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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.
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1. Introduction

Concerns for the viability of spotted owls (*Strix occidentalis*) profoundly influence forest management in the western United States. Conservation

* Corresponding author. Tel.: +1 707 825 2965; fax: +1 707 825 2901.
E-mail address: dclee@fs.fed.us (D.C. Lee).

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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 firs, 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). Preferential 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.,

2002). 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 covariates 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 $\geq$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 $\geq$50% CC class rather than with the $<$39% CC class. There are two reasons for this regrouping. First, the correlation with the adjusted mean RPI value is stronger when the 40% CC breakpoint is used ($r = 0.41$ 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

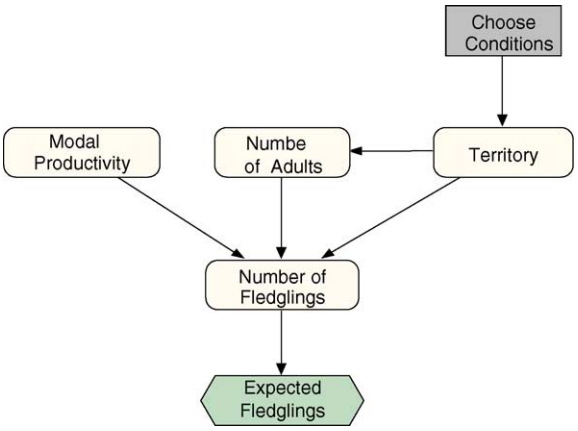

Fig. 1. Graphical model of influence diagram of California spotted owl (*Strix occidentalis occidentalis*) fledgling production as affected by territory canopy conditions and annual patterns in productivity. The shaded node, ''Choose Condition,'' is a decision node; ''Expected Fledglings'' is a utility node; all other nodes are chance nodes. Arrows indicate causal dependencies, i.e., the receptor node is conditionally dependent on the state of the donor nodes.

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):

If sparse CC > 0.55, then territory = ''Non-RPD''.
Else if {sparse CC < 0.55 and dense CC < 0.4}.
  Then territory = ''Moderate''.
otherwise, territory = ''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 1
California Wildlife Habitat Relationship (CWHR) forest classes used in the BayVeg model and initial proportions assigned to the archetypical territories for simulation

CWHR class	Description	Mean tree DBH (cm)	Canopy cover (%)	Proportion in each archetype[a]		
				Non-RPD	Moderate	High
2X	Saplings	2.5–15.2	0–100	0	0	0
3S	Pole trees	15.2–27.9	10–39	0.031	0.018	0.016
3M			≥40	0.011	0.008	0.018
4S	Small trees	27.9–61.0	10–24	0.089	0.053	0.045
4P			25–39	0.204	0.123	0.104
4M			40–59	0.137	0.095	0.222
4D			≥60	0.065	0.173	0.131
5S	Medium/large trees	> 61	10–24	0.056	0.034	0.028
5P			25–39	0.246	0.148	0.125
5M			40–59	0.042	0.029	0.069
5D			≥60	0.006	0.016	0.012
6X	Multilayer canopy	> 61	≥60	0.113	0.303	0.230

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

[a] 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 kellogii*), 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

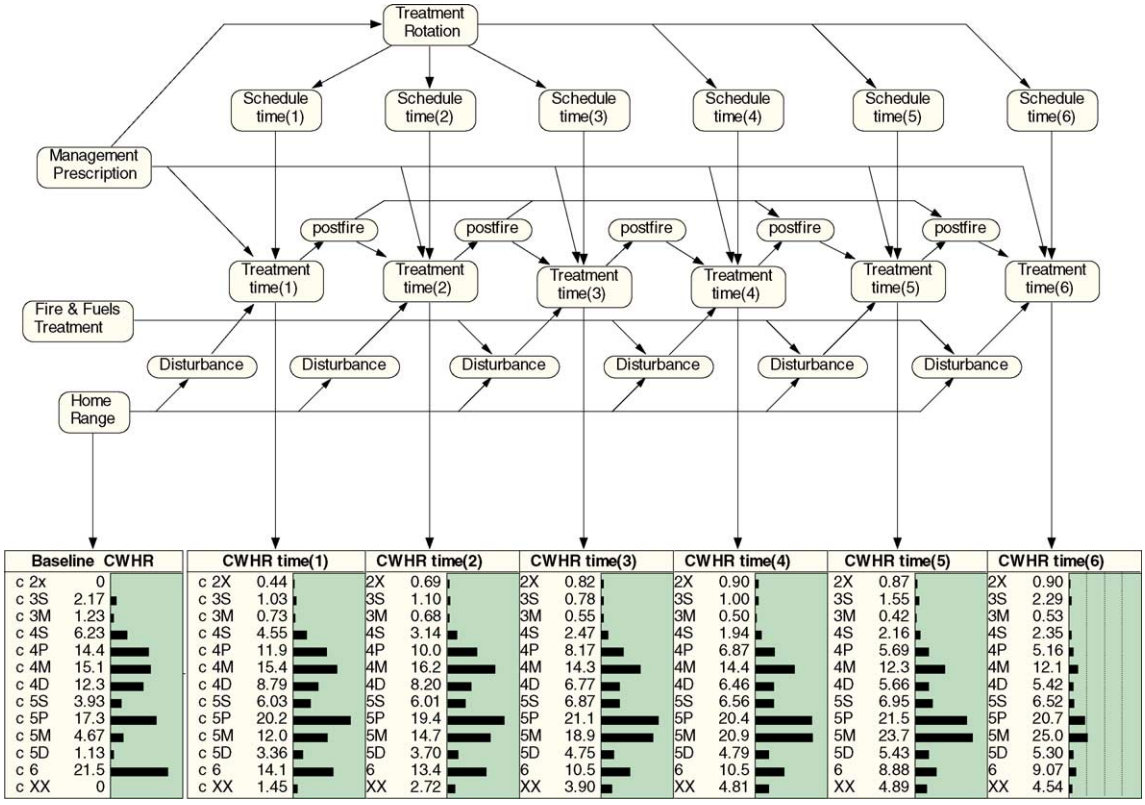

Fig. 2. Influence diagram of the BayVeg model's logic structure. Nodes in the upper portion of the diagram represent sequential events including stand treatments and possible disturbance events that can occur over 6 decades. The lower nodes contain histograms that reflect the probabilities of a randomly 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 ($R^2 = 0.62$; 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

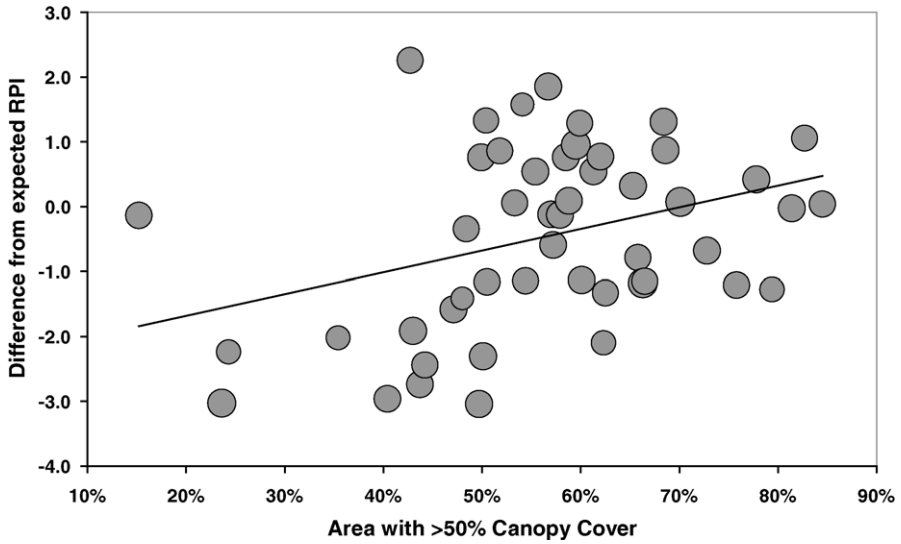

Fig. 3. Adjusted mean reproductive index (RPI) for 49 California spotted owl (*Strix occidentalis occidentalis*) territories in the Sierra National Forest plotted against the proportion of 430-ha area surrounding the center of activity with canopy cover estimated to be ≥50%. Sold line indicates linear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

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.

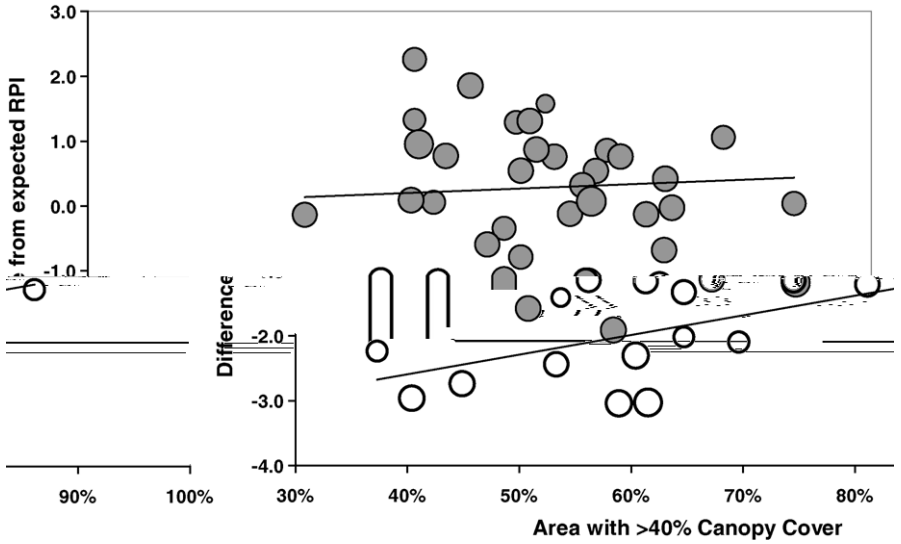

Fig. 4. Adjusted mean reproductive index (RPI) values plotted against the proportion of each 430-ha territory with canopy cover estimated to be ≥40%. Nest territories are in shaded circles, non-reproductive territories are in open circles, and lines represent linear regressions fitted to each subset independently. Size of circle reflects the expected RPI value for a given territory based on years sampled (larger circle = higher expected value).