstrated that apparent survival of northern spotted owls improved when the core area surrounding the nest (0.71-km radius circles) had a higher proportion of “owl habitat,” defined as dense stands (>70% canopy cover (CC)) with a mix of larger conifers and hardwoods (sensu Solis and Gutiérrez, 1990). Noting the low spatial variability across the study area, however, they suggested an “all-or-nothing-defense” hypothesis. They reasoned that once an owl locates a territory with adequate habitat to ensure high survival, the owl defends it against conspecific intruders. Because their study focused on territorial birds, low variability in survival is consistent with this hypothesis. Recent research based on radio tracking of adult owls suggests that topography, distance to water, and distance from the nest tree also contribute to habitat use by owls (Haufler and Irwin, 1994; Irwin et al., 2003). Undoubtedly, interspecific interactions with predators and competitors like the barred owl (Strix varia) also play a role (Kelly et al., 2003). As our understanding of owls increase, our ability to build predictive models for survival should improve.

While adult survival is key to long-term trends, annual variability and short-term trends in population numbers are driven primarily by fluctuations in reproduction and fledgling survival (Franklin et al., 2000, 2004; Blakesley et al., 2001; Seamans et al.,
Multiple studies demonstrate a high degree of variation in year-to-year production of young. The search for causal factors behind the variation consistently points to weather as a primary driving factor (Franklin et al., 2000; North et al., 2000; Ward, 2001; Seamans et al., 2002). Differences between studies, whether it is precipitation and temperature during the nesting period (North et al., 2000) or rainfall in the previous year (Seamans et al., 2002), suggest alternative mechanisms through which weather influences reproduction. Habitat quality can moderate or mitigate the effect of weather to varying degrees and affect the average productivity of a site. In a study of vegetative structure at the nest site, North et al. (2000) found reproduction to be higher at sites with greater above-nest foliage volume. Spatial position also may be important; Irwin et al. (2003) suggested that topography and proximity to productive riparian zones might influence reproductive success.

Quantitatively linking reproductive success to habitat conditions has proven challenging. Franklin et al. (2000) described a complex interaction of habitat quality and distribution that partially explains spatial variation in reproductive success. The habitat covariables in their model, which was derived through a sophisticated search of 177 candidate models, explained 75% of the spatial process variation. Interestingly, the best-fitting model included positive relations with the amount of edge between owl habitat and non-owl habitat. Higher reproductive success was noted in sites with intermediate numbers of owl habitat patches intermixed with non-habitat areas. By comparison, Blakesley (2003) found little effect of habitat in the ponderosa pine and mixed conifer forests in the northern Sierra Nevada near Mount Lassen. Using a modeling approach similar to Franklin et al. (2000), Blakesley (2003) reported a model of reproductive output that includes a year effect and negative relations with elevation and amount of non-owl habitat within the nest area. The coefficient for non-habitat was only 1.5 standard errors removed from zero, however, providing weak evidence of a relation. The addition of the non-habitat term explained little variation in reproduction ($R^2 = 0.25$) beyond that explained by a model with year and elevation alone ($R^2 = 0.24$). The Blakesley (2003) study highlights the difficulties of elucidating habitat relations in areas where the differences in habitat suitability may be subtle and not captured in relatively coarse measures of forest structure and composition. Differences in primary prey species between the Franklin et al. (2000) and Blakesley (2003) study sites also might affect habitat relations (Zabel et al., 1995).

A long-term demographic study of California spotted owl nest sites in the Sierra National Forest (Steger et al., 2002) provided data for an influential study of the effects of forest structure on spotted owl reproduction by Hunsaker et al. (2002). Hunsaker et al. (2002) reported a positive correlation ($r = 0.37$) between the amount of the 430-ha area surrounding nest and roost sites with >50% canopy cover (measured using photointerpretation) and a productivity score assigned to each site based on owl occupancy and reproduction. This finding, combined with the Bart (1995) conclusion that 30–50% of owl territories should be in suitable owl habitat to ensure replacement, motivated many of the protective measures incorporated in regional forest plan amendments for national forests within the Sierra Nevada (USDA, 2001).

Our objective in this paper is to demonstrate a process for risk assessment that uses existing information to quantify the threat to spotted owls of proposed forest thinning activities. The data used in the Hunsaker et al. (2002) analysis are particularly useful from the standpoint of examining competing risks because they fit the classification scheme used in regional vegetation mapping and analysis processes. Potentially one can use the same data to make informed judgments regarding both suitability for owls and fire risk.

### 2. Methods

Our approach to assessing risk involved two major steps. First, we examined the data from Hunsaker et al. (2002) to explore relations between canopy cover at the territory level and owl reproduction. We used these data to build a probabilistic model of juvenile production that incorporates interannual variation and habitat composition based on canopy cover. We then used an existing model of vegetation dynamics to model decadal changes in forest structure for synthetic, archetypical nest territories to illustrate
the magnitude of change that might be expected under different management and disturbance scenarios. The combination of results from these two steps indicates the magnitude of change in landscape conditions that might be expected, and how such change might influence owl reproduction.

2.1. Canopy cover and reproduction

Each spring from 1990 to 1998, 33 California spotted owl territories on the Sierra National Forest were systematically surveyed to determine occupancy, nesting success, and fledgling success; another 16 territories were monitored from 1994 to 1998. Study areas and owl survey methods are best described in Steger et al. (2002). Hunsaker et al. (2002) used reproductive data from these surveys to assign an annual index of reproduction (RPI) to each territory. RPI values were assigned based on one point for each adult or fledgling, plus two points for a nesting attempt, plus two additional points if young were fledged. Thus, annual RPI values came from the set {0, 1, 2, 4, 7, 8, 9}, ranging from no owls observed to a pair of adults and three fledglings. Sixteen territories were surveyed in all nine years, while others were missed in various years due to logistical problems. Average RPI scores were calculated by simply averaging over the years each territory was observed. Hunsaker et al. (2002) also used photointerpretation (PI) and satellite imagery (Landsat) to classify the landscape surrounding a central location (activity center) based on nesting and roosting sites in each territory. Estimates of canopy cover were divided into classes of 0–19%, 20–39%, 40–49%, 50–69%, and 70–100% CC. For each site, the percentage of the total area within each CC class was tabulated for concentric circles centered on the activity center and circumscribing 72, 168, and 430 ha. Hunsaker et al. (2002) equated these areas with estimated 50, 70, and 90% owl use areas using radio telemetry data from a subset of owls studied from 1987 to 1990 on the Sierra National Forest. Relationships between CC and reproduction were quantified through Pearson correlation coefficients calculated using the average RPI score and the percentage of the surrounding circle with ≥50% CC. Coefficients were reported for both Landsat and PI measurement techniques for all three circles.

The strongest correlation reported \((r = 0.37)\) involved canopy cover measured using PI in a 430-ha area. Thus, we limited our analysis to the 430-ha PI data, made available by George Steger (Pacific Southwest Research Station, Fresno, CA). A preliminary examination of the data suggested three relatively simple modifications of the Hunsaker et al. (2002) analysis. First, it seemed appropriate to adjust the average reproductive value to remove potential bias introduced by not sampling every territory every year. Some years had substantially higher overall reproductive success than others, and if territories were observed disproportionately in better or worse than average years, the mean values assigned to each would reflect this sampling bias. An adjustment was made by: (1) calculating an annual mean RPI value across all territories observed in a given year; (2) calculating an expected value for each territory by averaging the annual mean RPI values for the specific years in which a given territory was observed; and (3) calculating an overall adjusted RPI value by subtracting the territory-specific expected value from the arithmetic mean observed value.

The second modification was based on the observation that a nesting attempt was never observed in 16 of the 49 territories. That is, single or pairs of birds were observed periodically, but observed pairs were not recorded as having actively tried to nest. We labeled these territories “non-reproductive” to distinguish them from the “nest” territories where reproductive attempts were observed. Subsequent statistics were calculated separately for nest and non-reproductive territories to help elucidate differences between them.

The third modification was to group the 40–49% CC class with the ≥50% CC class rather than with the <39% CC class. There are two reasons for this regrouping. First, the correlation with the adjusted mean RPI value is stronger when the 40% CC break point is used \((r = 0.41 \text{ versus } r = 0.35)\), suggesting that the 40–50% CC class may help explain differences in observed reproduction. Second, the 40% CC threshold is useful when discussing fire risks and fuels treatments. In the Sierra Nevada, 40% canopy cover has been identified as a general rule-of-thumb for an upper bound on post-treated stands to minimize the probability of sustained crown fire, although “adjustments in stand density based on local condi-
tions certainly are appropriate” (Weatherspoon and Skinner, 1996).

The next step in our analysis was to examine whether further partitioning of the territories based on canopy cover might reveal useful patterns or relationships. The proportion of the territory with ≥40% CC was divided into two measures, 40–69% CC (intermediate CC), and >70% CC (dense CC). Our three-way classification into sparse (<40% CC), intermediate, and dense CC uses standard forest inventory breakpoints and matches Blakesley (2003) categorization of poor, normal, and good canopy classes. The 70% level also matches the Franklin et al. (2000) breakpoint for “owl habitat.” We also assessed possible differences between sites that were part of the original sample beginning in 1990 (Study A), versus the second group that was first observed in 1994 (Study B).

We next built an influence diagram (model) that accounts for both the influence of canopy cover at the territory level and annual variation in reproduction that affects all territories. In simplest terms, an influence diagram is a graphical, quantitative model that expresses causal or temporal relationships among various nodes in terms of conditional probabilities, including explicit decision choices (Pearl, 1988; Clemen, 1996). Influence diagrams are a form of Bayesian belief networks; the probabilistic axioms underlying both are well established in statistics and decision science (Pearl, 1988; Jensen, 2001). Examples of their use in ecological risk assessments include Lee and Rieman (1997), Rieman et al. (2001), and Marcot et al. (2001). We built our influence diagram using the Netica software system (Norsys Software Corp., http://www.norsys.com).

The objective of our model is to calculate a probability distribution for the number of fledglings produced at a randomly chosen owl territory, given the distribution of canopy cover in the chosen territory, and the expectation based on population-wide annual productivity. We used the annual observations of each territory to generate conditional probability distributions for the number of adults and fledglings observed on each territory. These conditional probability tables quantify the relationships between nodes in the model; directed arrows indicate causal dependencies graphically. As depicted in Fig. 1, the model has a single root node, modal productivity, which is not causally dependent on other nodes. Modal productivity is a binomial variable [poor, good] that indicates whether the number of owl pairs that produce young equals or exceeds the number that do not successfully reproduce (good years), or vice versa (poor years). Territory is also a root node, but it is causally dependent on the decision node, choose conditions. Territory denotes the composition of the landscape in terms of canopy cover, assigning territories into one of three classes. The breakpoints for the classes are based on an upper threshold (0.55) for sparse CC (<40% CC) and the approximate median proportion (0.4) of dense CC (≥70% CC):

$$\text{If sparse CC} > 0.55, \text{then territory} = \text{“Non-RPD”}. \\
\text{Else if} \{\text{sparse CC} < 0.55 \text{and dense CC} < 0.4\}, \\
\text{Then territory} = \text{“Moderate”}.
\text{otherwise, territory} = \text{“High”}.$$

Thus, “Non-RPD” denotes territories with a higher proportion of sparse CC where no successful reproduction was observed, “High” indicates territories with a larger proportion of dense CC, and “Moderate” denotes territories with an intermediate mix of CC classes. Choose conditions has three options: “Base case,” in which probabilities are assigned to territories following the frequency observed in the original data (i.e., 6% non-RPD, 43% moderate, and 51% high), and “Moderate” and “High,” in which the territory in
question is either in the moderate or high class, respectively. The number of adults at a site \( \{0, 1, 2\} \) is conditionally dependent on territory. Number of fledglings \( \{0, 1, 2, 3\} \) is conditionally dependent on modal productivity, number of adults, and territory. The utility node, expected fledglings, is simply the weighted average calculated from number of fledglings. The value of the utility node is reflected in the decision node, i.e., the model calculates the expected number of fledgling for each level of choose conditions and reports that in the graphical output.

2.2. Modeling vegetation dynamics

An understanding of vegetation dynamics is essential for anticipating how a blend of management activities and natural disturbances might affect owl habitat over the longer term. We used a probabilistic model of forest stand dynamics, BayVeg, to explore potential trajectories for nest territories experiencing different management and disturbance regimes. BayVeg was developed initially for use in planning for forest plan amendments in the Sierra Nevada (USDA, 2000, Appendix B). BayVeg is an influence diagram model that was parameterized using simulation results from the GAMMA vegetation simulation model developed by Larry Wilson (personal communication, Mason, Bruce, and Girard Inc.). GAMMA is a variant of the Forest Vegetative Simulator model, the USDA Forest Service’s nationally supported framework for forest growth and yield modeling (see Dixon, 2002, and references therein; also http://www.fs.fed.us/fmsc/fvs/). GAMMA is capable of using stand-inventory information to simulate detailed changes in stand composition and structure through time under various treatment prescriptions or disturbance regimes. Each prescription includes retention or cutting rules for management prescriptions as well as natural mortality and growth factors.

The GAMMA simulations used prescriptions developed by the USDA Forest Service, Region 5, and forest inventory data from 211 inventory plots on the seven Sierra Nevada national forests within the range of the California spotted owl (Klaus Barber, USDA Forest Service, personal communication). The Forest Inventory and Analysis (FIA) program managed by the Pacific Northwest Research Station collected and processed the initial inventory data (see http://www.fs.fed.us/pnw/fia/). For a single model run, GAMMA is a deterministic model that produces fixed outputs for a given set of input data and parameters. A probabilistic set of corresponding inputs and outputs were generated by using multiple input files, one for each inventory plot, where multiple plots were available for each forest stratum. The BayVeg model tracks forest conditions in terms of 12 strata, representing various combinations of mean tree size and canopy cover (Table 1). The BayVeg strata are

<table>
<thead>
<tr>
<th>CWHR class</th>
<th>Description</th>
<th>Mean tree DBH (cm)</th>
<th>Canopy cover (%)</th>
<th>Proportion in each archetype*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Non-RPD</td>
</tr>
<tr>
<td>2X</td>
<td>Saplings</td>
<td>2.5–15.2</td>
<td>0–100</td>
<td>0</td>
</tr>
<tr>
<td>3S</td>
<td>Pole trees</td>
<td>15.2–27.9</td>
<td>10–39</td>
<td>0.031</td>
</tr>
<tr>
<td>3M</td>
<td></td>
<td>≥40</td>
<td></td>
<td>0.011</td>
</tr>
<tr>
<td>4S</td>
<td>Small trees</td>
<td>27.9–61.0</td>
<td>10–24</td>
<td>0.089</td>
</tr>
<tr>
<td>4P</td>
<td></td>
<td>25–39</td>
<td></td>
<td>0.204</td>
</tr>
<tr>
<td>4M</td>
<td></td>
<td>40–59</td>
<td></td>
<td>0.137</td>
</tr>
<tr>
<td>4D</td>
<td></td>
<td>≥60</td>
<td></td>
<td>0.065</td>
</tr>
<tr>
<td>5S</td>
<td>Medium/large trees</td>
<td>&gt; 61</td>
<td>10–24</td>
<td>0.056</td>
</tr>
<tr>
<td>5P</td>
<td></td>
<td>25–39</td>
<td></td>
<td>0.246</td>
</tr>
<tr>
<td>5M</td>
<td></td>
<td>40–59</td>
<td></td>
<td>0.042</td>
</tr>
<tr>
<td>5D</td>
<td></td>
<td>≥60</td>
<td></td>
<td>0.006</td>
</tr>
<tr>
<td>6X</td>
<td>Multilayer canopy</td>
<td>&gt; 61</td>
<td>≥60</td>
<td>0.113</td>
</tr>
</tbody>
</table>

Proportions under each territory heading (non-rpd, moderate, high) sum to 1.0.

* Archetypical territories were assumed to have a mix of canopy cover conditions represented in a proportional distribution of CWHR classes.

The vegetation type is Sierran mixed conifer.
based on the California Wildlife Habitat Relationships System (CWHR, Mayer and Laudenslayer, 1988; see also http://www.dfg.ca.gov/whdab/html/cwhr.html). We limited our analysis to the Sierran mixed conifer vegetation type (Tappeiner, 1980); inventory plots suggested a diverse mix of stands containing Ponderosa pine (P. ponderosa), sugar pine (P. lambertiana), Douglas fir (Pseudotsuga menziesii), incense cedar, California black oak (Quercus kelloggii), and other associated species in varying proportions.

Our analysis included three prescriptions: no treatment, light mechanical thinning, and heavy mechanical thinning. The light mechanical thinning prescription paired mechanical treatment with prescribed burning and was designed to remove small-diameter trees, shrubs, and other surface fuels such that low-severity wildland fires or prescribed fire have a reduced chance of escalating or escaping. The heavy thinning prescription is more appropriate for defensive fuel protection zones (DFPZ) or other area treatments where the intent is to change wildland fire behavior and enhance fire suppression effectiveness. Both thinning prescriptions leave the larger trees regardless of species. Two disturbances were also included: lethal fire that killed most live trees, and mixed-lethal fires that mimicked a 6-foot flame length, which kills trees based on tree size and species-specific mortality coefficients. The individual tree mortality modeled in GAMMA is captured more simply in BayVeg as a transition (if it occurs) in CWHR stratum for the modeled stand as a whole. Initial conditions in BayVeg are defined as either a single CWHR stratum or a probabilistic mix of strata; various decision choices are made regarding treatments and effectiveness of fuel reduction strategies; and the model updates

![Influence diagram of the BayVeg model’s logic structure.](image)

**Fig. 2.** Influence diagram of the BayVeg model’s logic structure. Nodes in the upper portion of the diagram represent sequential events including stand treatments and possible disturbance events that can occur over 6 decades. The lower nodes contain histograms that reflect the probabilities of a randomly selected stand being assigned to a given California Wildlife Habitat Relations (CWHR) habitat strata, and the change in these probability distributions over 6 decades (time 1–6). CWHR strata are defined in Table 1.
probability vectors for forest conditions for up to 6 decades into the future (Fig. 2).

To simulate changes in owl territories, three archetypical territories were created that would be representative of the three habitat classes (non-RPD, moderate, or high) indicated in the canopy cover analysis. Each archetype was based on an actual data point randomly chosen from each class and assigned a distribution of CWHR habitat strata consistent with its observed canopy cover distribution. The assigned distributions were generated by scaling the overall distribution of CWHR strata in the mixed conifer type from forests of the Sierra Nevada based on forest inventory data. For example, if the proportion of the archetype in sparse CC = 0.32, then the Sierran-wide distribution of corresponding CWHR density strata were multiplied by a normalizing constant such that they summed to 0.32 (Table 1). Because ≥60% CC distinguishes the highest density strata in the CWHR system, the proportions in these strata were assigned to the dense CC category. The net result was that each archetype contained some proportion of all of the CWHR strata in mixed conifer, and only mixed conifer. Thus, they reflect a condition that is unlikely to be mimicked in the real world (i.e., there is no single territory that matches the range-wide average), but do serve as useful caricatures for simulation.

Seven scenarios were created and applied to each archetype. The scenarios included:

1. No treatment or major fire for 6 decades.
2. Light mechanical thinning on the entire territory in the first decade, retreatment every 2 decades, no major fire.
3. Light mechanical thinning on 80% and heavy thinning on the remaining 20% of the territory in the first decade, retreatment every 2 decades, no major fire.
4. Scenario 1, with a mixed-lethal fire in the second decade.
5. Scenario 2, with a mixed-lethal fire in the second decade.
6. Scenario 3, with a mixed-lethal fire in the second decade.
7. Lethal fire in the first decade.

The BayVeg model contains chance nodes that allow for random disturbances. These nodes were all set such that only the planned disturbances (mixed-lethal or lethal fire) occurred in each scenario.

3. Results

3.1. Canopy cover and reproduction

Our year-adjusted mean RPI value showed a positive correlation with the proportion of the 430-ha territory with ≥50% CC (r = 0.35), a result similar in magnitude to that reported by Hunsaker et al. (2002). Regressing the adjusted RPI on the proportion with ≥50% CC produced an estimated slope of 3.34 ± 1.29, but explained less than 13% of the variation (Fig. 3). Separating nest territories from non-reproductive territories suggested a different relationship between CC and reproduction, and improved overall fit substantially (R² = 0.62; Fig. 4). No significant relation was found between CC and adjusted RPI within nest territories when they were examined independently (estimated slope = 0.68 ± 1.76). The pattern suggested a possible minimum requirement rather than a trend, with no increasing benefit to reproduction of additional amounts of intermediate and dense CC. Intermediate and dense CC combined generally composed more than half of nest territories, averaging 70% of the territory. A logistic regression model fitted to the data suggested a lower threshold of 56% of the territory (i.e., if sparse CC < 0.56, the territory was predicted to be a nesting territory).

A significant positive trend occurred within the non-reproductive territories (estimated slope = 3.03 ± 1.22), when examined independently of nest territories. As the amount of adjoining landscape with ≥40% CC increased, non-reproductive territories more often were occupied by a pair of owls in a given year.

Aspects of the sampling scheme that might introduce bias clearly influenced classification of nesting and non-reproductive territories, and hence any subsequent estimates of relationships. Fifty-six percent of the territories that were added to the surveys in 1994 (Study B) were classified as non-reproductive, compared to 21% of the original (Study A) territories. Study B territories often were visited later in the season due to logistical difficulties of accessing these sites (George Steger, USDA Forest Service, personal communication). Some owl pairs could have
attempted to nest and were unsuccessful prior to being observed. Thus, they would have been recorded erroneously as “not nesting.” Study B territories also were not observed in the exceptional reproductive year of 1992. Of the 26 nest territories in Study A, 4 (15%) were classified as nesting based solely on nesting attempts observed in 1992; nesting was not observed in other years.

Fig. 3. Adjusted mean reproductive index (RPI) for 49 California spotted owl (Strix occidentalis occidentalis) territories in the Sierra National Forest plotted against the proportion of 430-ha area surrounding the center of activity with canopy cover estimated to be ≥50%. Solid line indicates linear regression line fitted to data (slope = 3.34 ± 1.29, $R^2 = 0.12$).

Fig. 4. Adjusted mean reproductive index (RPI) values plotted against the proportion of each 430-ha territory with canopy cover estimated to be ≥40%. Nest territories are in shaded circles, non-reproductive territories are in open circles, and lines represent linear regressions fitted to each subset independently. Size of circle reflects the expected RPI value for a given territory based on years sampled (larger circle = higher expected value).
A bubble plot of the territories and their adjusted mean RPI values in the triangular space defined by the proportion in sparse, intermediate, and dense CC suggests some differences between sampling areas (i.e., Study A versus Study B), but also overlap in composition (Fig. 5). The four territories with the highest proportion of dense canopy occurred within Study B. In contrast, Study A had 13 territories with levels of intermediate CC that exceeded the highest level observed in Study B. The greatest variation among all territories occurred along the dense CC axis. Our decision to subdivide territories further based on the median dense CC value (ca. 40%) reduced intraclass variation while maintaining relatively equivalent sample sizes in each class. Prior exploratory analysis of the data did not lead to any useful parametric models that could explain the observed variation in reproductive success.

Parameterization of the influence diagram involved 325 observations of various combinations of territory, adults, and fledglings. The influence diagram allows comparisons of the relative advantages of different territories or combinations thereof under fixed or probabilistic conditions. For example, Fig. 6 depicts the relative frequency of the various nodes exhibited in the original data set under the condition, “Base case,” and shows an expected number of fledglings per territory per year of 0.463. In comparison, Fig. 7a and b display expectations under good and poor year scenarios, respectively, for each option under choose conditions. In the “good years” most pairs attempted to nest and successful nests more often produced twins; in the “poor year” most pairs did not nest and most of those that did were unsuccessful at fledging young. Table 2 summarizes the results under these scenarios and demonstrates...
substantial differences due to fluctuating annual conditions relative to differences between territory conditions. The standard errors in Table 2 reflect the expected variation in mean values if a sample of 49 sites is taken. Based on the standard errors, we found no measurable differences in expected number of fledglings between moderate and high territories in a given year, while good years would be readily distinguishable from poor years.

3.2. Vegetation modeling

We used the BayVeg model to generate probability vectors for each CWHR class, decade, and scenario

Table 2

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Territory option</th>
<th>Expected fledglings</th>
<th>Standard deviation</th>
<th>Standard error</th>
<th>Difference from base</th>
<th>Normalized to base</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mix of years</td>
<td>Base case</td>
<td>0.463</td>
<td>0.90</td>
<td>0.13</td>
<td>0.000</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>0.489</td>
<td>0.93</td>
<td>0.13</td>
<td>0.026</td>
<td>1.06</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.497</td>
<td>0.91</td>
<td>0.13</td>
<td>0.034</td>
<td>1.07</td>
</tr>
<tr>
<td>Good year</td>
<td>Base case</td>
<td>1.066</td>
<td>1.10</td>
<td>0.16</td>
<td>0.603</td>
<td>2.30</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>1.129</td>
<td>1.20</td>
<td>0.17</td>
<td>0.666</td>
<td>2.44</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1.142</td>
<td>1.10</td>
<td>0.16</td>
<td>0.679</td>
<td>2.47</td>
</tr>
<tr>
<td>Poor year</td>
<td>Base case</td>
<td>0.237</td>
<td>0.68</td>
<td>0.10</td>
<td>−0.226</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>0.249</td>
<td>0.70</td>
<td>0.10</td>
<td>−0.214</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.255</td>
<td>0.69</td>
<td>0.10</td>
<td>−0.208</td>
<td>0.55</td>
</tr>
</tbody>
</table>

a Based on a presumed sample of 49 independent sites (i.e., S.E. = S.D./7).
b Mixed based on observed frequency in original data (poor = 73%, good = 27%).
c Assumes that the number of adult pairs that produce young is equal to or exceeds the number of pairs that produce no young in a given year.
d Assumes that the number of adult pairs that produce no young exceeds the number of pairs that produce young in a given year.
These vectors were used to map each archetype, scenario, and decade combination to plot a trajectory within a triangular plot based on canopy cover distribution (Fig. 8a–c). As expected, lethal fire resulted in the most pronounced change in canopy cover. The no treatment, light thinning, and light thinning plus DFPZ treatments had similar trajectories that were offset from each other, consistent with the
amount of canopy removed in the treatment sequence. The mixed-lethal disturbance had an effect greater than any of the mechanical treatments by themselves. Following the mixed-lethal disturbance, trajectories resumed in the general direction of the corresponding no-disturbance trajectory. All trajectories beginning in the “Non-RPD” zone (other than lethal fire) reached the “Moderate” reproductive zone by the end of the sixth decade. Trajectories beginning within the “Moderate” zone tended to stay within or near that zone. In contrast, trajectories beginning in the “High” zone moved towards the “Moderate” zone except in the no-treatment and lethal-fire scenarios. There was little relative movement in any of the scenarios towards higher proportions of dense CC.

4. Discussion

Our analysis of the southern Sierra Nevada data and the exploration of site trajectories using the BayVeg model have potential implications for management of fire-adapted forests within the range of the California spotted owl. The reanalysis of the southern Sierra Nevada data helps to clarify the Hunsaker et al. (2002) findings. Reproductive success increases with increasing levels of canopy cover because of a higher estimated frequency of nesting pairs, rather than greater reproduction by pairs that are known to be actively nesting. The distinction between pairs that nest and are unsuccessful versus those that do not attempt to nest is key to identifying non-reproductive territories. It also substantively influences the estimated RPI value, because non-successful nesting pairs are assigned a value twice as high as a pair alone (four versus two). If errors in estimating nesting attempt are common or systematic, then inferences that rely on estimated RPI values are suspect. Both the original Hunsaker et al. (2002) study and our regression analyses share this problem.

The influence diagram that we constructed avoids potential errors in estimating nesting attempts by
Fig. 8. (Continued).
looking directly at the conditional dependence between number of adults and number of fledglings. This simplification potentially loses some explanatory power that might arise from having a separate event node, “nesting attempt.” Alternative versions of our model had such a node, but we discarded them due to the identified bias in the data set. Note also that our analysis was limited to occupied sites; we had no basis in these data to discern how the observed sites would differ from a distribution of 430-ha circles placed at random on the landscape.

The influence diagram of fledgling production provides a useful tool for discerning patterns in the data and for demonstrating the relative importance of canopy cover versus weather or other regional environmental factors driving annual variation. The maximum expected gain in fledgling production from changing canopy cover alone was 7% (Table 2), which came primarily from improving non-RPD territories. In contrast, the average production in good years was 130% greater than the overall average, and 351% greater than in poor years. The singular influence of the 1992 brood year on recent population trends in the Sierra Nevada is well recognized (Franklin et al., 2004). Barring unforeseen and dramatic changes, near-future trends in population numbers likely will respond more dramatically to the frequency of good reproductive years than regional changes in canopy cover.

We recognize that reliance on canopy cover as a sole explanatory variable invites its own measurement problems. Hunsaker et al. (2002) clearly demonstrated that conclusions about canopy cover and owl reproductive success vary depending on whether aerial PI or Landsat data are used. Field comparisons among various ground-based methods and with PI raise further questions regarding the accuracy of PI estimates (Landram and Baldwin, 2002). If management guidelines are to incorporate canopy cover thresholds, then canopy cover and its measurement must be defined in a way that can be rigorously measured in the field.

Forecasting changes in vegetation conditions at appropriate scales, and linking the simulated changes to habitat features important to owls is essential to elucidating risk. Our use of the BayVeg model in combination with a single surrogate for site quality may oversimplify the issue, but it illustrates the types of analyses that are possible with interdisciplinary collaboration. Reliable forest dynamic models often are inaccessible to wildlife biologists or operate at inappropriate scales, making quantitative risk assessment problematic. The BayVeg model demonstrates one approach to making sophisticated forest dynamics models available to a wider set of users; we encourage further development in this direction.

Our study was motivated by concerns about proposed fuels treatments possibly having a negative effect, either short- or long-term, on spotted owls through reductions in canopy cover at the landscape scale. We focused on the types of treatments that have been proposed in the Sierra Nevada to reduce the risk of wildland fire by removing ground fuels and forest understories; we did not analyze silvicultural prescriptions to improve timber production, clear-cutting, or other intensive timber harvest methods. Our scenarios were more severe than proposed management direction (e.g., USDA, 2004) in that we did not avoid known owl activity centers or preferentially locate treatments based on existing stand conditions or topography.

The general trend of all scenarios except lethal fire was towards higher proportions of intermediate CC (40–69% CC) and lower proportions of sparse CC (0–39% CC). The mechanical thinning and mechanical thinning plus DFPZ construction scenarios resulted in less of the dense canopy class (70–100%), but equal or more amounts of intermediate canopy levels than the let-grow scenario through time. Mixed-lethal fire produced a pronounced effect in the decade that the simulated fire occurred (the second decade), which was still discernible 4 decades later. None of the simulated trajectories moved beyond the range of observed variation in the original data, suggesting that expected effects on owl reproduction would be essentially immeasurable. Our simulation results lend credence to the hypothesis that modest fuels treatments are compatible with territory-level canopy cover needs for spotted owl reproduction in the Sierra Nevada. We encourage empirical testing of this hypothesis.

The risk of wildland fire arises from a multitude of factors (e.g., live and dead fuels, forest structure, weather, topography, ignition sources). The same is true of site suitability for owls. Our analysis of fire effects was relatively simple and did not address...
complex fire behavior characteristic of most landscapes. Similarly, complex habitat elements important to owls were not analyzed here, such as nest trees with particular features and location of nests with respect to topography. Our analysis did not examine the spatial relationship of stands with different canopy classes within a territory (sensu Franklin et al., 2000), nor can we judge the preferential use or relative contribution of each stand type. We focused on reproduction because of its key role in population trends, but recognize that adult survival is also critical to long-term owl persistence. The entire complex of factors affecting owls should be considered when designing and implementing thinning projects in order to minimize risks to owls.

The complex interaction of fire and owls requires that risk assessments be site-specific to the extent practical. It also suggests the possibility of multiple options to reduce risks of fire to other resources while mitigating non-fire risks to owls. Greater appreciation is needed of the multiscale attributes of owl habitat and how they are created or maintained by characteristic fire regimes, or (potentially) the interaction of fire and active management. Additional development of risk-based tools for project-level planning could help explore various options.

Our analysis points to several hypotheses that would be amenable to empirical testing. For example, we found that the mix of intermediate and dense CC is relatively unimportant to spotted owl reproduction as long as the sum of the two composes the bulk of the owl territory. Treating territories to achieve a predetermined ratio may not have an identical effect, however, as the serendipitous combination of factors that shaped the landscapes examined here. We agree with Noon and Franklin (2002) that carefully designed manipulative experiments could advance understanding faster than relying on observational studies alone. We also recommend making previously collected data sets more widely available. Our analysis of the southern Sierra Nevada data illustrates the advantages of multiple researchers examining the same data.

Acknowledgments

We thank George Steger, Jared Verner, Carolyn Hunsaker, and Brian Boroski for generously sharing their data, time, and understanding of California spotted owls in the southern Sierra Nevada. Klaus Barber, Larry Wilson, and Andy Taylor were instrumental in helping to gather and format the data needed to build the BayVeg model. We thank them for their effort, and their patience in explaining the FVS and GAMMA models to us. We especially thank Jim Baldwin, William Laudenslayer, George Steger, Tom Munton, and two anonymous reviewers for their useful comments on the manuscript. Partial funding for this effort was provided under the National Fire Plan, Project 01.PSW.A.1.

References


