

Multi-scale Mexican spotted owl (*Strix occidentalis lucida*) nest/roost habitat selection in Arizona and a comparison with single-scale modeling results

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Abstract

Context Organisms commonly respond to their environment across a range of scales, however many habitat selection studies still conduct selection analyses using a single-scale framework. The adoption of multi-scale modeling frameworks in habitat selection studies can improve the effectiveness of these studies and provide greater insights into scale-dependent relationships between species and specific habitat components.

Objectives Our study assessed multi-scale nest/roost habitat selection of the federally “Threatened” Mexican spotted owl (*Strix occidentalis lucida*) in northern Arizona, USA in an effort to provide improved conservation and management strategies for this subspecies.

Methods We conducted multi-scale habitat modeling to assess habitat selection by Mexican spotted owls using survey data collected by the USFS. Each selected covariate was included in multi-scale models at their “characteristic scale” and we used an all-

subsets approach and model selection framework to assess habitat selection.

Results The “characteristic scale” identified for each covariate varied considerably among covariates and results from multi-scale models indicated that percent canopy cover and slope were the most important covariates with respect to habitat selection by Mexican spotted owls. Multi-scale models consistently outperformed their analogous single-scale counterparts with respect to the proportion of deviance explained and model predictive performance.

Conclusions Efficacy of future habitat selection studies will benefit by taking a multi-scale approach. In addition to potentially providing increased explanatory power and predictive capacity, multi-scale habitat models enhance our understanding of the scales at which species respond to their environment, which is critical knowledge required to implement effective conservation and management strategies.

Keywords Multi-scale modeling · Habitat · Scale · All-subsets · Scaling · Spotted owl · Habitat · Selection · Habitat preference

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Introduction

Robust habitat selection models are a critical component to developing effective conservation and management plans for threatened/endangered species.

These models are commonly used: (1) to infer the relationship between selected habitat covariates and use by a given species, (2) to develop predictive maps of species occurrence and/or relative abundance, and/or (3) to guide management actions and decisions relative to the species of interest. Regardless of the types of and/or statistical algorithms employed, in order for these models to be effective and to allow for robust inference they must include as full a suite of the covariates relevant to habitat selection by the species as is possible (Williams et al. 2012; Plischoff et al. 2014). In addition, each covariate should be included in the habitat selection models at relevant spatial scale(s) for the species of interest (Wiens 1989; Graf et al. 2005).

The concept that species respond to their environment across a range of spatial scales, both within and among specific habitat components, has long been appreciated in ecology, though the implementation of this concept into habitat selection studies has lagged considerably (Wiens 1989; Levin 1992). For example, in a review of the literature on multi-scale habitat modeling published between 2009 and 2014, McGarigal et al. (2016) found that scale optimization (i.e., “where all of the covariates are evaluated simultaneously across a continuous range of scales such that the best scale for each variable is identified conditioned on the other covariates”), which is critical to assess scale dependence, was conducted in less than 5 % of all habitat modeling papers and less than 25 % of papers that address “multi-scale” habitat analysis broadly defined. Commonly, all covariates are measured at the same spatial scale, which frequently is determined arbitrarily by researchers or justified based on expert biological knowledge of the species (Wheatley and Johnson 2009; Ashrafi et al. 2013; Dudus et al. 2014; Small et al. 2015). However, selecting a single-scale at which all covariates are measured is likely an oversimplification of how species respond to their environment and can reduce the effectiveness of the models via a reduction in the proportional variance explained and/or diminished predictive capacity of the models (DeCesare et al. 2012; Sanchez et al. 2013). Additionally, the estimated effect size and relative variable importance of covariates can vary depending on the selected scale of analysis for all covariates in habitat selection studies (Thogmartin and Knutson 2007; Feist et al. 2010; Martin and Fahrig 2012). In order to reduce investigator-driven bias in results and

to improve model performance, researchers should consider the use of multi-scale models in place of single-scale models when assessing habitat selection.

In this study we assessed multi-scale nest/roost habitat selection of the federally “Threatened” Mexican spotted owl (*Strix occidentalis lucida*) in northern Arizona, USA in an effort to provide improved conservation and management strategies for this subspecies. The Mexican spotted owl (hereafter “MSO”) is one of three subspecies of spotted owl in North America and ranges from the southwestern United States to central Mexico. This subspecies is typically associated with mature, late-seral forests, though it also inhabits rocky canyon slopes that occur in some portions of its range (U.S. Fish and Wildlife Service 2012). While the MSO has the largest range of the three spotted owl subspecies, its range is highly fragmented due to the patchy distribution of habitat suitable for survival and reproduction (Urban and Keitt 2001; Barrowclough et al. 2006). This subspecies was listed by the U.S. Fish and Wildlife Service as “Threatened” under the Endangered Species Act in 1993 primarily due to extensive habitat loss resulting from timber-management activities and increasingly extreme wildfire activity (U.S. Fish and Wildlife Service 2012). Since listing the owl as threatened, several studies have focused on determining MSO distributions and habitat requirements (Grubb et al. 1997; May et al. 2004; Ganey et al. 2013) in addition to assessing timber management and disturbance impacts on MSO populations (Ganey et al. 1999; Prather et al. 2008); however, to our knowledge none have done so in a true multi-scale framework.

We used MSO survey data collected by the U.S. Forest Service (USFS) between 1990 and 1993 throughout the Coconino and Apache-Sitgreaves National Forests combined with a suite of relevant environmental covariates to assess multi-scale habitat selection of this subspecies throughout these two National Forests. In addition, we use this as a case study to compare results obtained from multi-scale models to those obtained from single-scale models, primarily with respect to: (1) parameter estimates, (2) variable importance, (3) variance decomposition, and (4) model predictive performance. Results from this study will directly aid MSO conservation and management strategies, while concurrently serving as a case study to assess the value of employing a multi-scale framework in habitat selection studies.

Methods

Study area

All data were collected in the Coconino and Apache-Sitgreaves National Forests in central/north-central Arizona, USA (Fig. 1). The extent of these two National Forests encompass a wide diversity of vegetation communities ranging from Chihuahuan and Sonoran desert scrub at the lower elevations to alpine tundra on the highest peaks (Brown 1982). Data collection for this study occurred in the higher elevations where the majority of MSO are known to exist in these two National Forests, in areas typified by high plateaus dotted with isolated volcanic mountains dissected by deep canyons. These middle-to-upper elevation plateaus are dominated by extensive forests of ponderosa pine (*Pinus ponderosa*), often containing an understory of Gambel oak (*Quercus gambelii*). At higher elevations, or in cold air drainages, mixed-conifer forests containing Douglas fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) commonly dominate. Subalpine spruce-fir forests occur at the highest elevations in this study area, while areas just

below the ponderosa pine belt are dominated by pinyon-juniper woodlands (Brown 1982).

Owl locations

We used MSO survey data collected throughout the study area by the USFS during April–August (approximate nesting season throughout the study area) from 1990 to 1993 for all analyses in this study. USFS survey crews located MSO by imitating their vocalizations during nocturnal surveys and then listening for a response (Forsman 1983). Most surveys were conducted by stopping to call and listen for owls at calling stations spaced every 0.3–0.8 km along forest roads in a non-systematic fashion across the study area. Crews remained at these calling stations for 15 min or until an MSO responded. In roadless areas crews conducted surveys by hiking ridgetops or canyon bottoms and calling every 30–40 s. Surveys were concentrated in forests and canyonlands after initial efforts to locate owls outside of such areas failed. All surveys were conducted on calm nights and most locations were surveyed multiple times, especially in locations where MSO were encountered.

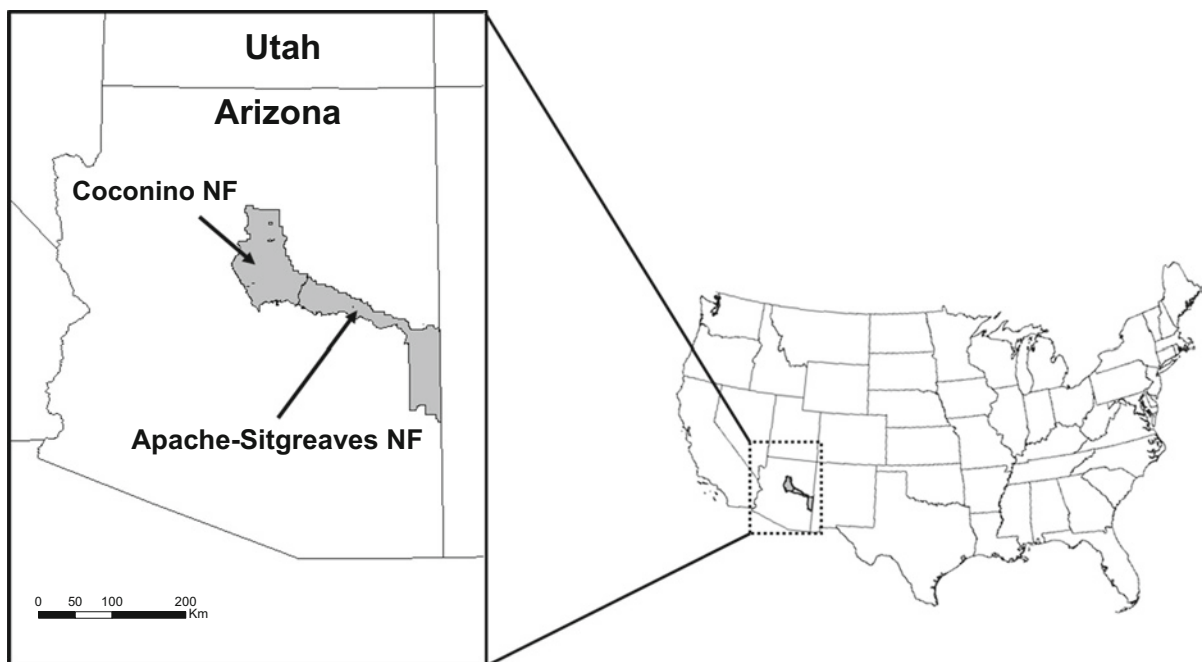


Fig. 1 Map of the study area

Survey crews mapped nocturnal MSO locations based on a compass bearing and estimated distance to the calling owl. Crews also revisited areas by day to locate roosting/nesting owls when possible. Crews located roosting MSO by calling during the day in areas where they were detected at night and tracking them until they were visually located in a nesting or roosting location. We excluded nocturnal locations from this current study due to the positional uncertainty associated with non-visual triangulation and given that MSO may be attracted in from relatively long distances at night by vocalization surveys. The remaining dataset was comprised entirely of nest ($n = 140$) and roost ($n = 68$) locations. Preliminary analyses indicated no significant differences between nest and roost data, which was consistent with our expectations given that many roosts during this period were likely locations of individuals roosting in close proximity to nests. Consequently, we combined these two datasets into a single nest/roost dataset ($n = 208$) for use in this study.

Pseudo-absence locations

Because survey locations where MSO were not encountered during surveys were not reliably recorded (i.e., this a presence-only dataset), we generated an equal number of random pseudo-absence points to be employed in logistic regression models following a standardized set of procedures. Specifically, for each nest/roost data point we extracted both the elevation (using a 30 m resolution elevation layer; LANDFIRE 2001) and the distance from the closest road (using a USFS roads data layer). We then buffered the range of observed elevations by 10 % of the difference between the minimum (1822 m) and maximum (2805 m) observed elevations to define the mask of available elevation cells throughout the study area. Next, we calculated the frequency of owl locations in each 100 m interval distance-from-road bin for the observed data, and we randomly sampled an equal number of pseudo-absence points in each distance bin from the elevation mask. The resulting dataset comprised the pseudo-absence locations dataset.

Habitat covariates

We developed a set of habitat covariates and spatial data layers considered important to habitat selection

by MSO from reviewing existing literature and from discussions with MSO experts. These included a set of four topographic variables, five landscape composition variables, and three climatic covariates. Topographic covariates were derived from the LANDFIRE digital elevation model, and included: (1) elevation (m), (2) slope (as a percentage), (3) topographic roughness index (calculated as the absolute value of the curvature index in Jenness 2013), and (4) topographic position index (Jenness et al. 2013). Landscape composition variables included: (1) percent cover of ponderosa pine, and (2) percent cover of mixed-conifer [both of these first two variables were derived from a 30 m resolution raster in which each USFS-delineated forest stand within the study area was classified to one of five cover classes (ponderosa pine, mixed-conifer, spruce-fir, pinyon-juniper, and other) according to a majority rule based on a 2001 LANDFIRE Existing Vegetation Type layer (LANDFIRE 2001)], (3) forest edge density (the number of forest-nonforest edge cells per unit area derived from the aforementioned forest stand cover layer), (4) forest edge proximity (distance to the nearest forest-nonforest edge; also derived from the forest stand cover layer), and (5) percent canopy cover calculated from a set of forest structural 30 m resolution rasters (see description in Dickson et al. 2014) which the project study area was nested within. Climate covariates included: (1) total monsoon-season (defined as May–August) precipitation, (2) cumulative annual degree-days (using a 10 °C threshold), and (3) solar radiation index (Fu and Rich 2002), all derived using 30-year normal (1981–2010) 800 m resolution PRISM climate data (PRISM Climate Group 2014) resampled using bilinear interpolation to 30 m. All habitat variables were mapped at 30 m resolution across the study area, which represented the finest resolution in the source data. Importantly, we held the spatial grain of the analysis constant at 30 m in the multi-scale analyses described below.

Habitat selection modeling

We employed standard logistic regression to develop a Resource Selection Function (RSF) of MSO nest/roost habitat selection within the study area. This is somewhat analogous to Johnson's (1980) second-order habitat selection (i.e., home range selection within the population range or study area), although

we used nest/roost sites instead of home ranges or random points within home ranges as the observations in the analysis. Prior to running regression analyses on the full set of covariates, we first conducted a univariate scaling analysis to empirically identify and select the characteristic scale and the functional form (i.e., standard logistic or quadratic logistic) combination for each covariate to be used in multi-scale models. Specifically, for each covariate we calculated the Gaussian kernel density value (i.e., the Gaussian weighted mean as a function of Euclidean distance) across a range of bandwidths extending from 100 to 5000 m at intervals of 100 m for each use and pseudo-absence location. We then employed each of these covariates in a single covariate logistic regression model using standard logistic and quadratic logistic functional forms independently, and we retained the scale and functional form combination with the lowest Akaike's Information Criterion corrected for small sample size (AICc) value among all candidates. We also conducted these aforementioned scaling analyses separately using uniform and Gaussian kernel density forms, as we also were interested in comparing results between these two commonly employed kernel density forms. Prior to running multiple logistic regression analyses, we calculated Pearson's correlations among all covariates to assess potential multicollinearity. In instances of high pairwise correlation between covariates (i.e., $|r| \geq 0.7$), we retained the covariate with the greater deviance explained and removed the other covariate from subsequent analyses. We calculated variance inflation factor (VIF) for all remaining covariates and confirmed that none of the retained covariates had a $VIF \geq 10$.

We used a custom spatial autocovariate approach to reduce the influence of residual spatial autocorrelation on results. Briefly, for each analysis, we ran the global model of retained covariates following the multicollinearity analyses and included an exponential spatial autocovariate term. We defined the autocovariate term as the kernel density of use points around the focal point based on an exponential distance decay function, in which we estimated the exponent of the decay function and the beta for the autocovariate term in the global model. We then forced this fitted autocovariate into each model in the all-subsets routine (detailed in the following section). Results from Moran's I analyses indicated considerable

reduction in residual spatial autocorrelation when including the estimated autocovariate term (Fig. 2).

Next, we conducted an all-subsets logistic regression analysis employing all remaining covariates and compared results using an information-theoretic framework. We limited the maximum number of covariates in logistic regression models to eight to ensure a minimum sample-to-variable ratio of 25:1. We then used AICc and Akaike's model weights (ω) to rank the candidate models and select the model(s) that best separated MSO use locations from pseudo-absence locations. We considered models < 2 AICc units from the best supported model to be jointly supported (Burnham and Anderson 2002). If no single model comprised > 90 % of the weight of the entire candidate model set, we used model averaging to derive parameter estimates from the top models that accounted for > 90 % of the cumulative model weights (Burnham and Anderson 2002). We conducted analogous routines for all single-scale models (across all bandwidths extending from 100 m to 5000 m at intervals of 100 m) to compare with results from multi-scale models.

Single-scale vs. multi-scale models

We compared results from single- and multi-scale models across several criteria, including: (1) covariate

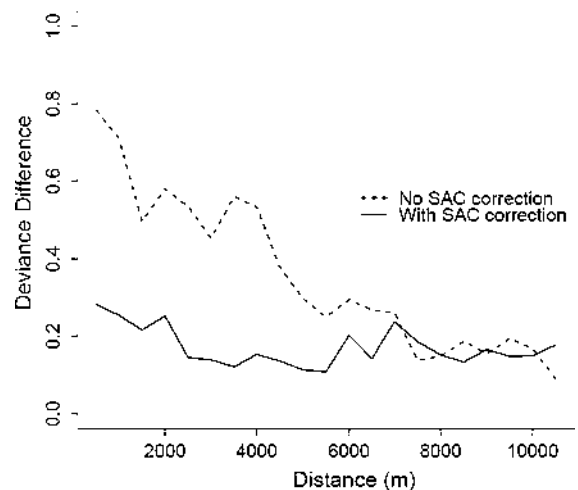


Fig. 2 Assessment of the effectiveness of the spatial autocovariate (SAC) approach we employed in reducing spatial autocorrelation of residuals. Shown are the Moran's I analysis results from the model-averaged multi-scale uniform kernel model as a representative example

effect size, (2) variable importance, (3) variance decomposition, (4) model explanatory power, and (5) model predictive performance. We define “single-scale models” in this context as models where all covariates are measured at the same scale. We used the difference in deviance between models with and without each covariate individually to compare relative effect sizes of covariates across scales. We estimated variable importance values for each covariate by summing model weights across all models containing that covariate. We used variance decomposition (using the “varpart” function in the “vegan” package in R; Oksanen et al. 2013) to assess the amount of variance explained independently and jointly by each of the three covariate groups (i.e., topographic, landscape composition, and climate). We used model-averaged proportion of deviance explained to evaluate model explanatory power.

We used a presence-only model validation method (Gegr and Trites 2008) to evaluate and compare model predictive performance. Briefly, this method calculates the (weighted) skewness of the distribution of model-derived predicted relative probability of occurrence values for a given presence-only dataset, whereby the more predictive the model is the higher the proportion of presence points that are at located at the higher end of the relative probability of occurrence values. Thus, the more left-skewed the distribution (i.e., the higher the proportion of the presence points that are located at the high end of the relative probability of occurrence values) the more predictive the model is in terms of accurately predicting use locations. To account for inter-model variability in the distribution of pseudo-absence relative probability of occurrence values across the defined study extent, the count of presence points in each relative probability of occurrence bin is weighted by the proportion of total pseudo-absence points that are in the associated bin and then the skewness is calculated on this weighted distribution of counts. We used this weighted skewness method to assess model predictive performance using both a cross-validation and independent validation dataset approach. For the cross-validation approach, we conducted a five-fold cross validation for each model at each scale. We built models for each fold using a randomly selected 4/5ths of the data and used the remaining 1/5th of the data as the presence-only dataset for calculating the weighted skewness. We then averaged the calculated weighted skewness

across the five-folds as the cross-validated weighted skewness value for the given model and scale. For the independent dataset approach, we built models at each scale using the entirety of the data and calculated weighted skewness on an independent MSO presence-only nest location dataset collected within the Coconino NF (USFWS unpubl. data).

We conducted all analyses in the R computing environment (R Development Core Team 2014).

Results

Results obtained from analyses employing uniform kernel densities were consistent with and comparable to those using Gaussian kernel densities; thus, for purposes of clarity we focus primarily on the uniform kernel results, unless otherwise specified.

The optimized scale identified for each covariate in the univariate scaling analyses varied considerably among covariates (Table 1); slope, topographic position index, percent mixed-conifer, and forest edge density were all most strongly related to MSO nest/roost selection at relatively fine scales (i.e., ≤ 500 m), whereas the remaining four covariates (i.e., percent canopy cover, percent ponderosa pine cover, monsoon-season precipitation, and cumulative degree-days) were all most strongly related at much coarser scales (i.e., > 2500 m). In addition, quadratic functional forms explained a greater proportion of the deviance in the data than linear functional forms for all of the topographic and climate covariates.

Absolute and relative effect size (as measured by deviance difference) of individual covariates varied substantially among scales in the single-scale models (Fig. 3). Most showed either a monotonic decay or a concave unimodal relationship between absolute effect size and increasing spatial scale. In general, landscape composition covariates and slope peaked at relatively fine spatial scales and decayed steeply thereafter, whereas other topographic and climate covariates displayed more of a unimodal relationship with peaks at coarser spatial scales than landscape composition covariates. As a consequence, relative effect sizes among covariates varied across scales, in some instances changing the rank ordering of covariates with respect to effect size. Thus, conclusions regarding the absolute and relative effects of individual covariates varied dramatically with the choice of

Table 1 Habitat covariates and the univariate optimized uniform and Gaussian kernel scale for each used in the multi-scale models assessing Mexican spotted owl nest/roost habitat selection

Covariate	Class	Data source	Top uniform scale (m)	Top Gaussian scale (m)
Slope (Q)	Topographic	LANDFIRE (2001)	400	200
Topographic position index (TopPos) (Q)	Topographic	LANDFIRE (2001)	500	300
Canopy cover (CanCov)	Composition	Dickson et al. (2014)	2700	1500
Ponderosa pine (PondPine)	Composition	USFS Stand Map with LANDFIRE (2001)	5000	5000
Mixed-conifer (MixCon)	Composition	USFS Stand Map with LANDFIRE (2001)	500	300
Forest edge density (Edge)	Composition	USFS Stand Map	400	200
Monsoon-season precipitation (MonPre) (Q)	Climate	PRISM Climate Group (2014)	3300	5000
Cumulative degree-days (DegDays) (Q)	Climate	PRISM Climate Group (2014)	5000	5000

Q a quadratic fit was the best for a given covariate

scale in the single-scale models and differed from the multi-scale model. Importantly, the scale with the greatest effect size for individual covariates in the single-scale models was largely inconsistent with the optimized scale identified for that covariate (Fig. 3). For example, the optimized scale for canopy cover was 2700 m and its effect size in the multi-scale model was roughly 8.6. Its effect size in the single-scale models was less than that of the multi-scale model across all scales (<8.0), but was greatest at the finest scale evaluated (100 m uniform kernel). Thus, based on the single-scale modeling approach we would conclude that canopy cover had its greatest effect on MSO nest/roost site occurrence at 100 m, whereas in the multi-scale modeling approach we would conclude that canopy cover has a greater effect at 2700 m.

Variable importance of individual covariates displayed a similar pattern with respect to spatial scale as was observed with effect size (Fig. 4). In general, variable importance of individual covariates varied dramatically across scales in the single-scale models, in many cases changing the status of variables from relatively important (e.g., >0.8) to unimportant (e.g., <0.3). In addition, variable importance of individual covariates in the multi-scale model often differed dramatically from that of the single-scale models. For some covariates (canopy cover, slope, and monsoon-season precipitation) variable importance was greatest in the multi-scale model, for other covariates (mixed-conifer and degree-days) variable importance was

consistently greater across all scales in the single-scale models, and for other covariates (ponderosa pine, edge density, and topographic position) variable importance was greater in the single-scale models at some scales but not at others. Thus, as with effect size, conclusions regarding the absolute and relative importance of individual covariates varied dramatically with the choice of scale in the single-scale models and differed from the multi-scale model.

The multi-scale models explained a greater proportion of total deviance in the data than any single-scale model for the corresponding kernel form (Fig. 5). In addition, the multi-scale uniform and Gaussian models consistently outperformed their single-scale counterparts with respect to predictive performance across all single-scales assessed, with exception to the 500 m-scale uniform kernel model evaluated against an independent dataset (Fig. 6). In general, predictive performance of the single-scale models was best in the 300–1000 m neighborhood scale and declined substantially beyond this range. Interestingly, despite the generally superior performance of the multi-scale model over the single-scale models, the best single-scale model (i.e., the 400 m radius scale model, as determined by proportional deviance explained) was not that different from the multi-scale model with respect to model-averaged parameter estimates (or odds ratios) and variable importance (Table 2).

The suite of top multi-scale nest/roost models (i.e., the top-ranked models that, combined, accounted for

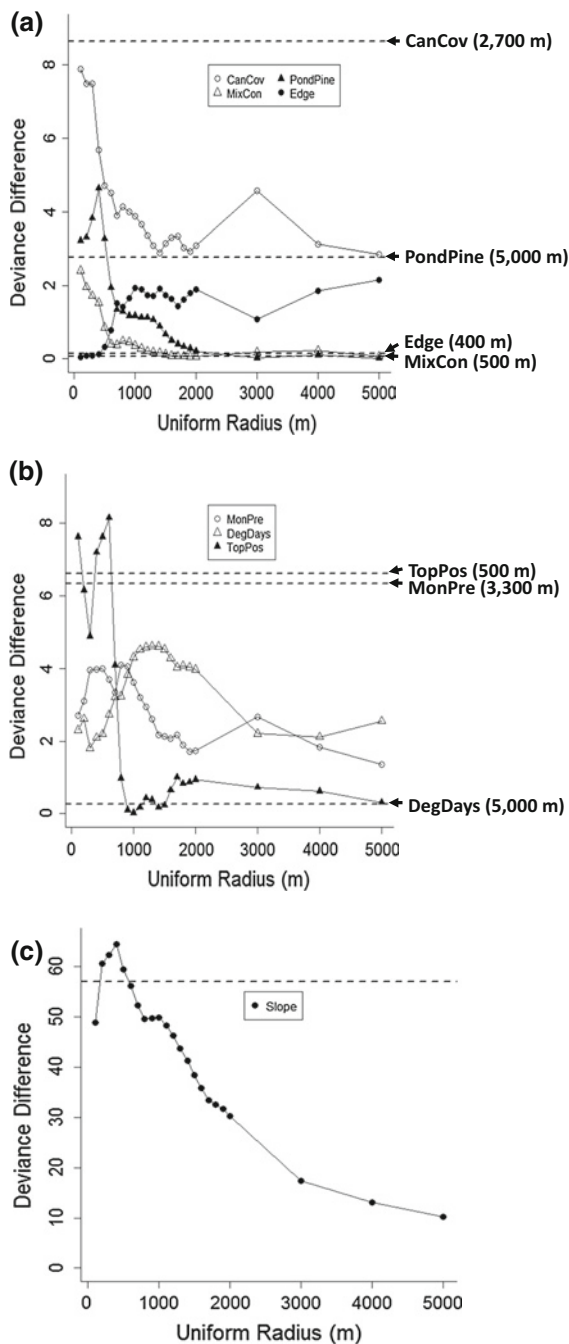


Fig. 3 Deviance difference between models with and without each given covariate across all uniform kernel, single-scale models. The horizontal lines show the deviance difference for each covariate from the optimized, uniform kernel, multi-scale model for comparison (and the optimized scale for each covariate is shown in parentheses). A larger deviance difference indicates greater explanatory power of that covariate across all models that covariate is in

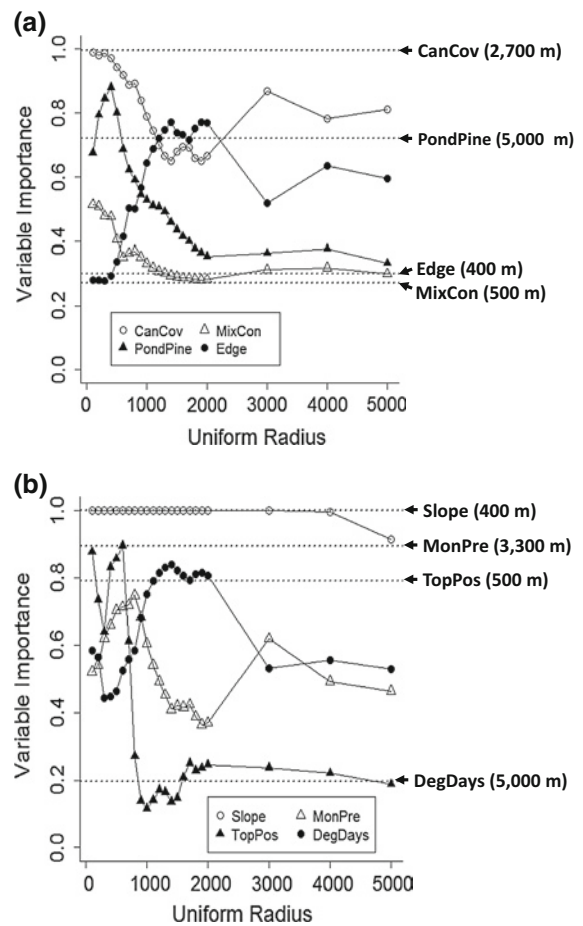


Fig. 4 Variable importance values for all covariates across all uniform kernel, single-scale models. The horizontal lines display variable importance values for each covariate from the optimized, uniform kernel, multi-scale model for comparison (and the optimized scale for the covariate is shown in parentheses)

>90 % of the cumulative model weights) all contained percent canopy cover and slope with a subset of other covariates (Table 3). MSO nest/roost selection was positively related to percent canopy cover and showed a broad concave unimodal relationship with slope. Model-averaged variance decomposition analyses indicated that the marginal and conditional effects of topographic covariates accounted for most of the total variance explained in the multi-scale models, with the remainder approximately equally distributed between landscape composition and climate covariates (Fig. 7).

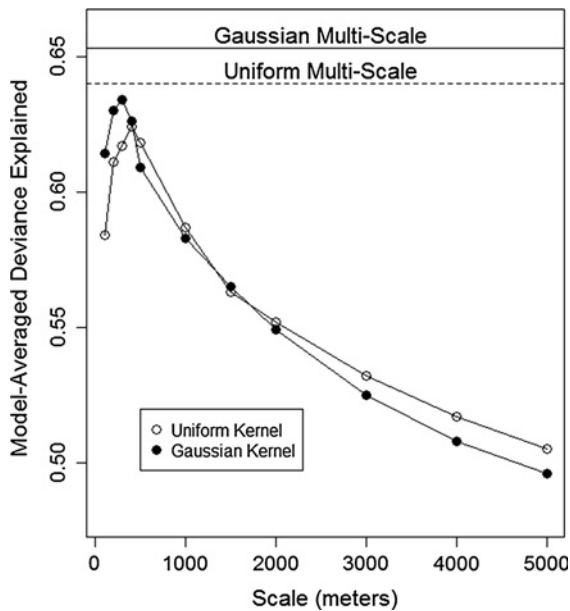


Fig. 5 Model-averaged proportion of deviance explained from all single-scale uniform and Gaussian kernel models. *Horizontal lines* show the deviance explained by the optimized multi-scaled models for both functional forms. A larger deviance difference indicates greater explanatory power across all models at a given scale

Discussion

Multi-scale MSO nest/roost habitat selection

Results from the multi-scale habitat selection modeling indicate that MSO nest/roost selection was most strongly related to slope and percent canopy cover, and to a lesser extent topographic position, monsoon-season precipitation, and ponderosa pine cover. The strong (and positive) relationship with percent canopy cover is consistent with other studies assessing nest-site selection by MSO (Seamans and Gutiérrez 1995; Grubb et al. 1997; May et al. 2004; Ganey et al. 2013) as well as for the other two North American spotted owl subspecies (Northern spotted owl: Forsman and Giese 1997; Hershey et al. 1998; Loehle et al. 2015; California spotted owl: Bias and Gutierrez 1992; Blakesley et al. 2005), and it has been suggested that these owls select areas with high canopy cover because these locations provide moderate microclimates and refuge from predators (Barrows 1981; Carey 1985; Gutiérrez 1985; Ganey et al. 1999). The strong relationship with slope and, to a lesser extent,

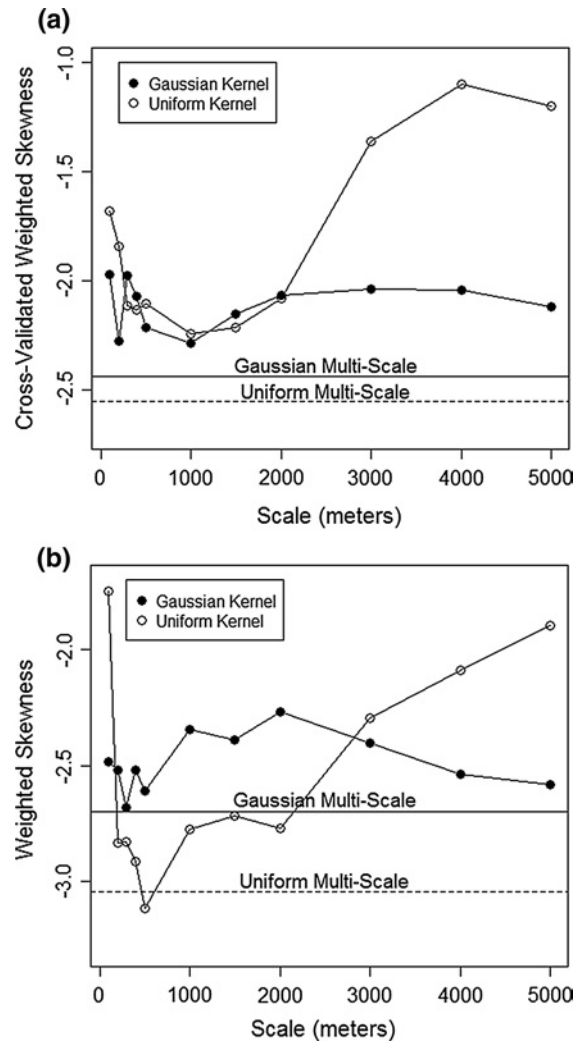


Fig. 6 Predictive performance, as measured by a weighted skewness metric (GREG and Trites 2008), from all single-scale uniform and Gaussian kernel models using both a cross-validation (a) and an independent dataset approach (b). *Horizontal lines* show weighted skewness for the optimized multi-scaled models for both functional forms. Note that a greater negative weighted skewness value indicates better predictive performance

topographic position also is consistent with previous studies (Ganey and Balda 1989; May et al. 2004), and is likely primarily indicative of the extensive use by MSO of relatively steep, narrow, forested canyons throughout the study area, which is readily apparent in predicted surfaces generated from the multi-scale models (e.g., Fig. 8). These narrow canyons likely provide relatively cool, moist microclimates, with high structural habitat diversity (most notably multi-

Table 2 Model-averaged interquartile range odds ratios, 95 % confidence intervals, and variable importance for the top uniform kernel, single-scale (i.e., 400 m radius) model and the uniform-kernel, multi-scale model

Covariate	Single-scale model (400 m)		Multi-scale model	
	Odds ratio (95 % CI)	Importance	Odds ratio (95 % CI)	Importance
Intercept	1.631e−07 (4.295e−15 to 6.197e04)	1.00	1.721e−04 (3.705e−18 to 7.994e09)	1.00
CanCov	4.136 (1.567–10.918)	0.97	4.856 (1.811–13.019)	1.00
MixCon	1.755 (0.706–4.369)	0.48	1.098 (0.593–2.031)	0.27
PondPine	4.963 (1.015–24.266)	0.88	2.537 (0.996–6.460)	0.72
Edge	0.860 (0.411–1.799)	0.29	0.832 (0.420–1.649)	0.30
Slope	160.508 (11.507–2.238e05)	1.00	343.778 (29.052–406.806)	1.00
Slope ²	0.195 (0.031–1.215)	1.00	0.090 (173.778–461.106)	1.00
TopPos	247.630 (1.197 to 5.121e04)	0.83	122.025 (0.682–218.429)	0.79
TopPos ²	0.007 (3.51e−05 to 1.256)	0.83	0.001 (7.662e−07 to 2.368)	0.79
MonPre	0.042 (9.274e−05 to 19.407)	0.66	0.002 (1.757e−06 to 2.062)	0.90
MonPre ²	10.152 (0.038–2.697e03)	0.66	150.401 (0.240–9.427e04)	0.90
DegDays	63.474 (0.456–8.842e03)	0.45	13.629 (0.0754–2.461e03)	0.20
DegDays ²	0.011 (6.473e−05 to 1.810)	0.45	0.060 (2.742e−04 to 13.338)	0.20
SAC	11.876 (5.637–25.019)	1.00	13.673 (5.948–31.434)	1.00

Covariates are defined in Table 1 (SAC = spatial autocovariate, see text for details)

layered canopies). Though we were unable to assess habitat selection associated with canopy-layering in this study (due to a lack of data sources to estimate this study area wide), the importance of canopy layering for MSO (Seamans and Gutiérrez 1995; Hathcock and Haarmann 2008) and other spotted owl subspecies (Northern spotted owl: Mills et al. 1993; Everett et al. 1997; McComb et al. 2002; California spotted owl: LaHaye et al. 1997; Moen and Gutiérrez 1997) has been well-documented, and has been attributed to increased prey availability, protection from potential predators, and moderated microclimates. The use of these forested canyons may also be an indirect result of previous management activities (May et al. 2004) combined with historic fire patterns in these landscape settings (Beier and Maschinski 2003). Specifically, due to reduced timber harvest and firewood gathering in areas of steep terrain (U.S. Fish and Wildlife Service 2012) combined with a reduced fire frequency in canyons (Beier and Maschinski 2003), these areas may retain larger and more suitable trees for nesting.

Of particular note was the low effect size and variable importance of percent mixed conifer in our study given that MSO have been documented primarily nesting in mixed conifer settings in forested landscapes in the southwestern U.S. (Ganey and Balda

1989; Seamans and Gutiérrez 1995; May and Gutiérrez 2002). One potential explanation to this seemingly contradictory finding may be the extensive use of pine-oak cover by Mexican spotted owls in the study landscape (Ganey et al. 1999; May and Gutiérrez 2002; May et al. 2004), which may have provided a suitable alternative to mixed conifer. Though poorly mapped throughout the entire extent of our study area, ponderosa pine—Gambel oak (*Quercus gambelii*) cover is widespread and abundant throughout the study area, and has a number of attributes that are consistent with preferred nesting and roosting habitat by MSO. Notably, these pine-oak stands are typically characterized by high canopy cover, with a multi-layered canopy, and with relatively high prey densities (Ward and Block 1995). Additionally, MSO nest extensively in Gambel oak cavities, and owls have been observed nesting in the same cavity for up to 7 years, which may be preferred over other available nest settings (e.g., platform nests) due to the cool and sheltered environment it provides for the incubating female and nestlings (May et al. 2004). Another potential/partial explanation for the apparent limited importance of mixed conifer cover in nest/roost habitat selection in this study relates to the study design during the initial data collection phase.

Table 3 The top-ranked uniform kernel, multi-scale logistic regression models assessing foraging habitat selection by Mexican spotted owls

Model	D ²	AICc	ΔAICc	wgtAICc
CanCov + PondPine + Slope* + MonPre* + TopPos* + SAC	0.64	225.34	0.00	0.22
Edge + CanCov + PondPine + Slope* + MonPre* + TopPos* + SAC	0.64	227.28	1.94	0.08
MixCon + CanCov + PondPine + Slope* + MonPre* + TopPos* + SAC	0.64	227.29	1.94	0.08
CanCov + Slope* + MonPre* + TopPos* + SAC	0.64	227.49	2.15	0.08
CanCov + PondPine + Slope* + MonPre* + SAC	0.63	228.21	2.86	0.05
CanCov + Slope* + MonPre* + TopPos* + DegDays* + SAC	0.64	229.06	3.71	0.04
CanCov + PondPine + Slope* + MonPre* + TopPos* + DegDays* + SAC	0.65	229.06	3.72	0.04
Edge + MixCon + CanCov + PondPine + Slope* + MonPre* + TopPos* + SAC	0.65	229.18	3.84	0.03
MixCon + CanCov + Slope* + MonPre* + TopPos* + SAC	0.64	229.56	4.22	0.03
Edge + CanCov + Slope* + MonPre* + TopPos* + SAC	0.64	229.58	4.24	0.03
MixCon + CanCov + PondPine + Slope* + MonPre* + SAC	0.63	229.83	4.48	0.02
CanCov + Slope* + MonPre* + SAC	0.63	229.85	4.50	0.02
CanCov + PondPine + Slope* + TopPos* + SAC	0.63	229.97	4.63	0.02
Edge + CanCov + PondPine + Slope* + MonPre* + SAC	0.63	230.13	4.78	0.02
Edge + CanCov + PondPine + Slope* + TopPos* + SAC	0.63	230.19	4.85	0.02
Edge + CanCov + Slope* + MonPre* + TopPos* + DegDays* + SAC	0.64	230.92	5.58	0.01
Edge + CanCov + PondPine + Slope* + MonPre* + TopPos* + DegDays* + SAC	0.65	230.92	5.58	0.01
MixCon + CanCov + PondPine + Slope* + MonPre* + TopPos* + DegDays* + SAC	0.65	231.06	5.72	0.01
MixCon + CanCov + Slope* + MonPre* + TopPos* + DegDays* + SAC	0.64	231.17	5.82	0.01
CanCov + Slope* + MonPre* + DegDays* + SAC	0.63	231.60	6.25	0.01
Edge + MixCon + CanCov + Slope* + MonPre* + TopPos* + SAC	0.64	231.66	6.32	0.01
Edge + MixCon + CanCov + PondPine + Slope* + MonPre* + SAC	0.63	231.67	6.32	0.01
Edge + CanCov + Slope* + MonPre* + SAC	0.63	231.92	6.57	0.01
MixCon + CanCov + Slope* + MonPre* + SAC	0.63	231.92	6.58	0.01
MixCon + CanCov + PondPine + Slope* + TopPos* + SAC	0.63	231.99	6.64	0.01
CanCov + PondPine + Slope* + MonPre* + DegDays* + SAC	0.63	232.01	6.66	0.01
Edge + MixCon + CanCov + PondPine + Slope* + TopPos* + SAC	0.63	232.29	6.94	0.01

* Covariates where the linear + quadratic terms were used. Covariates are defined in Table 1 (SAC = spatial autocovariate, see text for details) and D² is the proportion of deviance explained by the model. Models were ranked using change in Akaike's information criterion corrected for small sample size (ΔAICc) and Akaike's model weights (wgtAICc)

Specifically, most of the owl surveys were conducted at sites where management activities were proposed, which was largely within ponderosa pine stands at the time, thus surveys in mixed conifer stands were likely underrepresented in this dataset. Unfortunately we did not have adequate documentation identifying the full suite of sites sampled, both where MSO were recorded and sites where they were not, thus we cannot estimate the potential bias introduced by this sampling scheme. Finally, based on a visual inspection of the LAND-FIRE raster which was used as the basis for the input land cover layer for these analyses, it was apparent that mixed conifer cover in the study area was considerably

underestimated, which could have also contributed to a downward-biased variable importance for mixed conifer in the analyses.

The optimized scale identified for each covariate to enter multi-scale models varied considerably among covariates in this study, as discussed below. In addition to providing for robust multi-scale models, results from the scaling analysis component of the multi-scale modeling allowed us to gain improved insight regarding the scales at which MSO responded to different components of the landscape. The two topographic covariates (i.e., slope and topographic position index) entered at relatively fine scales, which,

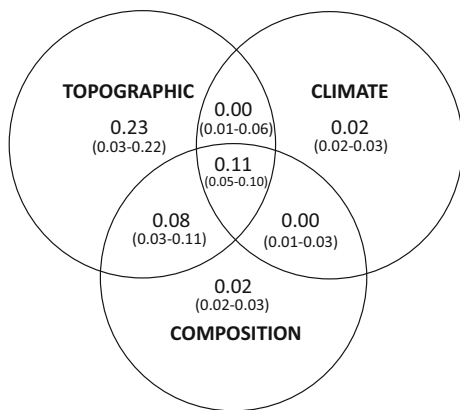


Fig. 7 Model-averaged variance decomposition results from the uniform kernel models, showing proportions of variance explained by different suites of covariates. Proportions shown in *larger font* are results from the multi-scale model whereas those in the smaller font and in *parentheses* are the range of results across all single-scale models

as discussed previously, is likely the result of the extensive use of relatively steep, narrow, forested canyons throughout the study area for nesting by MSO. The two climate covariates (i.e., monsoon-season precipitation and cumulative degree-days) entered at much coarser scales, which was to be expected given that these two metrics vary at relatively coarse resolutions. Interestingly, of the four landscape composition covariates used in the multi-scale models, percent mixed-conifer cover and forest edge density entered at relatively fine scales (though both with low variable importance values) whereas percent canopy cover and percent ponderosa pine cover entered at considerably coarser scales. This suggests that percent mixed-conifer cover and forest edge density are more relevant to conditions in the immediate vicinity of the nest/roost (e.g., microclimate and exposure to potential predators), whereas percent canopy cover and percent ponderosa pine cover are more relevant to conditions in the broader landscape surrounding the nest (e.g., foraging habitat suitability).

Results from the variance decomposition analysis indicated that topographic covariates contributed the greatest amount of variation explained in the data, whereas the variance explained by landscape composition and climate variables was considerably reduced in comparison. As it is difficult to hypothesize a robust mechanistic relationship between MSO nest/roost selection and these topographic covariates, this finding

is likely the result of these topographic covariates acting largely as a proxy for microhabitat and/or microclimate conditions (as discussed previously). The relatively minor effect of climate was somewhat surprising as this species is hypothesized to be negatively affected by high temperatures (Barrows 1981; Ganey 2004); however, the climate rasters that we employed were constructed at an 800 m resolution, which likely were at too coarse of a resolution to adequately assess selection for these climatic covariates.

Lastly, results from models using Gaussian kernels and those using uniform kernels did not vary substantially in our study, which was counter to our expectations. It makes intuitive ecological sense that organisms are most strongly affected by habitat conditions within their immediate vicinity and that this effect likely decays with increasing distance from the organism, thus we expected that measuring habitat covariates using a functional form that emulates such a pattern would outcompete a standard uniform kernel. Though we did not find a difference in this study, we strongly encourage researchers in future habitat selection studies to include non-uniform kernels to more broadly assess the effect of kernel form on modeling efficacy.

Single-scale vs. multi-scale MSO nest/roost habitat models

While several previous studies assessed MSO habitat use and habitat selection at multiple scales (Grubb et al. 1997; Peery et al. 1999; May and Gutiérrez 2002; Ganey et al. 2013), our study was the first to do so in a multi-scale framework that allowed covariates to enter models at different spatial scales. Multi-scale models outcompeted all single-scale models in our study with respect to explanatory power and all but one single-scale model with respect to predictive performance. This is consistent with our current understanding of MSO biology throughout their range, whereby they appear to select nest sites that provide moderate microclimates at the nest and the immediate vicinity, while at the same time locating the nest such that it is in relative close proximity to high quality foraging habitat. Our findings are consistent with a growing body of habitat selection studies across a range of species supporting the superiority of multi-scale models over their single-scale counterparts (Boscolo

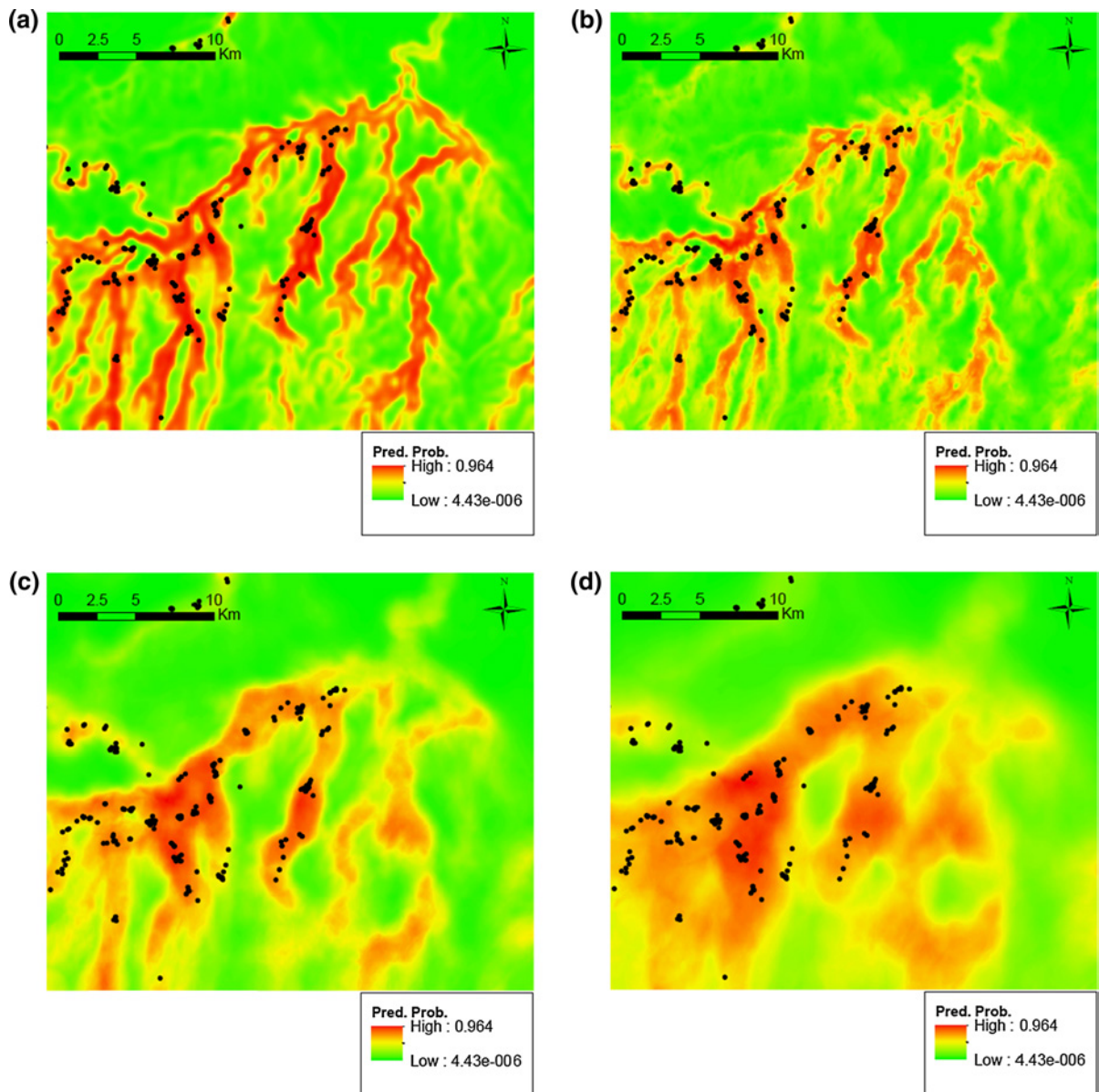


Fig. 8 Predicted nest/roost habitat suitability surface for a subarea of the entire study area using model-averaged **a** multi-scale, uniform kernel, **b** 500 m-radius uniform kernel, **c** 1 km-radius uniform kernel, and **d** 2 km-radius uniform kernel. Filled

circles on the surfaces indicate MSO nest/roost locations from a separate dataset provided by USFWS that was not used to build the habitat models

and Metzger 2009; Kuhn et al. 2011; Sanchez et al. 2013, but see Martin and Fahrig 2012 for an exception).

Results from single-scale MSO nest/roost models varied considerably as a function of scale. For example, the greatest effect size obtained for seven of the eight covariates occurred at scales ≤ 1 km and tended to monotonically decay, in some cases quite

precipitously, with increasing spatial scale thereafter. The ordering of covariates also changed in terms of relative effect size and variable importance across the scales that we assessed. Thus, inferences made regarding the MSO nest/roost habitat selection could change considerably depending upon the selected scale of analysis in a single-scale modeling approach. Employing a scale-optimized, multi-scale model

provided for a more objective and ecologically robust method of selecting the scale at which each covariate would enter the analysis, thus reducing the amount of researcher bias potentially injected into the results.

Management and conservation implications

Our results provide an empirical assessment of multi-scale nest/roost habitat selection for MSO throughout a substantial and important portion of their current range. These results can be used to help guide extensive management efforts that are currently underway in the region aimed at restoring ponderosa pine stands to pre-settlement conditions following a century of fire suppression and other land uses such as livestock grazing. Largely the result of this fire suppression and human land use, much of the current landscape exists as unnaturally dense stands of ponderosa pine that has dramatically increased the threat and incidence of extensive high mortality wildfires (Covington et al. 1994; Allen et al. 2002; Brown et al. 2004). The threat of these high mortality wildfires is high in many MSO Protected Activity Centers (PACs), as thinning efforts have been limited in these areas due to perceived conflicts with the closed-canopy nesting requirements of spotted owls and increased regulatory restrictions in these locations (U.S. Fish and Wildlife Service 2012). However, more recently managers have appreciated that a lack of active management (e.g., thinning) within PACs may have a negative impact on the long-term persistence of MSO habitat due to the increasing likelihood of stand-replacing crown fires (Prather et al. 2008; U.S. Fish and Wildlife Service 2012). An MSO-specific relative probability of occurrence map generated throughout the study area from this current modeling effort will allow for more effective treatment prescriptions aimed at MSO conservation and management.

Consistent with previous studies, MSO nest/roost sites were positively correlated with canopy cover (Seamans and Gutiérrez 1995; Grubb et al. 1997; Ganey et al. 1999, 2000; May et al. 2004), indicating a need to retain areas with abundant canopy cover to provide adequate nest/roost habitat in the study area. While much of the current landscape exists as dense canopied ponderosa pine cover, the majority of these areas are characterized by unnaturally high density of small-diameter trees. As suggested previously (e.g., in Prather et al. 2008), conducting low intensity thinning

in these areas would allow for increased tree growth (Mast 2003), providing large trees and snags used by MSO for nesting and roosting while at the same time reducing the threat of high severity crown fires. Due to the consistent finding across numerous studies of the considerable importance of canopy cover in nest site selection by MSO, experimental work assessing potential threshold effects of canopy reduction with respect to MSO nesting habitat suitability would be extremely valuable for land managers.

Scope, limitations, and future directions

Our findings must be interpreted with regard to several major considerations. First, our data were collected in a considerably human-altered landscape, as noted above. Thus, the degree to which our habitat selection estimates (e.g., covariate beta estimates) reflect those exhibited under the historic, pre-settlement landscape setting in which this species evolved is unknown. Second, the habitat data we used were entirely GIS-based, as we didn't have comprehensive field-collected habitat data for both use and pseudo-absence locations. MSO are known to cue in on specific microhabitat features (e.g., trees with mistletoe infections, snags, trees with existing cavities) and forest structural conditions (e.g., multi-layered canopies) in close proximity to nest trees that were not available in our GIS layers. The extent to which the inclusion of these data would have impacted the results is unknown. Third, the amount of canopy cover within 100 m of the nest/roost for the best single-scale model or within 2700 m of the nest/roost for the multi-scale model was one of the strongest predictors of nest/roost habitat for MSO in this study, though the effect of the spatial configuration of canopy cover, especially at fine scales, on habitat use/selection is unknown. Based on preliminary analyses we conducted for a small subset area of our study area, it appears that fine-scale canopy configuration may be an important predictor of habitat use by this species. We are currently in the process of constructing a fine-scale canopy raster for the entire extent of our study area using a supervised remote-sensing classification scheme, which we plan to employ to assess the effect of selected canopy configuration metrics on MSO habitat use and selection. Lastly, it is plausible that our assessment of scale dependency was influenced by the varying texture and quality of the input data. In particular, the cover type

map was derived from LANDFIRE (2001) and in general had a relatively coarse texture, whereas the canopy cover map was derived by Dickson et al. (2014) and had a relatively fine texture. Given the disparity in textures and accuracy among data sources we opted not to include a suite of potentially important vegetation configuration metrics in the analysis, other than forest-nonforest edge density and proximity which we deemed suitable as derived from the LANDFIRE-based cover type map. In addition, we also used Gaussian kernel smoothing over 100–5000 m bandwidths for all of the independent variables which should be relatively insensitive to variations in fine-grained texture of the input layers. Thus, by carefully selecting predominantly landscape composition metrics and using kernel smoothing over relatively coarse scales, we deemed our results relatively robust to variations in texture and accuracy of the input data sources.

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