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NORTHERN SPOTTED OWL HABITAT MODELS FOR RESEARCH AND MANAGEMENT APPLICATION IN CALFORNIA (USA)

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Abstract. In order to test the veracity of currently accepted ideas about Northern Spotted Owl (*Strix occidentalis caurina*) habitat associations in the Klamath Province of northern California (USA) we compared different habitat descriptions using predictive habitat-association models. The current description used by federal agencies and new descriptions based on research results and field biologists' best estimates of owl nesting/roosting habitat and foraging habitat were evaluated. For each habitat description, three habitat metrics and three forms of the relationship between owl occupancy and quantities of these habitat metrics were evaluated, each at three spatial scales. Our refined descriptions of owl nesting and roosting, and foraging habitat, were better at predicting owl occupancy than the habitat description currently used by federal land managers. The best-fitting model for predicting owl occupancy was at the 200-ha scale and exhibited a pseudo-threshold relationship to nesting and roosting habitat and a quadratic relationship to foraging habitat. This model correctly classified owl-occupied sites 94% of the time for the developmental data set and between 85% and 92% of the time on four independent test data sets. The current description of owl habitat in northern California ranked among the worst in the collection of models we examined. The testing of multiple models on the four independent data sets was very important for determining the goodness-of-fit and predictive capabilities of the best models. We explored the use of the best-fitting model to predict number of owls on several independent study areas and found a strong correlation between predicted and observed number of owls. The results of this study are beginning to be used to make land-management decisions regarding harvesting and prescribed-burning activities on federal forestlands and were specifically designed to be amenable to adaptive resource management.

Key words: Akaike's information criterion, AIC; Bayesian posterior probability; correct-classification analysis; habitat associations; Klamath Province (California, USA); national forests; northern California (USA); Northern Spotted Owl; owl habitat; predictive models; Strix occidentalis caurina.

Introduction

Wildlife biologists have long sought to develop habitat-based models to predict presence/absence (Verner et al. 1986, Morrison et al. 1992, Block and Brennan 1994, Carroll et al. 1999, Dettmars and Bart 1999), indices of abundance (Block et al. 1997), and demographic attributes (Van Horne 1982, Ostfeld et al. 1985, Adler 1987, Donovan et al. 1995, Dunk et al. 1997, Franklin et al. 2000) of wildlife species, as well as population trends (Forsman et al. 1996, Paradis et al. 2000). The major assumption behind the development of accurate predictive habitat-based models is that subsequent estimation of a species' presence/absence or demographic attributes may be possible without extensive and expensive field surveys. Thus, large geographic areas may be assessed in a much more time- and cost-effective manner compared to field surveys. Furthermore, predictions regarding various anthropogenic disturbances can be evaluated and possibly modified in order to reduce negative impacts.

The final product of most habitat-based modeling projects is the development of a quantitative model, based on a representative data set. Unfortunately, biologists have typically lacked additional independent data to test their models. More rigorous evaluations have at least included cross-validation methods to evaluate the accuracy and robustness of models (e.g., Carroll et al. 1999, Dettmars and Bart 1999). In most cases, however, it is left to others to discover, evaluate, and implement the model results. We were able to overcome these difficulties by using multiple independent test data sets to evaluate our model results. In addition, we

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moved away from a traditional null vs. alternative hypothesis testing approach towards a model selection and inference paradigm described by Burnham and Anderson (1998) that compares a collection of plausible competing models.

The Northern Spotted Owl (NSO) is among the most studied and well-known bird species in the world (Gutiérrez et al. 1995). NSO habitat selection has been intensively evaluated in many study areas throughout northern California (LaHaye 1988, Sisco 1990, Solis and Gutiérrez 1990, Blakesley et al. 1992, Folliard 1993, Hunter et al. 1995, Zabel et al. 1995, Gutiérrez et al. 1998, Thome et al. 1999, Franklin et al. 2000). However, NSO habitat associations have not been systematically evaluated throughout their northern California range. Thomas et al. (1990) recognized that NSOs in northern California appeared to use habitat differently than in the more northern part of their range in Oregon and Washington. At least part of this difference has been attributed to differences in prey (Zabel et al. 1995). In general, NSO diets contain a larger proportion of bushy-tailed and dusky-footed woodrats (*Neotoma cinerea* and *N. fuscipes*, respectively) in northern California and southern Oregon (Barrows 1980, Ward et al. 1998) and a larger proportion of northern flying squirrels (*Glaucomys sabrinus*) further north (Forsman et al. 1984, Carey et al. 1992).

Because of this difference in the NSO's biology in northern California, one habitat description for this species throughout the three states may not be adequate. It is possible that certain habitats provide thermal benefits, nest-site availability, and protection from predators while other habitat types provide foraging opportunities, at least in portions of their range (Franklin et al. 2000). One of the NSO's primary predators, Great Horned Owls (*Bubo virginianus*), was encountered at its highest densities near NSOs in the mixed-conifer forests of the Klamath Mountains (northwest California, USA) (Carey et al. 1992). These authors suggested that NSOs may use mature and old-growth forests to avoid predation by Great Horned Owls because the latter do not use those forest types. There is general agreement among researchers that NSOs disproportionately select areas with mature and late-successional forest characteristics for nesting and roosting (Solis and Gutiérrez 1990, Blakesley et al. 1992, Hunter et al. 1995, Gutiérrez et al. 1998). Less is known about foraging-habitat associations because it is more difficult to obtain radiotelemetry locations on moving NSOs than on roosting or nesting NSOs. However, the importance of edges between ''suitable'' NSO habitat and other habitat types for foraging has been documented (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000). It also has been suggested that younger age classes may be used for foraging, at least in the Klamath Province of California, because the highest densities of woodrats occur in young stands in this region (Sakai and Noon 1993). NSOs in northwestern California preferred woodrats to other prey species and hence used foraging areas near ecotones between mature and young-growth stands where woodrats were most abundant and accessible (Ward et al. 1998).

Until the work of Franklin et al. (2000), biologists working with the NSO and most other wildlife species apparently assumed that a linear relationship existed between quantity of suitable habitat and the quality of an area. Franklin et al. (2000) documented nonlinear habitat relationships for the NSO. It is conceivable that NSOs require a certain quantity of ''suitable'' habitat for particular life-history needs (e.g., nesting or roosting), but too much might have negative impacts or limit the variety and quantity of other habitat types that are required to meet other needs (e.g., foraging).

We developed, tested, and compared the ability of vegetation models to predict NSO presence/absence throughout national forest lands in northern California. Land managers desired a quantitative and empirically derived model that they could use to evaluate existing landscapes, and future landscapes based on projections of tree growth and harvesting, that would minimize negative impacts on this threatened species.

METHODS

We evaluated habitat descriptions developed by a team of USDA Forest Service and USDI Fish and Wildlife Service biologists (the ''NSO Baseline Team''). They had created a seamless, ecologically based habitat map within the four northern California national forests within the range of the NSO (Northern Spotted Owl) in California, USA. In essence, they ''dissolved'' forest boundaries and used ecological-zone boundaries. These zones were derived and modified from Ecological Units of California (Bailey 1978) and Natural Vegetation of California (Kuchler 1977). The habitat descriptions were refined for the following five zones: Western Klamath, Interior Coast, Eastern Klamath, Modoc, and West Cascades (Fig. 1). Habitat descriptions were developed incorporating the knowledge of the local forest biologists, NSO database inquiries, and published research. Descriptions included new habitat types (e.g., smaller tree size classes) and new attributes (e.g., elevation, aspect, and Dunning's soil site class) that the FSEIS description (USDA/USDI 1994) had not included (Appendices A and B).

To develop models, we used a data set of 74 NSO-survey locations spread throughout the range of NSOs in northern California national forests that were surveyed in 1990 and 1991 (Research Development and Application [RDA] data set, USDA 1988). These locations were randomly selected to be surveyed and were not selected based on timber sales or any other management action or inaction; nor were they constrained to be near roads or any other feature. In addition, we had four independent data sets to test the models. These data sets were from areas within the National Forest lands of our study area. Each indepen-

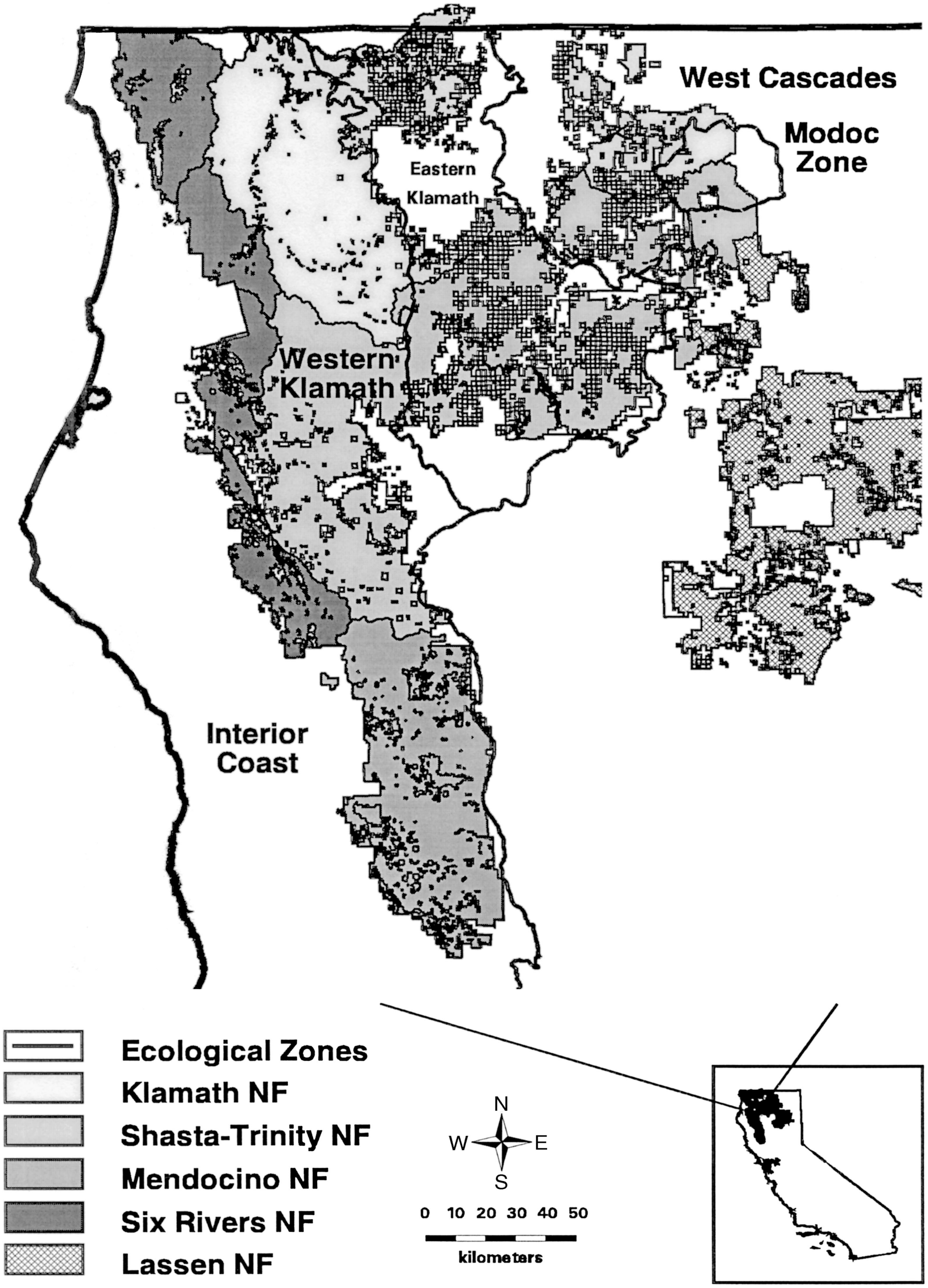

FIG. 1. Map indicating ecological zones in the Klamath Province for northern California, USA; NF = National Forest.

dent study area had been completely surveyed for NSOs so both presence and absence were documented. Standard NSO survey protocols (Forsman 1983, Franklin et al. 1996) were used on all of the surveyed areas.

We tested six different map layers (hereafter, ''descriptions'') representing NSO habitat: (1) the existing FSEIS description; (2) a revised FSEIS (FSEIS$_{new}$) description developed by our team using the FSEIS attributes (e.g., tree size class and canopy cover) on updated vegetation data provided to us by the national forests, with GIS habitat map layers updated for timber sales and fires that had occurred since the original 1979

TABLE 1. Acronyms and symbols used to describe habitat covariates, together with the forms of relationships of habitat covariates for habitat-selection models for Northern Spotted Owls in northern California, USA.

Meaning	Abbreviation
Habitat descriptions	
Final Supplemental Environmental Impact Statement	FSEIS
New FSEIS	$\text{FSEIS}_{\text{new}}$
Nesting and roosting	NR
Foraging	F
Nesting, roosting, and foraging	NRF
Nesting and roosting plus foraging	NR + F
Edge	E (e.g., NRE)
Core	C (e.g., FC)
Examples of forms of relationships	
Linear nesting and roosting	NR
Pseudothreshold nesting and roosting core	LOGNRC
Quadratic nesting and roosting	$\text{NR} + \text{NR}^2$
Pseudo-threshold foraging core plus linear nesting and roosting	LOGFC + NR

aerial-photo typing; (3) nesting and roosting habitat (NR) that was thought to represent habitats primarily selected by the NSO for these activities (essentially including all FSEIS habitat as well as a few smaller-diameter tree size classes to account for differences thought to represent additional NSO habitat in California) (Appendix A); (4) foraging (F) habitat that was thought to represent habitats primarily selected by NSOs for hunting for prey, but that occasionally are used for nesting/roosting as well, and generally included smaller-diameter tree size classes and more-open canopy than NR (Appendix B); (5) a combination of nesting, roosting, and foraging (NRF) habitat that did not distinguish between the relative quantities of NR and F habitat (combining maps from descriptions 3 and 4); and (6) NR+F habitat (Table 1) in which the relative quantity of these habitat types could be considered independently and forms of the relationship between owl occupancy and quantity of habitat could be different (this also represented combining maps from descriptions 3 and 4, but retained their individual attributes). It is important to note that by using the terms ''NR'' and ''F'' we do not mean to imply that NR habitat is solely used for nesting and roosting and that F habitat is solely used for foraging. More accurately, we assume that NR habitat provides most of the nesting and roosting habitat, along with some foraging habitat. Similarly, we assume that F habitat is primarily used for foraging, but we also know that in some instances it is used for nesting and roosting as well. We began our analyses without the $\text{FSEIS}_{\text{new}}$ description, but an evaluation of the FSEIS map revealed that it was so coarse and inaccurate that it required updating (see Fig. 2). We used an identical process to revise the FSEIS map as was used in the creation of the NR, F, and NRF base maps. By creating the $\text{FSEIS}_{\text{new}}$ map we allowed that habitat description to be fairly evaluated (i.e., we did not want it to perform poorly or well due to known inaccuracies in the base layers) along with the new descriptions. The $\text{FSEIS}_{\text{new}}$ map was more up-to-date relative to fire and timber harvesting that occurred between 1993 and 1999 than the FSEIS map. These changes in the landscape, however, were relatively minor as timber harvesting within the study area was dramatically reduced during that same time.

We examined NSO presence and absence at three different spatial scales around each sample location: 200-ha, 550-ha, and 900-ha circles. The smallest spatial scale was based on the estimated size of average core home-range area for NSOs in northern California (Bingham and Noon 1997). The largest scale was based on estimates of mean nearest-neighbor distance between NSOs in the 1100 km^2 Hayfork Adaptive Management Area (Northern California, USA) and six adjacent late-successional reserves that was completely surveyed during 1996 and 1997 (C. J. Zabel and K. S. McKelvey, *unpublished data*). The midpoint between these two scales was used for the third scale. For each habitat description we estimated three habitat metrics around each sample location: total quantity (total), linear distance of edge between that habitat type and any other (edge), and quantity of core habitat area defined by 100-m buffers from an edge (core).

Three functional forms of each covariate were evaluated: linear, quadratic, and pseudo-threshold (sensu Franklin et al. 2000). The linear form assumed that the probability of NSO presence was a monotonic function of the amount of the habitat metric within the sampling unit. The quadratic form allowed for some intermediate level of the habitat metric to be optimal or suboptimal (i.e., hump-shaped or bowl-shaped) for probability of NSO presence. The pseudo-threshold form, based on a logarithmic transformation, allowed for the possibility that once the quantity of the habitat metric reached some ''threshold'' level the probability of occupancy did not increase or decrease substantially with more habitat.

Statistical methods

Developing and comparing models.—We used logistic regression for the analyses and a parsimonious

FIG. 2. Final Supplemental Environmental Impact Statement (FSEIS) and revised FSEIS (FSEIS$_{new}$) map overlays for the Northern Spotted Owl in northern California.

model-selection and inference strategy based on the bias-corrected Akaike's Information Criterion (AIC$_c$; Akaike 1973) to compare the models (Sugiura 1978, Hurvich and Tsai 1989, Burnham et al. 1995, Burnham and Anderson 1998). This information-theoretic measurement of model fit accounts for both bias and precision. The models with the lowest AIC$_c$ values are the best-fitting models to the data. We began by identifying a collection of plausible candidate models, based on the field experience of the biologists on our team and extensive published literature on the NSO. For each of the six habitat descriptions we had three metrics and three functional forms, resulting in nine combinations at each of three scales, with the exception of NR+F for which we had a total of 27 combinations (9 combinations of forms for each of NR and F total, core, and edge).

We used a two-stage process for selecting our best-fitting models. First we compared a collection of models for each of the six habitat descriptions, selecting the best-fitting models. Within each habitat description, the most competitive one-covariate models (i.e., those within two $\mathrm{AIC_c}$ units of the model with the lowest $\mathrm{AIC_c}$; Burnham and Anderson 1998) were determined. Each competing model was then combined with the model that had the next lowest $\mathrm{AIC_c}$, but that was an estimate of a different metric. For example, if the lowest $\mathrm{AIC_c}$ was for the NR pseudo-threshold description (total), we would not combine that further with any other NR (total) descriptions (linear or quadratic). Instead, we would search among the three edge and three core covariate models for the lowest $\mathrm{AIC_c}$, subject to the constraint of not being highly correlated with the original covariate ($r > 0.50$). The best two-covariate model was then compared to the best univariate model. If it was a better model, based on $\mathrm{AIC_c}$, we then evaluated three-covariate models using the same criteria, and tested them against the two-covariate model. For the NR+F description, up to six covariates could be in a model. For each habitat description, model building was terminated when the more complex model failed to have a lower $\mathrm{AIC_c}$ than the model with fewer covariates. At the second stage, we compared the pooled collection of the top two best-fitting models from each of the six habitat descriptions ($n = 12$ models). Because our evaluation of habitat descriptions included the description currently used by federal land managers along with several ''challenging'' descriptions, it was important for us to keep the best-fitting models from each description throughout the model development and testing process.

We estimated the variance inflation factor c from our full model (i.e., the model containing the covariates from all of the models) and adjusted our corrected $\mathrm{AIC_c}$ accordingly to obtain the quasi-corrected $\mathrm{QAIC_c}$ that accounts for overdispersion in the data (Wedderburn 1974). Overdispersion due to dependencies in the data creates a variance larger than that expected by the binomial assumptions underlying the logistic regression model.

Akaike weights (Buckland et al. 1997) ($[w_i = \exp(-\Delta_i/2)]$ where $\Delta_i = (\mathrm{AIC}_{c_i} - \mathrm{minimum}(\mathrm{AIC}_{c_k})$ for the ith model; the kth model is the best-fitting model) were used to evaluate the relative competitiveness of the leading models. Akaike weights can be interpreted as the Bayesian posterior probabilities for the collection of models, describing their relative likelihoods of best fitting the data (see Carlin and Louis 2000).

For the independent test data sets, we evaluated the top two models within each habitat description. We sequentially analyzed the test data sets, calculating Akaike weights for each of the models, and multiplied those weights by the posterior probabilities of the previously analyzed data sets, viewed as prior probabilities of the new data set. These provided us with revised Bayesian posterior probabilities for our collection of models, based on the sequence of data sets previously analyzed and the new test data set. By evaluating models in this manner, each subsequent data set was considered both individually (the $\mathrm{AIC_c}$ values and weights for that data set) and collectively with all previously analyzed data sets. By examining whether the posterior probabilities of the models remained constant or varied substantially over multiple data sets, we evaluated the stability of our best-fitting models. This approach had the benefit of synthesizing new information with previous information. The practical management benefit was that each new data set could stand on its own, but its overall weight could also be evaluated relative to other information that was available.

Predictive accuracy of our best-fitting models was evaluated using a correct-classification (CC) analysis. We determined the proportion of NSO-occupied sites ($\mathrm{CC_{NSO}}$) (i.e., the sensitivity) and the proportion of unoccupied sites ($\mathrm{CC_{absent}}$) (i.e., the specificity), as well as the total proportion of sites ($\mathrm{CC_{total}}$) that were correctly predicted by our best-fitting models. Correct-classification estimates were derived for both the RDA and test data sets. We established an ''optimal'' probability cutoff point for each estimated model in order to have a way of classifying sites as ''occupied'' or ''unoccupied.'' Locations with estimated probabilities greater than the cutoff point were classified as occupied, and those with probabilities less than or equal to the cutoff point were classified as unoccupied.

For the two leading models for each habitat description a range of probability cutoff points, in increments of 0.05 from 0.25 to 0.65, was evaluated. We determined an ''optimal'' cutoff point using two criteria: (1) correct classification of NSO-occupied sites had to be $\geq$75%, and (2) an increase in the probability value of the cutoff point had to result in a greater increase in $\mathrm{CC_{absent}}$ than the reduction in $\mathrm{CC_{NSO}}$. This protocol reflected the conservation priority to avoid errors of omission (i.e., predicting absence when NSOs were present) rather than errors of commission (i.e., predicting presence when NSOs were absent). We also recognized that suitable habitat is sometimes vacant for a variety of reasons (e.g., it is occupied by a predator, the occupant recently died). Furthermore, the smaller spatial scales are likely to represent relatively small portions of a NSO's home range and therefore be predisposed to predict occupancy when NSOs are absent. Thus, a 200-ha scale model applied to a home range of 1000 ha that is composed of all high-quality habitat (i.e., high predicted probability values) would correctly predict presence in one of five 200-ha polygons overlaid on the home range.

Overall model rankings within each scale were based on an average of $\mathrm{AIC_c}$ and $\mathrm{CC_{NSO}}$ ranks. We decided to use this composite ranking system in order to maintain and balance the positive attributes of each tool. $\mathrm{AIC_c}$ can heavily penalize a model for its outliers (although less so than traditional statistics based upon Pearson residuals). An outlier, on the other hand, regardless of magnitude will have a relatively small fixed effect on $\mathrm{CC_{NSO}}$, misclassifying at most one point. Correct classification, however, will be highly dependent on the data set, and $\mathrm{AIC_c}$ will be more sensitive to possible biases created by specific data sets.

Testing models on independent data.—We tested the models on the four independent data sets using both $\mathrm{AIC_c}$ and $\mathrm{CC_{NSO}}$ to evaluate model performance at each spatial scale. We compared model rankings for the test data sets to the original rankings for the developmental RDA data set. We also used the iterative Bayesian process, looking at posterior distributions for the models with the data sets to examine the stability of the model rankings within and between spatial scales. We were particularly interested in the scale that would give us the most consistent best-fitting model(s): the 200-ha scale that estimated the core nesting-roosting area of the NSO, the 900-ha scale that estimated the home range, or the intermediate scale.

Estimating numbers of NSOs.—We estimated probability of NSO occupancy within each independent study area using a ''focal point'' method. We used the ''best'' model at the best scale (200 ha; see *Results: All models*, below) to estimate probabilities of NSO occupancy at potential nesting locations, positioned at incremental points 40 m apart throughout the region. This allowed us to effectively create a continuous probability contour map over the 2.2×10^6 ha study area. Areas of interest to land managers could be classified and used as an indicator of its value to NSOs.

We explored the ability of our ''best'' model to estimate NSO numbers. We evaluated the relationship of NSO numbers to the sum of probabilities within nine independent study areas that had been completely censused. For this exploratory evaluation, we used each of the four independent study areas mentioned near the start of *Methods*, above (for this evaluation each of the five relatively small Klamath National Forest areas were treated separately) in addition to the Willow Creek Study Area (see Franklin et al. 2000). Because these areas were completely surveyed, we had estimates of the total number of territorial NSOs. We then summed the probability values from each 40 × 40 m pixel within each study area and divided by 5625 (the number of pixels within a 900-ha area). We chose 900 ha because it approximates the mean size of a NSO home range in the Klamath Province. We used simple linear regression to evaluate this relationship. If our ''best'' model is a good predictor of owl numbers we would expect that the intercept term would not be significantly different than zero and the slope term would be positive and not significantly different than one.

RESULTS

Sample sizes for the RDA (Research, Development and Application) data set (USDA 1988) varied at different scales because at the larger scales, 550 ha and 900 ha, we encountered more private land for which we had no data and thus excluded those locations. The number of occupied sites and total sample sizes were 33 of 74, 18 of 41, and 15 of 35 sites at the 200-ha, 550-ha, and 900-ha scales, respectively. The four test data sets had total (presence plus absence) sample sizes ranging from 24 to 180.

Differences in habitat covariates (total, core, and edge) between owl-occupied and unoccupied sites were greater at the 200-ha scale than at either the 500-ha or 900-ha scales for FSEIS, $\mathrm{FSEIS_{new}}$ (a revised FSEIS), NRF, and NR (nesting and roosting) habitat descriptions (i.e., GIS map layers) but not for F (foraging) habitat. Subsequently, ''all models'' refers to all models developed at a particular spatial scale and ''reduced set of models'' refers to the evaluation of the two top-ranking models within each habitat description (12 models total: 6 habitat descriptions × 2 models).

200-ha models

All models.—Ninety-two 200-ha models were developed and compared using the RDA data set (Appendix C). Using $\mathrm{AIC_c}$, the FSEIS linear model (the model in use by the federal government when our work began) ranked 55th, while the highest-ranking FSEIS model ranked 46th. Using two $\mathrm{AIC_c}$ units as the criterion for determining competing models, there were three competing 200-ha RDA models. The competing RDA models were

$$\mathrm{LOGNRE} + \mathrm{LOGNRC} + \mathrm{NR} + \mathrm{NR}^2 + \mathrm{F} + \mathrm{F}^2$$

$$\mathrm{LOGNR} + \mathrm{F} + \mathrm{F}^2$$

$$\mathrm{LOGNR} + \mathrm{F} + \mathrm{F}^2 + \mathrm{LOGNRE} + \mathrm{FE}$$

(see Table 1 for explanation of symbols). The cumulative Akaike weight of these three models was 0.5476 (the cumulative Akaike weight of all 92 models = 1.0). All three models contained F and NR covariates, with the functional form of F being identical in each model and NR exhibiting either a quadratic or threshold functional form.

The top-ranking model based on $\mathrm{AIC_c}$ was 15 449 times more likely to be the best model than the FSEIS linear model based on Akaike weights. However, the top-ranking model was only 1.39 and 2.09 times more likely to be the best model than the second- and third-ranking models.

Reduced set of models.—Among the reduced set of models, the two top-ranking models had a cumulative Akaike weight of 0.87 based on the RDA data set (Table 2). $\mathrm{CC_{NSO}}$ (correct classification of the site as NSO occupied) of the RDA data at the 200-ha scale varied from 81.8% to 93.9% among these 12 models. We es-

TABLE 2. Bias-corrected Akaike Information Criterion (AIC$_c$), percentage correct classification of Northern Spotted Owl occupancy (CC$_{NSO}$), and Bayesian posterior probabilities (w_B) for the developmental (RDA) data set and four test data sets, for the five top-ranking models based on the RDA data set at each of three spatial scales.

	RDA			Hayfork		
Models†	AIC$_c$	CC$_{NSO}$ (%)	w_B	AIC$_c$	CC$_{NSO}$ (%)	w_B
200-ha scale						
LOGNRE + LOGNRC + NR + NR^2 + F + F^2	74.63	87.88	0.506	264.15	81.11	$<$0.001
LOGNR + F + F^2	*75.29*	*93.94*	*0.363*	*208.40*	*92.22*	*0.670*
LOGNRFC + NRF + NRF^2 + NFE	79.44	87.89	0.046	216.44	92.22	0.002
LOGNRE + LOGNRC	79.65	84.85	0.041	205.50	92.22	0.323
LOGNRE	79.70	90.91	0.040	232.00	92.22	$<$0.001
550-ha scale						
NRE + LOGFE + NR + NR^2 + LOGF	48.75	94.44	0.367	237.75	61.11	$<$0.001
NRE + NRE^2 + LOGFE + NRC + NRC^2 + FC	49.62	83.33	0.238	264.31	62.22	$<$0.001
NRC + NRC^2	50.40	77.78	0.161	260.77	60.00	$<$0.001
NRC + NRC^2 + NRE	51.58	77.78	0.089	250.95	63.33	$<$0.001
LOGFSEIS$_{\text{new}}$C	53.09	77.78	0.042	240.52	42.22	$<$0.001
NRF	*54.69*	*88.89*	*0.019*	*223.19*	*92.22*	*0.006*
900-ha scale						
F + F^2	41.70	80.00	0.292	299.47	64.44	$<$0.001
LOGNR + F + F^2	43.11	93.33	0.144	302.60	70.00	$<$0.001
NR + F + F^2	43.16	86.67	0.119	246.93	64.44	$<$0.001
FC + FC^2	43.49	86.67	0.092	322.77	68.89	$<$0.001
LOGNRF	44.02	80.00	0.067	218.96	83.33	0.263
LOGFSEIS$_{\text{new}}$*E*	*47.88*	*86.67*	*0.013*	*213.45*	*81.11*	*0.599*

Notes: Bayesian posterior probability values (w_B) represent the relative probability of each model among the set of 12 models compared at each scale, given the ''performance'' of the model on all previous data sets.

† These models are the top five among the 12 models we evaluated at each scale on each data set. The model in italics is the top-ranking model considering *all* data sets; at some scales this is an additional model. For an explanation of model symbols see Table 1.

timated a variance inflation factor c of 1.01, using a full model with the 19 covariates from these 12 models. There was no evidence of overdispersion in the data so we did not use the quasi-corrected QAIC$_c$.

We summarized the AIC$_c$ and CC$_{NSO}$ rankings along with the Bayesian posterior probabilities of the top five models at the 200-ha scale for the RDA data and evaluated how well these models performed on test data sets (Table 2). Except for one notable exception, AIC$_c$ and CC$_{NSO}$ rankings of the top models were generally in agreement for the RDA and test data sets, though the Akaike weights fluctuated considerably. Most of the top models at this scale exhibited similar rankings among the test data sets. The top-ranking RDA model was the one inconsistent model that performed poorly among the test data sets. This top-ranked RDA model, based on AIC$_c$, was the most complex of the 12 and had seven parameters. The FSEIS models were consistently ranked low among the different data sets. Based on our composite rankings of AIC$_c$ and CC$_{NSO}$, the best 200-ha model (LOGNR + F + F^2), ranked first with both the RDA data and the test data sets. For this model, CC$_{NSO}$ averaged 90% (range 85.2 to 93.9%) on the RDA and test data sets. The estimated logit for this model was as follows:

$$-4.35700 + 2.00760 \log(\mathrm{NR} + 1)$$
$$+ 0.06700(\mathrm{F}) - 0.00049(\mathrm{F}^2)$$

and standard errors of the coefficients were 1.12167, 0.57413, 0.02759, and 0.00025, respectively.

550-ha models

All models.—Ninety-five models were developed at the 550-ha scale using the RDA data (Appendix C). Based on AIC$_c$, the FSEIS linear model ranked 46th while the highest-ranking FSEIS model ranked 27th. Six of the 95 550-ha RDA models were competing models (within two AIC$_c$ units; Appendix C). The competing models were

NRE + LOGFE + NR + NR^2 + LOGF

NRE + NRE^2 + LOGFE + NRC + NRC^2 + FC

NRE + LOGFE + NRC + NRC^2 + LOGFC

NRE + LOGFE + NRC + NRC^2 + FC

NRC + NRC^2

NRE + LOGFE.

The cumulative Akaike weight of these models was 0.433. These six competing models shared many covariates with NRE appearing in five, LOGFE appearing in five, and NRC appearing in four. The top-ranking model was only 2.3 times more likely to be the best model than the sixth-ranked model. The top-ranking RDA model was 32.2 times more likely to be the best model than the FSEIS linear model. The top-ranking RDA model was 194 times more likely to be the best model than the 95th-ranking model (contrast this to the difference between the best and worst 200-ha RDA

TABLE 2. Extended.

Mendocino 1			Mendocino 2			Klamath		
AIC$_c$	CC$_{NSO}$ (%)	w_B	AIC$_c$	CC$_{NSO}$ (%)	w_B	AIC$_c$	CC$_{NSO}$ (%)	w_B
84.22	62.96	<0.001	65.45	8.33	<0.001	198.94	66.67	<0.001
61.07	*85.19*	*0.680*	*37.88*	*91.67*	*0.005*	*131.76*	*87.04*	*0.321*
68.21	77.78	0.0178	32.97	83.33	<0.001	152.00	74.07	<0.001
48.16	88.89	0.215	38.72	91.67	0.952	144.63	83.33	0.104
49.62	96.30	<0.001	40.22	91.67	<0.001	148.34	88.89	<0.001
57.62	81.48	<0.001	69.94	83.33	<0.001	216.26	46.30	<0.001
62.46	70.37	<0.001	63.51	83.33	<0.001	204.77	38.89	<0.001
66.61	62.96	<0.001	35.17	83.33	<0.001	145.62	42.59	<0.001
68.13	62.96	<0.001	35.73	83.33	<0.001	146.00	46.30	<0.001
59.26	81.48	<0.001	40.02	66.67	<0.001	144.36	53.70	<0.001
61.04	*100.00*	*0.001*	*36.49*	*75.00*	*0.041*	*140.06*	*70.37*	*0.327*
105.93	55.56	<0.001	64.82	8.33	<0.001	154.18	62.96	<0.001
89.91	62.96	<0.001	65.57	8.33	<0.001	159.10	64.81	<0.001
107.74	55.56	<0.001	66.97	8.33	<0.001	156.22	62.96	<0.001
119.80	59.26	<0.001	45.96	16.67	<0.001	154.61	68.52	<0.001
56.60	85.19	0.017	42.88	0.00	0.786	148.00	51.85	0.272
73.88	*100.00*	*0.769*	*36.93*	*100.00*	*0.599*	*141.39*	*83.33*	*0.059*

models where the top model was 1 361 128 more likely to be the best model).

Reduced set of models.—Among the reduced set of models there was no evidence of overdispersion in the data. CC$_{NSO}$ ranged from 77.8 to 94.4% using the RDA data set. The top three models of this group had a cumulative Akaike weight of 0.766. Nonetheless, the five top-ranking (based on the RDA data set) models of this group performed very poorly on the test data sets (Table 2). The top-ranking model using our composite rank by CC$_{NSO}$ and AIC$_c$ was NRF (Table 2). Of the 12 models, on the RDA data set this model was the eighth ranked using AIC$_c$ and fourth ranked using CC$_{NSO}$. Using the RDA data set the relative likelihood of this model being the best of the 12 models was 0.019 (Table 2). Nonetheless, it performed the best and most consistently when considering the developmental and four test data sets. CC$_{NSO}$ for this model averaged 85.3% (range 70.4 to 100%) across all data sets. The estimated logit for this model was

$$-1.359 + 0.00423(\mathrm{NRF})$$

and standard errors of the coefficients were 0.7778 and 0.00262, respectively.

900-ha models

All models.—One hundred five models were developed at the 900-ha scale using the RDA data set (Appendix C). Using AIC$_c$, the FSEIS linear model ranked 86th and the highest-ranking FSEIS model ranked 48th. The top-ranking model was 28.4 times more likely to be the best model than the FSEIS linear model and 98.4 times more likely to be the best model than the lowest ranked model.

There were five competing 900-ha RDA models. The competing models were

$$\mathrm{F} + \mathrm{F}^2 \qquad \mathrm{LOGNR} + \mathrm{F} + \mathrm{F}^2$$

$$\mathrm{NR} + \mathrm{F} + \mathrm{F}^2 \qquad \mathrm{FC} + \mathrm{FC}^2 \qquad \mathrm{LOGFC}.$$

The cumulative Akaike weight of these models was 0.1803. Three of the five competing models included a quadratic functional form of F, with the other two models including either a quadratic or threshold form of FC.

Reduced set of models.—Among the reduced set of models we found no evidence of overdispersion. Using the RDA data set on the reduced set of models, the cumulative Akaike weight of the top-ranking five models was 0.789 (Table 2). CC$_{NSO}$ among the 12 models ranged from 80–93.3% on the RDA data set. Of the five top-ranking models only one (LOGNRF) performed very well on the test data sets (though it had 0% CC$_{NSO}$ on one data set and 52% on another; Table 2). The top-ranking model using our composite rank by CC$_{NSO}$ and AIC$_c$ was LOGFSEIS$_{new}$E (Table 2). Of the 12 models, on the RDA data set this model was the eleventh ranked using AIC$_c$ and tied for second based on CC$_{NSO}$ (86.67%) with four other models (two models tied for first with 93.33%). Using the RDA data set the relative likelihood of this model being the best of the 12 models was 0.0133 (Table 2). Nonetheless, it performed most consistently when considering all data sets. CC$_{NSO}$ for this model averaged 90.2% (range

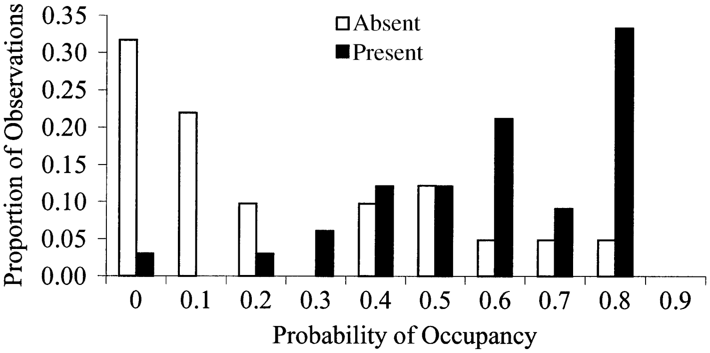

FIG. 3. Distribution of Northern Spotted Owl presence and absence locations relative to predicted probability of occupancy classes based on the LOGNR + F + F^2 model at the 200-ha scale applied to the Research Development and Applications (RDA) data set, Klamath Province, California, USA.

81.1–100%; Table 2) across all data sets. The estimated logit for this model was

$$-2.120 + 0.466(\mathrm{LOGFSEIS}_{\mathrm{new}}\mathrm{E} + 1)$$

and standard errors of the coefficients were 2.1348 and 0.5032, respectively

Determining the ''best'' model and estimating NSO numbers

Of the 36 models evaluated on all five data sets (12 at each spatial scale), the model that performed most consistently across all data sets was the LOGNR + F + F^2 model at the 200-ha scale. Thus, this model was used for subsequent estimation of owl numbers in the independent study areas. The distribution of predicted probabilities relative to NSO presence and absence showed good separation using the RDA data set (Fig. 3).

Observed number of NSOs in the nine independent study areas ranged from 4–45 birds. Estimated number of NSOs in the independent study areas (based on the sum of probabilities from 40 × 40 m pixels divided by 5625) ranged from 3.5 to 63.4 birds. We found a high correlation between actual number of NSOs within independent study areas and estimated number of NSOs from the sum of probabilities ($r = 0.89$, $P = 0.0012$). Futhermore, the estimated y-intercept (5.883) had a wide 95% confidence interval (−1.31–13.07) and did not differ from an intercept of zero ($t = 1.93$, $P = 0.09$). The estimated slope coefficient (0.674) had a 95% confidence interval (0.36–0.98) that was close to but did not overlap 1. Four of the nine estimates were within two NSOs of the actual number.

DISCUSSION

It was critical to our analyses that we included a rigorous test of the models on independent data. A survey of recent journal articles found that only 3% of the habitat-modeling papers had conducted independent field-testing of models and an additional 16% had used some form of statistical validation ($n = 382$ articles; T. Edwards, *personal communication*). We used a parsimonious model-selection and inference methodology based on $\mathrm{AIC_c}$ (bias-corrected Akaike Information Criterion) to determine our best-fitting models. $\mathrm{AIC_c}$ provides a method for comparing models but does not provide information about goodness of fit of the model to the data, as Burnham and Anderson (1998) have emphasized. Although parametric bootstrapping approaches have been suggested for goodness-of-fit tests with logistic regression, there is not a consensus among statisticians about the effectiveness of this approach. The Hosmer-Lemeshow test (Hosmer and Lemeshow 1989) is a standard goodness-of-fit test recommended by statisticians for logistic regression, but it is a somewhat arbitrary test, depending on the grouping of the data into categories. AIC is a relative measure of the fit of data to a model, and thus we used it to evaluate relative fit of the various models. We also chose to evaluate model correct-classification rates, using optimal cutoff points for the models, and examining the $\mathrm{CC_{NSO}}$ (correct classification of the site as occupied by a Northern Spotted Owl). Comparing multiple models will always result in one (or a few) being considered ''the best.'' However, whether any of them (including the best) are useful for making accurate predictions is another issue. Evaluating $\mathrm{CC_{NSO}}$ for each model allowed us to address this issue of goodness of fit. Furthermore, we used multiple test data sets to critically test our results.

We concluded that the LOGNR + F + F^2 model at the 200-ha scale worked best considering its performance on the developmental and test data sets. Models at the 550-ha and 900-ha scales had reduced $\mathrm{CC_{NSO}}$ and performed more erratically across the various test data sets (see Table 2). Testing multiple models at multiple scales on the independent data sets revealed major inconsistencies among many of the top-ranking models based on the developmental data set. These results suggest that researchers should be extremely cautious about inferences they make based on models that have not been adequately evaluated on independent test data. Using $\mathrm{AIC_c}$ to draw inferences from a single data set could be extremely misleading. Even though our developmental data set was based on a random sampling of the study area, many of the models that appeared to be good were apparently good only because they fit that particular data set, not because they were in general good models. Burnham and Anderson (1998) discuss issues such as this. Our findings simply re-emphasize the interpretation of ''the best model, *given the data*.''

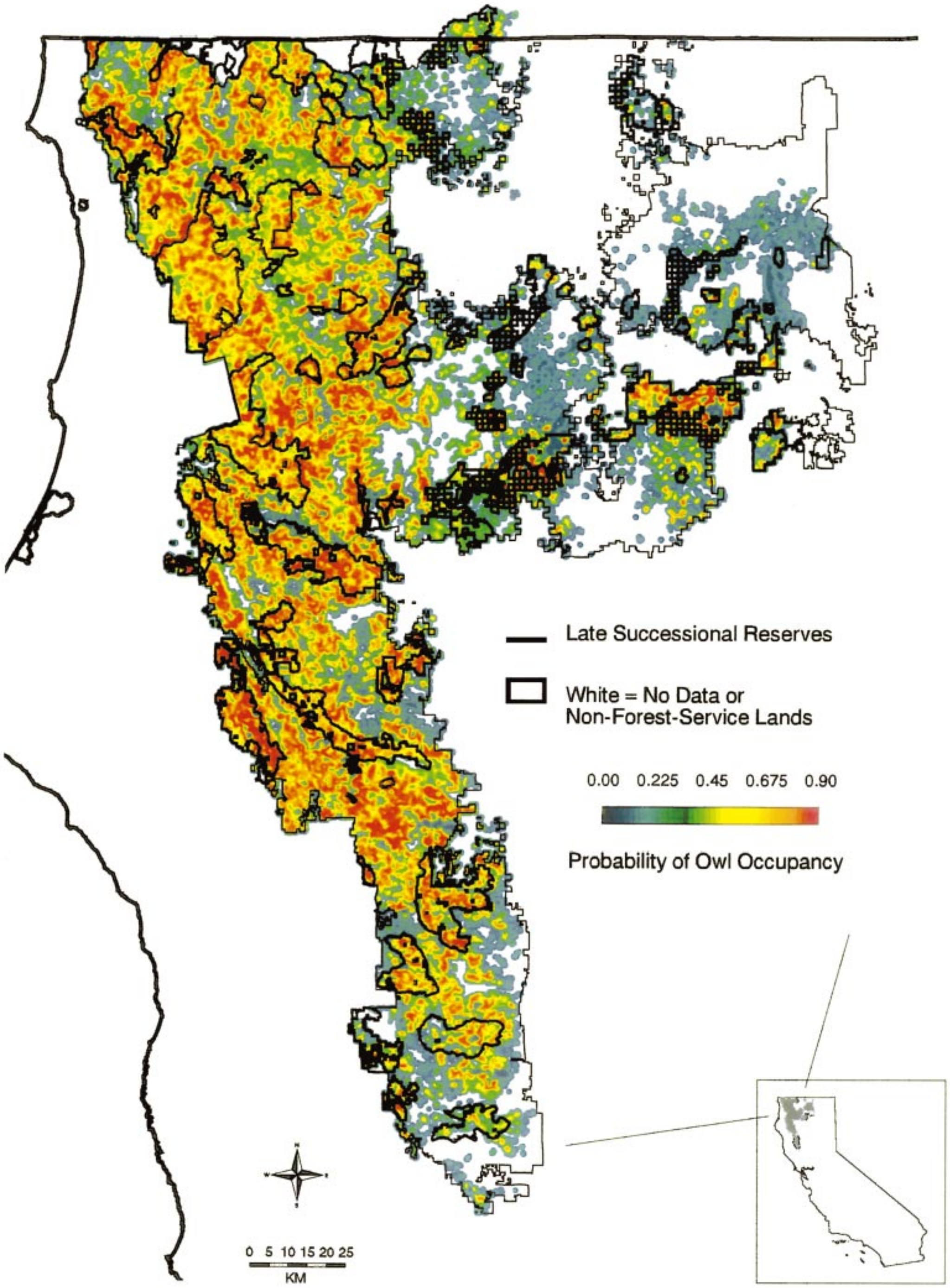

FIG. 4. Predicted probability of Northern Spotted Owl occupancy for every 40 × 40 m pixel within USDA Forest Service lands in the Klamath Province, California, USA, based on the LOGNR + F + F^2 model at the 200-ha scale.

Beyond the ''best'' model, given the data set, the suite of competing models needs to be subjected to the same cautious interpretation.

Our data sets had small sample sizes at the larger scales; therefore, we need to accept our results of 200 ha being the best scale with some caution. The spatial scale at which Northern Spotted Owls respond to habitat features has been reported by others (Lehmkuhl and Raphael 1993, Hunter et al. 1995, Bingham and Noon 1997, Ripple et al. 1997, Meyer et al. 1998, Swindle et al. 1999, Thome et al. 1999). Most found that NSO sites differed from non-NSO sites at relatively small scales (e.g., 200 ha); however, differences have also been reported at relatively large scales (e.g., >3600 ha; Meyer et al. 1998). These estimates are consistent with published estimates of NSO home-range sizes (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, Blakesley et al. 1992, Zabel et al. 1995), indicating that tremendous variation in size exists throughout their range (Gutiérrez et al. 1995).

Although we chose the LOGNR + F + F^2 model as the best model, our analyses suggested that there were three highly competitive leading models at the 200-ha scale. All three models produced consistently high classification success rates for the RDA and test data sets. We considered whether to use weighted averages to predict probabilities of NSO occupancy, based on these three models, but decided this was unnecessary because predicted values were similar for each of the three models. Nonlinear effects were prevalent in our top models. Our results differed from other NSO studies in northern California and southern Oregon that did not examine nonlinear effects (Carey et al. 1990, Solis and Gutiérrez 1990, Hunter et al. 1995, Meyer et al. 1998). Only one other study evaluated nonlinear forms of the relationship between habitat and NSOs and their conclusions were similar to ours (Franklin et al. 2000). The FSEIS and $\text{FSEIS}_{\text{new}}$ habitat descriptions did not perform very well at the 200- or 550-ha scale, but $\text{LOGFSEIS}_{\text{new}}\text{E}$ was the ''best'' 900-ha model. Consistently, we found that descriptions that incorporated NR and F habitat better predicted CC_{NSO} than the older FSEIS descriptions.

For land managers our results provide a predictive tool that may be useful for NSO habitat monitoring and adaptive land management in California. Our best-fitting model, LOGNR + F + F^2, was used to provide a current assessment of habitat for NSO occupancy on federal forestlands in northern California (Fig. 4). It can be used in the future to compare the effects of various proposed management prescriptions on NSO occupancy. The effect of proposed changes in habitat on NSO probabilities of occupancy can be evaluated using GIS by comparing probabilities before and after any prescribed activity.

The LOGNR + F + F^2 model was designed and tested using data from federal forest lands in northern California, but could be applied to other lands with similar habitat types. It should not be applied to other habitat types such as coastal Douglas–Redwood without first being tested in those areas. It provides an index of NSO occupancy. Although it consistently demonstrated high success rates at predicting habitat where NSOs can be found, its success rates at predicting NSO absence were lower. Furthermore, all of our test data sets came from areas that were thought to be relatively good habitat for NSOs prior to being surveyed. Test data from a random sample of locations throughout the entire study area would be a more critical and rigorous test of our models.

This study began with the primary objective of comparing new NSO habitat descriptions, based on nesting–roosting and foraging habitat. The older FSEIS description was based on mature forest stands and described NSO habitat the same in Oregon, Washington, and California. However, evaluations of NSO foraging ecology (Ward et al. 1998), prey use and home-range characteristics (Zabel et al. 1995), and habitat use (Solis and Guttierez 1990, Blakesley et al. 1992, Hunter et al. 1995, Thome et al. 1999) in California have suggested that NSOs use habitat differently in relatively xeric conditions in the south compared to more mesic conditions further north. Our findings were consistent with previous results suggesting that NSOs use and perhaps need a broader variety of habitats in California than in the remainder of their range.

Climate explained almost all of the temporal process variation in the life-history traits estimated for the NSO in northwest California (Franklin et al. 2000). The period when life-history traits were most affected by climate was during the spring, i.e., the breeding effort was impacted by rainfall. Franklin et al. (2000) hypothesized that precipitation may decrease hunting efficiency, prey activity, and prey populations. They stressed that climate variation may negatively affect NSO populations, even if no further habitat loss occurs. They concluded that temporal variation, as influenced by climate, is an important factor to consider when developing conservation plans.

Our exploratory analysis of the relationship of the focal-point probabilities to NSO abundance was encouraging. Due to the small sample size ($n = 9$ study areas), our results must be viewed as preliminary, subject to more thorough evaluation of using our model (or other models) to estimate owl numbers. Nonetheless, the high correlation between observed and estimated number of NSOs was encouraging.

Our models represent an association of NSOs to the habitat features we evaluated. We do not suggest that these habitat features are causally tied to NSO life-history characteristics. We do believe, however, that the habitat features we evaluated are correlated with features that are causally tied to NSO life-history characteristics. An evaluation of the relationship between NSO fitness and our best model predictions would be an important step toward determining the degree to which our model might serve as an index of NSO fitness throughout the Klamath Province (California, USA).

Our determinations of the ''best'' models at each spatial scale were also biased toward correctly classifying owl presence. We recognize that other individuals and groups might wish to place more (perhaps all) weight on predicting owl absence. For example, rural communities within our study area are particularly concerned about catastrophic wildfires. However, if NSOs are thought to occupy areas adjacent to these communities, additional regulations might hamper proactive fuel-reduction efforts. Thus, from a pragmatic standpoint, if our ''best'' model is to be used for estimating NSO occupancy, we recommend that areas having predicted probabilities near the center of the frequency distribution (e.g., from 0.20 to 0.50; see Fig. 3) be considered equivocal predictions, perhaps triggering on-the-ground surveys.

We found that using data from a randomized sampling design over a large (2.2×10^6 ha) study area resulted in the development of accurate-habitat-association models when applied to relatively small spatial scales (e.g., the much smaller study areas from which the test data came). We encourage federal and state agencies and other institutions to invest in such studies. The degree to which results from small-scale habitat-association studies can be extrapolated to larger areas outside of the study area has long been suspect. Furthermore, study areas are often chosen because they are presumed to be good habitat for the organism(s) of interest (and will result in larger sample sizes), making the generality of findings from such areas tenuous. Our results provide evidence that ''scaling down'' from larger study areas to smaller portions within them is feasible, and we believe more defensible. Initially these larger scale studies will be more expensive than smaller, more localized, studies. However, in the longer term we believe they are more cost-effective and provide more defensible information.

ACKNOWLEDGMENTS

Our project would not have been possible without a collaborative effort among research scientists and land managers. The research was motivated by management requirements to assess habitat relationships associated with the Northern Spotted Owl. Management involvement was required at the early stages of the project to provide relevant objectives that were important to land managers and at the final stages to implement the results. Researchers were needed to do the analyses. Without the participation of both scientists and managers, this project would not have been successfully completed. We thank Alan Franklin, Kevin McKelvey, and Darrin Thome for many ideas they contributed at the beginning of this project. Kelly Wolcott, David Solis, Brian Woodbridge, Mike Gertsch, Sherri Keckler, Jesse Plumage, Greg Goldsmith, and George Mayfield were on the ''Owl Team'' and provided numerous contributions throughout the project. We thank Jim Baldwin, Thomas Edwards, Danny Lee, Brian Maurer, and two anonymous reviewers for providing extremely helpful comments on earlier versions of the manuscript.

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APPENDIX A

New descriptions of Northern Spotted Owl ''nesting and roosting'' (NR) habitat by ecological zone in northern California (USA) developed for the USDA Forest Service Land Management Planning vegetation database are available in ESA's Electronic Data Archive: *Ecological Archives* A013-017-A1.

APPENDIX B

New descriptions of Northern Spotted Owl ''foraging'' (F) habitat by ecological zone in northern California (USA) developed for the USDA Forest Service Land Management Planning vegetation database are available in ESA's Electronic Data Archive: *Ecological Archives* A013-017-A2.

APPENDIX C

The list of all vegetation models evaluated at each of three spatial scales is available in ESA's Electronic Data Archive: *Ecological Archives* A013-017-A3.