Modeling Nesting Habitat Selection of California Spotted Owls (*Strix occidentalis occidentalis*) in the Central Sierra Nevada Using Standard Forest Inventory Metrics

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ABSTRACT. California spotted owl (*Strix occidentalis occidentalis*) nest sites are associated with large trees, moderate-to-high tree densities, high canopy cover, and structural complexity. Therefore, forest managers need accurate estimates of these characteristics. Standard forest inventory metrics, such as those estimated from Forest Inventory and Analysis (FIA) data, are used by silviculturists to assess forest trends and condition, and are a source of data for assessing wildlife habitat. We estimated which FIA metrics best predicted California spotted owl nesting habitat by developing a nesting-habitat model comparing owl nest stands with randomly chosen forest stands in potential nesting habitat (stands dominated by 30–60.9- and ≥61-cm diameter trees and ≥40% cover) in the central Sierra Nevada. Number of large trees (≥76.2 cm) and canopy cover were the best predictors of owl nesting habitat. We present a nesting-habitat selection model based on our analysis. FIA metrics may be useful for quantifying California spotted owl habitat in our study area, but because forest conditions are highly variable in the Sierra Nevada, our results should be tested further in other geographic regions. FOR. SCI. 50(6):773–780.

Key Words: California spotted owl, Forest Inventory and Analysis, model selection, Sierra Nevada, *Strix occidentalis occidentalis*.

LATE SERAL STAGE FORESTS provide critical habitat for many species of wildlife and enhance biological diversity (Spies and Franklin 1996), but are among the most altered habitats in the Sierra Nevada, California (SNEP 1996). A history of selective harvesting that typically removed the largest and oldest trees from a stand has shifted tree-diameter distributions in the Sierra Nevada over the past century (McKelvey and Johnston 1992). As a result, wildlife species that are closely associated with late seral stage forests in the Sierra, such as the California spotted owl (*Strix occidentalis occidentalis*), are of management concern (Verner et al. 1992b).

A combination of large trees and high canopy cover has been found consistently at California spotted owl nest and roost sites in the central Sierra Nevada (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and

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Gutiérrez 1997). As a result of the owl's habitat associations, the USDA Forest Service adopted temporary measures to conserve the subspecies by protecting large-diameter (≥76.2 cm) trees, retaining ≥70% canopy cover in nesting and roosting stands, and retaining 50–90% canopy cover in foraging stands (Verner et al. 1992b). Later it was recognized that owls sometimes inhabit sites that were classified as mid-seral stage forest, but these sites almost always had residual large trees (Moen and Gutiérrez 1997). Residual trees are the large remnant trees in an area that has lost much of its large-tree component (Bond and Hunter 2001). To manage for California spotted owls, land managers must be able to accurately estimate important habitat metrics at stand and landscape scales.

The USDA Forest Service uses stand metrics derived from field data measured on permanent Forest Inventory and Analysis (FIA) plots to estimate forest conditions and trends at stand and landscape scales (USDA Forest Service 1994). FIA has been used for more than two decades to assess conditions and monitor changes in the quality of habitat for various wildlife species throughout the country (see references in Rudis 1991). Ohmann and Mayer (1987) and Ohmann (1992) assessed current and future availability of suitable habitat for selected wildlife species in hardwood forests by linking FIA data to habitat associations developed from the California Wildlife Habitat Relations Program.

The FIA network of plots is also a promising source of information for quantifying habitat for spotted owls. Chojnacky and Dick (2000) used FIA data to calculate stand density metrics of potential Mexican spotted owl (*S. o. lucida*) habitat in New Mexico at a landscape level, and to estimate how much habitat in the Gila National Forest met conditions of the recovery plan for that subspecies. McComb et al. (2002) developed habitat-capability models representing a range of spatial scales relative to northern spotted owl (*S. o. caurina*) nest occurrences, based on a vegetation map derived from FIA sampling. Determining which FIA metrics best predict actual nesting habitat used by spotted owls at a stand level is valuable to managers who need to decide how best to use FIA data to monitor quantity and changes in habitat at a landscape level. For example, Ohmann and Mayer (1987) noted that validation of California Wildlife Habitat Relations models about wildlife habitat preferences is necessary to improve predictions of habitat suitability made with FIA inventory data. Therefore, we investigated which of several habitat metrics that can be derived from FIA data most appropriately reflect the habitat features associated with California spotted owl nest sites in the central Sierra Nevada.

We used 2,000-m^2 rectangular plots (Krebs 1989) to sample vegetation at California spotted owl nest sites and to estimate habitat metrics that can be obtained using FIA data (*q*-factor, stand density index, large-tree density, canopy cover, Berger-Parker index, tree diameter variance). We also sampled randomly located nonowl plots in potential nesting habitat for comparison. We considered these metrics to be potential factors associated with nest-site selection based on previous research on spotted owls (Gutiérrez et al. 1992, Moen and Gutiérrez 1997, LaHaye and Gutiérrez 1999, North et al. 1999). We hypothesized that abundance of larger trees relative to smaller trees, overall stand density, density of large trees, canopy cover, and stand heterogeneity would be greater at owl nest sites than at random sites. Our objectives were to compare habitat metrics between known nest sites and randomly selected forest stands to evaluate which FIA-type metrics best predicted nesting-habitat selection by California spotted owls, and to develop nesting-habitat selection models using FIA-type metrics. Our management objective was to provide information on how FIA data could be used to quantify California spotted owl nesting habitat at a landscape level, although we acknowledge that nonhabitat factors such as a site's prey density, foraging history, and presence of predators can also influence nest-site selection.

Study Area

Our 34,627-ha Eldorado Study Area was located in the central Sierra Nevada, ~16 km northeast of Georgetown, in Eldorado and Placer counties, California. Elevation ranged from 366 to 2,257 m. The study area had cold, wet winters and hot, dry summers, with an average annual precipitation of ~130 cm (Elford 1974). Temperatures averaged 15° C at lower elevations and 13° C at higher elevations, and ranged from −1° C in winter to 35° C in summer (Elford 1974).

The study area was 63% public (USDA Forest Service) and 37% private land. Vegetation was Sierran Montane Forest (SMF: Küchler 1977). SMF was dominated by ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*) from 600 to 1,500 m. Above 1,500 m, a transition zone was dominated by red fir (*A. magnifica*). Other common tree species that occurred within the study area included sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), canyon live oak (*Quercus chrysolepis*), California black oak (*Q. kelloggii*), Pacific dogwood (*Cornus nuttallii*), and tanoak (*Lithocarpus densiflorus*).

Methods

Vegetation Sampling Using Rectangular Plots

We limited our vegetation sampling to potential California spotted owl nesting habitat within our study area because we were interested only in modeling habitat selection within these habitat types. Based on previous research on spotted owls in the Sierra Nevada, we considered potential nesting habitat to be in stands dominated by medium- (30–60.9 cm diameter at breast height [dbh]) and larger-sized trees (>61-cm dbh) with greater than 40% canopy cover (Gutiérrez et al. 1992, Verner et al. 1992a, Moen and Gutiérrez 1997). Nonowl plots were randomly located within forest stands in strata that represented potential nesting habitat (see below), but they did not occur within any known owl nest stands. Thus, we limited our inference to strata that could potentially be used by spotted owls for nesting.

The USDA Forest Service commonly uses "strata" to describe forest type. Nest sites of spotted owls in our study area have been found consistently in four strata: M3N, M3G, M4N, and M4G, where M = westside mixed conifer; 3 = dominated by medium trees 30.5–60.9 cm dbh, and 4 = dominated by larger-sized trees ≥61 cm dbh; and N = 40–69% canopy and G = ≥70% canopy. Therefore, we investigated nest-site selection using the criteria for these four strata. We used a USDA Forest Service geographic information system (GIS) map developed from 1996 Landsat data, used by the FIA program and provided to us by the USDA Forest Service Remote Sensing Lab, Sacramento, California, to identify the four strata in which to locate our random plots. The GIS map assigned each polygon, which represented a land form or forest stand, to a tree-size class and canopy-cover class. Because the GIS map used a finer resolution to classify vegetation than we used to assess owl habitat (i.e., canopy cover in 10% classes and tree diameters in five classes), we collapsed canopy classes into N and G and tree-size classes into medium- and larger-sized trees using ArcView GIS 3.2 (ESRI, Inc., Redlands, CA). As a point of clarity, the USDA Forest Service defines larger-sized trees in stratum 4 as ≥61 cm dbh, whereas we defined "large" trees in our analysis as ≥76.2 cm dbh, because this size reflects the smallest-diameter spotted owl nest tree from our study area.

We initially selected 20 plots per GIS-mapped stratum to conduct an accuracy assessment of the GIS map. We selected sample plot locations from a list of random Universal Transverse Mercator (UTM) coordinates. After sampling the vegetation on the ground, we assessed the accuracy of the initial stratum designated by the GIS map and assigned the correct stratum to each plot. As part of the accuracy assessment, we sampled 79 randomly placed plots as follows: 21 plots in the M3N stratum, 20 plots in the M3G stratum, 18 plots in the M4N stratum, and 20 plots in the M4G stratum. Using the original GIS map, we estimated the area covered by each of the four strata within our study area. We then randomly selected a subsample of plots in each stratum for use in our spotted owl nesting-habitat analysis. The number of subsamples was proportional to the amount of that stratum on the landscape (i.e., stratified random sample). We used all 21 plots in M3N, and randomly selected 2 plots in M3G, 3 plots in M4N, and 1 plot in M4G. Our results can be extrapolated only to these forest types within our study area.

Random UTM coordinates were located in the field using Garmin 12XL Global Positioning System units. We centered a 2,000-m^2 rectangular-shaped plot, 100 m long and 20 m wide (10 m on each side of a line bisecting the length of the plot), on the UTM coordinates and oriented it in a random direction. Thus, our rectangular plot was a 0.2-ha bounded transect within which tree size and canopy closure were measured. On the GIS map, an 80-m buffer was created on the inside of each forest-type polygon, and all random points located within the buffer zone were discarded to reduce the chance of a plot crossing the boundary into an adjacent polygon. Fifteen locations could not be sampled because of dangerous terrain (e.g., cliffs) and were replaced with other randomly selected locations. All vegetation sampling was conducted from May through Aug. 2001.

To estimate canopy cover, we recorded overstory using a vertical densitometer (Stumpf 1993) at 1-m intervals beginning at meter 1 and proceeding along the center line of the plot for 100 readings. Canopy cover for each plot was expressed as the percentage of readings with closed canopy above sample points. The dbh of all woody stems ≥15.2-cm diameter within each plot was measured using a Biltmore stick or measuring tape if the tree was ≥76.2-cm diameter. All trees were measured at breast height (1.37 m above ground level from the root collar, on the uphill side of the tree). Trees were considered within the plot if their midpoint was ≤10 m from the center of the plot.

Owl Surveys and Nest Locations

This study was part of a long-term demography study in which owls were surveyed and banded annually. We limited our vegetation sampling for this study to nests ($n = 22$) used by owls from 1996 through 2001 to reflect the relevant characteristics identified on the 1996 satellite image. All nests were geo-referenced using Garmin 12XL Global Positioning System units. We used the same vegetation sampling methods for owl plots as we did for random plots.

Data Analysis

We used an information-theoretic approach to objectively rank a set of a priori models in terms of their ability to explain our data regarding nesting-habitat selection. The response variable was the probability of plot being a nest site (P_{nest}) and the independent variables were individual habitat covariates or combinations of six habitat covariates. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank models based on their ability to explain the data, and we used Akaike weights (w) to estimate the relative likelihood of each model given the data (Akaike 1973, Burnham and Anderson 1998). We used logistic regression (PROC LOGISTIC, SAS Institute, Inc. 1999) to model data, where the probability of a plot being a nest (P_{nest}) was the response variable (nest = 1, random = 0). The binary logit model estimated parameter values for explanatory variables using maximum likelihood. We assessed the strength of the correlation between the predictors and response variable by examining sign and 95% confidence intervals for the regression coefficients (Franklin et al. 2001). We also evaluated the predictive power of the best-ranked model using the rescaled R^2 value, which was the generalized R^2 value divided by the upper bound of the conventional R^2 value (Allison 1999). The generalized R^2 was based on the likelihood ratio chi-square for testing the null hypothesis that all the coefficients in the model are zero (Allison 1999).

Based on the literature regarding spotted owl habitat selection, we constructed a suite of 14 a priori candidate models (hypotheses) to predict nesting-habitat selection before analyzing the empirical data (Table 1). We used the following six habitat covariates in the hypothesized models (models were developed from metrics obtained from our plot data, and are standard metrics derived from FIA data).

Table 1. Description of the 14 a priori habitat models used to investigate the association of tree size distribution (*q*-factor), stand density (stand density index = SDI), canopy cover (cc), number of large trees (large), structural diversity (Berger-Parker index = BPI), and forest structure heterogeneity (var) with nesting habitat selection by California spotted owls in the central Sierra Nevada, California.

Model	Model structure	Expected result
Hypothesis for nest site (logit P)		
1. Negative association with high *q*-factor (<1.7)		
P_{qfact}	$\beta_0 + \beta_1(P_{\text{qfact}})$	$\beta_1 < 0$
More small than large trees is negatively associated with selection.		
2. Positive association with increasing SDI		
P_{SDI}	$\beta_0 + \beta_1(P_{\text{SDI}})$	$\beta_1 > 0$
High density of trees, especially larger trees, is positively associated with selection.		
3. Negative association with low ($<25\%$) or high ($>60\%$) SDI*		
$P_{\text{SDI+(SDI)}^2}$	$\beta_0 + \beta_1(P_{\text{SDI}}) - \beta_2(P_{\text{SDI}})^2$	$\beta_1 > 0, \quad \beta_2 < 0$
Medium stand density is positively associated with selection.		
4. Threshold association with SDI		
P_{lnSDI}	$\beta_0 + \beta_1(P_{\text{lnSDI}})$	$\beta_1 > 0$
High density of trees is positively associated with selection to a threshold point.		
5. Negative association with high *q*-factor and quadratic SDI*		
$P_{\text{qfact+SDI+(SDI)}^2}$	$\beta_0 + \beta_1(P_{\text{qfact}}) + \beta_2(P_{\text{SDI}}) - \beta_3(P_{\text{SDI}})^2$	$\beta_1 < 0, \quad \beta_2 > 0, \quad \beta_3 < 0$
Too high a density of small trees is negatively associated with selection.		
6. Positive association with high number of large trees		
P_{large}	$\beta_0 + \beta_1(P_{\text{large}})$	$\beta_1 > 0$
Many large trees is positively associated with selection.		
7. Positive association with high number of large trees and high canopy cover		
$P_{\text{large+cc}}$	$\beta_0 + \beta_1(P_{\text{large}}) + \beta_2(P_{\text{cc}})$	$\beta_1 > 0, \quad \beta_2 > 0$
Many large trees and high canopy cover is positively associated with selection.		
8. Positive association with high dbh variance		
P_{var}	$\beta_0 + \beta_1(P_{\text{var}})$	$\beta_1 > 0$
High forest heterogeneity is positively associated with selection.		
9. Positive association with high number of large trees and high dbh variance		
$P_{\text{large+var}}$	$\beta_0 + \beta_1(P_{\text{large}}) + \beta_2(P_{\text{var}})$	$\beta_1 > 0, \quad \beta_2 > 0$
Many large trees and high forest heterogeneity is positively associated with selection.		
10. Positive association with high number of large trees, high canopy, and high dbh variance		
$P_{\text{large+cc+var}}$	$\beta_0 + \beta_1(P_{\text{large}}) + \beta_2(P_{\text{cc}}) + \beta_3(P_{\text{var}})$	$\beta_1 > 0, \quad \beta_2 > 0, \quad \beta_3 > 0$
Many large trees, high canopy cover, and high forest heterogeneity is positively associated with selection.		
11. Positive association with high canopy cover and quadratic SDI*		
$P_{\text{cc+SDI+(SDI)}^2}$	$\beta_0 + \beta_1(P_{\text{cc}}) + \beta_2(P_{\text{SPI}}) - \beta_3(P_{\text{SDI}})^2$	$\beta_1 > 0, \quad \beta_2 > 0, \quad \beta_3 < 0$
High canopy cover and medium stand density is positively associated with selection.		
12. Positive association with high number of large trees, high canopy cover, and high BPI		
$P_{\text{large+cc+BPI}}$	$\beta_0 + \beta_1(P_{\text{large}}) + \beta_2(P_{\text{cc}}) + \beta_3(P_{\text{BPI}})$	$\beta_1 > 0, \quad \beta_2 > 0, \quad \beta_3 > 0$
Many large trees, high canopy cover, and evenness of height classes is positively associated with selection.		
13. Positive association with high number of large trees and high canopy cover with low *q*-factor and quadratic SDI*		
$P_{\text{large+cc+qfact+SDI+(SDI)}^2}$	$\beta_0 + \beta_1(P_{\text{large}}) + \beta_2(P_{\text{cc}}) + \beta_3(P_{\text{qfact}}) + \beta_4(P_{\text{SDI}}) - \beta_5(P_{\text{SDI}})^2$	$\beta_1 > 0, \quad \beta_2 > 0, \quad \beta_3 < 0, \quad \beta_4 > 0, \quad \beta_5 < 0$
Many large trees and high canopy cover, with more large than small trees and medium stand density is positively associated with selection.		
14. Positive association with high number of large trees, high canopy cover, high BPI, and high dbh variance, with low *q*-factor and quadratic SDI*†		
$P_{\text{large+cc+BPI+var+qfact+SDI+(SDI)}^2}$	$\beta_0 + \beta_1(P_{\text{large}}) + \beta_2(P_{\text{cc}}) + \beta_3(P_{\text{BPI}}) + \beta_4(P_{\text{var}}) + \beta_5(P_{\text{qfact}}) + \beta_6(P_{\text{SDI}}) - \beta_7(P_{\text{SDI}})^2$	$\beta_1 > 0, \quad \beta_2 > 0, \quad \beta_3 > 0, \quad \beta_4 > 0, \quad \beta_5 < 0, \quad \beta_6 > 0, \quad \beta_7 < 0$
Many large trees, high canopy cover, evenness of height classes, and high forest heterogeneity with more large than small trees and medium stand density is positively associated with selection.		

* The quadratic form of these models suggests an optimal SDI associated with nest-site selection, with too-low or too-high stand densities being suboptimal.

† Global model.

1. *q*-Factor, the ratio of trees in a specified diameter class compared to number of trees in the next larger class, is a measurement of tree distribution within a stand. Each tree was placed into a 5-cm size class. The *q*-factor for each plot was obtained by regressing each size class onto the natural logarithm of trees/acre (Chojnacky and Dick 2000). The regression slope (β_1) was then converted to $q = \exp(-2\beta_1)$. A smaller

Table 2. Ranking of 14 a priori habitat models investigating the association of tree size distribution (*q*-factor), stand density (stand density index = SDI), canopy cover (cc), number of large trees (large), structural diversity (Berger-Parker index = BPI), and variance in tree size (var) with nesting-habitat selection by California spotted owls in the central Sierra Nevada, California.

Model*	K†	AIC_c‡	$\Delta\mathrm{AIC}_{ci}$	w_i§
$P_{\text{large+cc}}$	3	52.44	0	0.35
$P_{\text{large+cc+var}}$	4	53.88	1.44	0.17
$P_{\text{large+cc+BPI}}$	4	54.48	2.03	0.13
P_{lnSDI}	2	55.02	2.57	0.10
P_{SDI}	2	55.80	3.36	0.07
$P_{\text{cc+SDI+(SDI)+large+qfact}}^{2}$	6	56.34	3.90	0.05
$P_{\text{qfact+SDI+(SDI)}}^{2}$	4	56.55	4.11	0.05
$P_{\text{SDI+(SDI)}}^{2}$	3	57.93	5.49	0.02
$P_{\text{cc+SDI+(SDI)}}^{2}$	4	57.99	5.54	0.02
$P_{\text{cc+SDI+(SDI)+large+qfact+BPI+var}}^{2}$	7	58.50	6.05	0.02
P_{large}	2	58.51	6.07	0.02
$P_{\text{var+large}}$	3	60.57	8.13	0.006
P_{var}	2	63.89	11.44	0.001
P_{qfact}	2	64.91	12.46	0.0007

* Corresponds to models outlined in Table 1.
† Estimable number of parameters.
‡ Akaike's information criterion adjusted for small sample size.
§ Akaike's information criterion weights.

q-factor indicates greater densities of larger trees (Meyer 1952, Fiedler and Cully 1995, Chojnacky and Dick 2000), which are associated with spotted owl habitat (Gutiérrez et al. 1992).

2. Stand density index (SDI) combines tree size and density to indicate densities of stands with different-sized trees (Long and Daniel 1990, Long 1998, Chojnacky and Dick 2000). SDI for the *i*th tree in the *j*th plot is obtained using the formula

$$\mathrm{SDI}_i = (\text{trees/acre})_j * (\mathrm{dbh}_i/10)^{1.6}$$

and calculating a mean SDI per plot. Maximum SDI for mixed conifer forests in California is 750 (Reineke 1933), so the SDI of a plot can be represented as percentage of maximum SDI. High stand densities may impede movement of spotted owls, but low densities may be too open for owl nesting and roosting (Gutiérrez et al. 1992). Either a high or medium SDI is predicted to be associated with nesting-habitat selection.

3. High numbers of large (or residual) trees ≥76.2 cm dbh (30 in.) have been documented at California spotted owl nest sites (Gutiérrez et al. 1992, Moen and Gutiérrez 1997). Large (or residual) trees may moderate temperature, provide cover, provide nest sites, and add structure and coarse woody debris to the stand (Moen and Gutiérrez 1997).

4. High percent canopy cover, generally ≥70%, has been associated with California spotted owl nest sites (Gutiérrez et al. 1992, Moen and Gutiérrez 1997). High canopy cover likely moderates temperature and provides concealing cover from weather and predation (Verner et al. 1992a).

5. The Berger-Parker index (BPI) is a measure of the evenness of canopy layers. BPI for a plot is calculated as $N_{\text{total}}/N_{\max}$, where N_{total} is the total number of trees and $N_{\max}$ is the number of trees in the height class with the most trees (North et al. 1999). We did not measure tree heights but instead used size class as a surrogate for height: 25.2–30.4 cm, 30.5–60.9 cm, and ≥61 cm. High BPI indicates greater structural diversity, more evenness, and less structural dominance among canopy layers. Structural diversity may increase foraging success by providing low perches and openings for prey capture (North et al. 1999).

6. The variance of tree diameters has been associated with Mexican and northern spotted owl nest sites (Seamans and Gutiérrez 1995, LaHaye and Gutiérrez 1999). High variation in tree diameters, a measure of forest structure heterogeneity, indicates multi-storied habitat that may create suitable microclimates and variable perch sites for spotted owls.

Results

We did not need to correct for overdispersion because deviance divided by degrees of freedom was <1 in the global model. The best approximating a priori hypothesized model (Table 1) for nesting-habitat selection by California spotted owls in the sampled strata was $\{P_{\text{large+cc}}\}$ (Table 2). This model suggested that the probability of nesting-habitat selection by California spotted owls increased as a function of increasing numbers of large trees (≥76.2 cm dbh) and greater canopy cover [$\beta_1(P_{\text{large}}) = 0.2179$, 95% CI = 0.0542–0.4211; $\beta_2(P_{\text{cc}}) = 0.0541$, 95% CI = 0.0156–0.1044]. The confidence intervals of both of the parameter estimates did not overlap zero, indicating that their slopes were different from zero. This suggested that the effects of both parameters on nest-site selection of California spotted owls were real (Franklin et al. 2001).

The second-ranked model $\{P_{\text{large+var+cc}}\}$ was only 49% as likely as the best ranked model (Table 2). Both variables, number of large trees and canopy cover, appeared in the top three ranked hypothesized models. The combined weights of all the models containing large trees was ~0.75, and the combined weights of all the models containing the canopy cover was 0.73. These two variables appeared to be strongly associated with nesting-habitat selection.

The equation representing the best model for California spotted owl nesting-habitat selection in the central Sierra Nevada was

$$P_{\text{nest}} = 5.2693 + 0.2179(P_{\text{large}}) + 0.0541(P_{\text{cc}}).$$

The maximum rescaled R^2 value for this model was 0.47, indicating moderate power to predict nest-site selection by California spotted owls in our study area.

Discussion

We assessed the utility of six habitat metrics that are typically or easily derived from FIA data for estimating California spotted owl nesting habitat in the central Sierra Nevada. We modeled nest-site selection using these metrics to estimate which were the best predictors of nesting habitat. Our study contributes to ongoing efforts to model habitat selection of wildlife species using FIA metrics as parameters derived from empirical data (McComb et al. 2002).

Not surprisingly, our top-ranked model suggested that number of large trees (≥76.2 cm) and canopy cover were the best predictors of nesting-habitat selection by California spotted owls in M3 and M4 habitat in our study area. Average number of large trees at our nest plots was 8.73 (95% CI = ±1.88) compared with 4 large trees (95% CI = ±1.56) at random forest plots. Canopy cover at nest plots averaged 77.41% (95% CI = ±6.40%) compared with 55.04% (95% CI = ±8.72%) at random plots.

Number of large trees and canopy cover were found to be greater at spotted owl nests than at random forested areas in several previous habitat studies (Gutiérrez et al. 1992, Moen and Gutiérrez 1997). In our study area, Bias and Gutiérrez (1992) showed that nests of California spotted owls also occurred in habitats with greater basal areas of live trees, snags, medium, mature, and old-growth trees, and higher total canopy closure than random plots. Moen and Gutiérrez (1997) found that nest plots contained more and larger trees than did random plots. However, in both studies, plots were randomly placed on the entire landscape rather than solely within potential nesting habitat. Tree-size variance, which was found to be greater at Mexican and northern spotted owl nests than random sites (Seamans and Gutiérrez 1995, LaHaye and Gutierrez 1999), appeared with large trees and canopy cover in our second-ranked model, although this model was only half as likely as the top-ranked model. BPI, a measure of diversity of tree height classes, was higher at foraging areas used by northern spotted owls (North et al. 1999). However, BPI appeared in the third-ranked model along with number of large trees and canopy cover, which was only 37% as likely as the top model.

Both stand density index and *q*-factor have been suggested as metrics for quantifying habitat and for developing silvicultural prescriptions to manage habitat for Mexican spotted owls (Fiedler and Cully 1995, Chojnacky and Dick 2000). Fiedler and Cully (1995) suggested using stand density index rather than basal area to compare site occupancy between traditional silvicultural prescriptions and prescriptions designed to maintain or facilitate development of Mexican spotted owl habitat. Stand density index and *q*-factor estimated from FIA data were used to quantify amount of Mexican spotted owl habitat in the Gila National Forest of New Mexico (Chojnacky and Dick 2000). However, our study indicated that neither of these metrics were particularly useful for identifying California spotted owl nesting habitat in the central Sierra Nevada. Thus, our foremost recommendation is to use large tree and canopy cover variables for California spotted owl nest stand management.

The number of large trees and canopy cover are clearly important variables associated with California spotted owl nesting habitat. However, we found that the GIS map we used to place our random plots was relatively inaccurate in its estimates of canopy cover and tree size at a scale appropriate for spotted owl management. The GIS map correctly classified a polygon's canopy cover and tree size about 60% of the time (M. Bond, unpublished data). Overall, the map had a tendency to underestimate tree-size class and canopy cover on the landscape. Therefore, the development of vegetation maps that integrate FIA plot data with imagery and other spatial data may be a better technique for accurately estimating quantity and quality of California spotted owl habitat than currently available GIS maps. We quantitatively measured canopy cover with a vertical densitometer in our plots, whereas FIA usually estimates crown cover on vertical aerial photographs (USDA Forest Service 1994). Because different estimation methods can yield different results, our ground-based estimates should be tested against aerial photography-derived estimates to determine whether both methods demonstrate similar relationships to canopy cover in California spotted owl nesting habitat.

The results from our study could prove useful when developing silvicultural prescriptions for timber harvest or reducing risk of severe fire within the range of the California spotted owl, and for quantifying amount of nesting habitat at a landscape level to meet management guidelines. However, the generality of our conclusions needs to be further tested in other geographic locations and other vegetation strata because our top model could only moderately predict nest-site selection (maximum rescaled R^2 value = 47%). This suggests that there may be additional stand-level metrics of value in predicting owl nesting-habitat selection, or there are other factors such as presence of nest site, coarse woody debris, overall landscape pattern, or nonhabitat factors such as prey densities, presence of predators, and foraging history, that contribute to owl habitat selection processes. We agree with the cautious approach suggested by North et al. (1999) that management should not follow a singular focus on one or two stand characteristics that does not take into account the complexity of forest ecosystems.

Conclusion

The results of our study suggest that large trees and canopy cover as estimated by FIA data should be used in future studies of the spotted owl subspecies. Estimates of numbers of large trees and canopy cover as derived from FIA inventories might be used at regional scales to monitor amount of suitable nesting habitat for California spotted owls in the central Sierra Nevada. Because FIA data are geo-referenced, habitat at the stand scale and the home-range and landscape scale could be quantified (Chojnacky and Dick 2000). In addition, because FIA data continue to be collected, it may be possible to track changes in suitable nesting habitat over time in a given area if the sampling intensity of FIA plots is sufficient. Future research should include identifying additional factors influencing nesting-habitat selection, mapping and quantifying currently available nesting habitat, investigating the relationship of nesting habitat to landscape patterns, and estimating effects of habitat variation on demographic parameters such as survival and reproduction.

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