



RESEARCH ARTICLE

Meta-replication reveals nonstationarity in multi-scale habitat selection of Mexican Spotted Owl

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Submitted February 17, 2017; Accepted May 19, 2017; Published August 9, 2017

ABSTRACT

Anthropogenic environmental changes are leading to habitat loss and degradation, driving many species to extinction. In this context, habitat models become increasingly important for effective species management and conservation. However, most habitat studies lack replicated study areas and do not properly address the role of nonstationarity and spatial scales in determining factors that limit species occurrence under different environmental settings. Here we provide an optimized multi-scale framework for analyzing habitat selection of the threatened Mexican Spotted Owl (*Strix occidentalis lucida*) between 2 meta-replicated study areas: the Sacramento Mountains, New Mexico, and the Mogollon Plateau, Arizona. The optimized scales of habitat variables strongly differed between the 2 study areas. Percent cover of mixed-conifer was more strongly associated with the relative likelihood of Mexican Spotted Owl occurrence in the Sacramento Mountains than in the Mogollon Plateau. Topographic covariates strongly explained variance in the habitat model in the Mogollon Plateau, but not in the Sacramento Mountains. Topographically constrained habitat availability may be affecting the relative likelihood of owl occurrence in the Mogollon Plateau, but not in the Sacramento Mountains. In the Sacramento Mountains, suitable habitat and owl distributions show dissimilar spatial autocorrelation patterns, indicating that the relative likelihood of occurrence may be influenced by factors in addition to habitat. Owl distribution shows a periodic spatial pattern, suggesting that the relative likelihood of owl occurrence in the Sacramento Mountains might be influenced by territoriality. Differences in habitat relationships between the 2 study areas suggest that management strategies should be tailored to local conditions. This study underscores the advantage of scale optimization and replicated studies in analyzing nonstationary habitat selection.

Keywords: climate change, conservation, endangered species, habitat suitability, modeling, niche differentiation

La meta-replicación revela la falta de estacionariedad en la selección de hábitat a múltiples escalas para *Strix occidentalis lucida*

RESUMEN

Los cambios ambientales antropogénicos están provocando pérdida y degradación de hábitat, conduciendo a muchas especies a la extinción. En este contexto, los modelos de hábitat se tornan cada vez más importantes para el manejo y la conservación efectiva de las especies. Sin embargo, la mayoría de los estudios de hábitat no presentan réplicas de las áreas de estudio y no abordan adecuadamente el rol de la falta de estacionariedad y de las escalas espaciales para determinar los factores que limitan la ocurrencia de las especies bajo diferentes escenarios ambientales. En este estudio brindamos un marco de trabajo optimizado de múltiples escalas para analizar la selección de hábitat de la especie amenazada *Strix occidentalis lucida* entre dos áreas de estudio meta-replicadas – las Sierras de Sacramento, Nuevo México y la Meseta de Mogollón, Arizona. Las escalas optimizadas de las variables de hábitat variaron fuertemente entre las dos áreas de estudio. El porcentaje de cobertura de los bosques de coníferas mixtas estuvo más fuertemente asociado con la probabilidad relativa de ocurrencia de *S. o. lucida* en las Sierras de Sacramento que en la Meseta de Mogollón. Las covariables topográficas explicaron en gran medida la varianza en el modelo de hábitat en la Meseta de Mogollón, pero no en las Sierras de Sacramento. La disponibilidad de hábitat ajustada por la topografía podría estar afectando la probabilidad relativa de ocurrencia del búho en la Meseta de Mogollón, pero no en las Sierras de Sacramento. En las Sierras de Sacramento, el hábitat adecuado y la distribución del búho mostraron patrones de autocorrelación espacial diferentes, indicando que la probabilidad relativa de ocurrencia podría estar influenciada por otros factores además del hábitat. La distribución del búho mostró un patrón espacial periódico, sugiriendo que la probabilidad relativa de ocurrencia del búho en las Sierras de Sacramento podría estar influenciada por la

territorialidad. Las diferencias en las relaciones de hábitat entre las dos áreas de estudio sugieren que las estrategias de manejo deberían estar ajustadas a las condiciones locales. Este estudio subraya las ventajas de la optimización de la escala y la réplica de los estudios para analizar la selección de hábitat no estacionaria.

Palabras clave: aptitud de hábitat; cambio climático; conservación; diferenciación del nicho; especies en peligro; modelado

INTRODUCTION

Species extinction rates in the Anthropocene are increasing exponentially (Barnosky et al. 2011). Many species are declining in response to major anthropogenic environmental changes, such as biological invasion, pollution, altered fire regimes, and climate change. Identifying and monitoring the populations and habitats of species of concern has become a critical task for conserving biodiversity as many species experience habitat loss and degradation.

The development of statistical models to quantify species' resource selection and predict habitat distributions have garnered increasing interest in wildlife management and conservation (Hegel et al. 2010). Because species may be limited by different factors across their range, depending on spatial variation in local habitat conditions, replicated study areas are often needed to ascertain potential nonstationary species–habitat relationships over extensive species' ranges that encompass differing environmental conditions (e.g., Short Bull et al. 2011, Shirk et al. 2014). Replicated study areas can improve our understanding of factors that influence species occurrence and how they differ between study areas because of environmental variation (Cushman et al. 2011, Shirk et al. 2014). However, studies in different areas usually are conducted independently and often differ in the type of data collected, sampling scheme, experimental design, and statistical approach, making comparison difficult.

Moreover, many habitat studies do not address the issue of scale in their analyses (McGarigal et al. 2016) despite the longstanding recognition of the scale dependency of species–habitat relationships (Wiens 1989, Levin 1992, Mayor et al. 2009), and many that incorporate scale do not do so in rigorous fashion (McGarigal et al. 2016). A misconception about multi-scale modeling is that using multiple scales promises stronger inference (McGarigal et al. 2016), but the reality is that multi-scale models may still lead to prediction errors if the scales are chosen arbitrarily or are not optimized (Thompson and McGarigal 2002, Grand et al. 2004, Wasserman et al. 2012, Shirk et al. 2014).

Timm et al. (2016) analyzed the habitat selection of the Mexican Spotted Owl (*Strix occidentalis lucida*; MSO), a federally listed threatened species, in the Mogollon Plateau of Arizona, and demonstrated that an optimized multi-scale modeling approach provided large improvements in predictive performance over single-scale models that were

not scale optimized. Although their study area was large, they did not include a replicated study area, providing little inference on how the MSO might respond to different environmental conditions in other areas. Both multi-scale optimized modeling and spatial replication are required to facilitate robust inference and reliable predictions regarding nonstationary species–habitat relationships (e.g., McGarigal and Cushman 2002).

Our objective was to demonstrate a multi-scale optimization framework for evaluating whether environmental factors that influenced habitat relationships were stationary or nonstationary across the range of a species. We accomplished this by using the threatened MSO, a species of high conservation interest, as a case study. We contrasted the results between 2 study areas dominated by forested habitat: the Sacramento Mountains of New Mexico and the Mogollon Plateau of Arizona. In both study areas, owl nesting is concentrated in mixed-conifer forest with high canopy cover (USFWS 2012). We developed single-scale and multi-scale habitat selection models, and identified factors in each study area that led to differences in the models. We also evaluated the relationship between scale and spatial pattern of owl and habitat distributions in the Sacramento Mountains. Our analysis was guided by 3 hypotheses:

- (1) The scale-optimized model will outperform the unoptimized models, and will illustrate qualitative differences in the interpretation of habitat relationships of MSO.
- (2) MSO will exhibit nonstationarity in habitat selection between the 2 study areas. Specifically, the scale-optimized model for the Sacramento Mountains will differ from that reported for the Mogollon Plateau because of different physiographic environments. In the Sacramento Mountains, we expect forest composition variables such as percent canopy cover and forest type will be more important than topographic variables because topography is dominated by a single high-elevation massif where mixed-conifer forests are fairly widespread and not restricted by topography. In contrast, mixed-conifer forests on the Mogollon Plateau are more topographically driven, occurring mostly in high mountains, canyons, or buttes.
- (3) The Sacramento Mountains model will explain substantially less variance than the Mogollon Plateau model because the Sacramento Mountains are char-

acterized by extensive, high-elevation closed-canopy mixed-conifer forests, which we expect to provide high quality habitat for the MSO. This will lead to less contrast between used and available points, and thus lower model discrimination. On the Mogollon Plateau, the heterogeneous pattern of suitable forested habitat distribution will lead to large differences between used and available sites, and thus higher model discrimination.

METHODS

Study Area

We modeled MSO habitat selection within a study area in the Sacramento Mountains in south-central New Mexico, and compared the resulting model to a model developed in a separate study area located along the Mogollon Plateau in north-central Arizona (Timm et al. 2016; Figure 1; approximate distance between study areas = 300 km).

The Sacramento Mountains study area encompassed much of the Sacramento Ranger District of the Lincoln National Forest and included approximately 150,000 ha in a montane sky-island surrounded by a matrix of desert and semi-desert habitat. Terrain within the study area consisted of heavily forested montane ridges and slopes interspersed with meadows in the larger valley bottoms. Elevation ranged from 2,000 to 2,800 m. Precipitation averaged 65 cm yr⁻¹ with summer thunderstorms providing more than 60% of annual precipitation and most of the remainder occurring as winter snowfall (Kaufmann et al. 1998). Higher-elevation forest was dominated by mixed-conifer of white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*). Southwestern white pine (*Pinus strobiformis*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*) were also common in this area (Kaufmann et al. 1998, Ward 2001). Maples (*Acer* spp.) and Gambel oak (*Quercus gambelii*) were common in the understory at some sites, and the most common shrub species was rock spirea (*Holodiscus dumosus*). At the lower elevations, drier forest types dominated the landscape, with pinyon pine (*P. edulis*) and alligator juniper (*Juniperus deppeana*) dominating many ridgetops and most south-facing slopes. North-facing slopes were dominated by ponderosa pine forest, sometimes with a prominent component of Gambel oak. Gray oak (*Q. griseus*) and wavyleaf oak (*Q. undulatus*) also were present in some areas. Mixed-conifer forests in these areas were restricted to cooler microsites such as drainage bottoms and north-facing slopes.

The Mogollon Plateau study area used by Timm et al. (2016) included much of the Coconino and Apache-Sitgreaves National Forests (Figure 1). Most surveys for

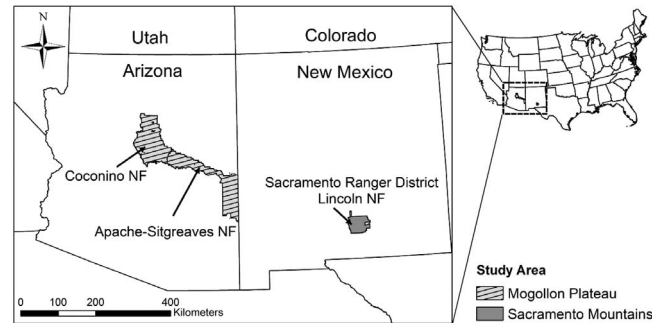


FIGURE 1. Locations of our study areas within the United States. Also shown are locations of the Mogollon Plateau study area in Coconino and Apache-Sitgreaves National Forests of Arizona, and the Sacramento Mountains study area in Lincoln National Forest of New Mexico.

Spotted Owls occurred in the higher-elevation forests that occurred on high plateaus having isolated volcanic mountains and deep canyons. The low-to-middle elevation of these plateaus was dominated by extensive forests of ponderosa pine, often containing an understory of Gambel oak. At higher elevations, or in cold-air drainages, mixed-conifer forests containing Douglas-fir and white fir commonly dominated. Subalpine spruce-fir (*Picea* spp. – *Abies* spp.) forests occurred at the highest elevations, while areas just below the ponderosa pine belt were dominated by pinyon-juniper woodlands (Brown 1982).

Model Development

We modeled habitat relationships of MSO using a suite of compositional, topographic, and climatic covariates (described below). To enhance comparability of results between study areas, we repeated the procedures of Timm et al. (2016) to develop our models and used the same data source when possible (Table 1). We summarized these procedures below, and noted any differences between Timm et al. (2016) and our modeling methods.

Owl Locations

We used conventional protocols for studying Spotted Owl demography to conduct owl surveys (Franklin et al. 1996; see also Forsman 1983). Briefly, we determined areas occupied by owls using nocturnal calling surveys. Once areas occupied by an individual or pair of owls were determined, we conducted daytime surveys to locate roost or nest sites. Nocturnal locations were based on the intersection of 2 or more compass bearings or a single bearing and estimated distance to the calling owl, whereas roost and nest locations were documented using global positioning system (GPS) units, with accuracy within 10 m. We excluded nocturnal locations from model development because of the positional uncertainty related to non-visual

TABLE 1. Descriptions of covariates and the corresponding univariate optimized scale used in the multi-scale MSO habitat selection models developed for the Sacramento Mountains study area and for the Mogollon Plateau study area (Timm et al. 2016). Covariates were classified into 3 groups: composition covariates, topographic covariates, and climate covariates.

Covariate	Description	Class	Data source	Top scale (m)	
				Sacramento Mountains	Mogollon Plateau
Canopy	Percent canopy cover	Composition	Varied ^d	100	2,700
Edge	Forest edge density	Composition	USFS Stand Map	3,700	400
Mixcon	Percent cover of mixed-conifer	Composition	USFS Stand Map with LANDFIRE	5,000	500
PonderosaPine ^a	Percent cover of ponderosa pine	Composition	USFS Stand Map with LANDFIRE	3,600	5,000
Proximity ^b	Proximity index of forest	Composition	USFS Stand Map	4,000	Not provided
Slope	Slope	Topographic	LANDFIRE	500	400
TPI	Topographic position index	Topographic	LANDFIRE	300	500
TRI ^c	Topographic roughness index	Topographic	LANDFIRE	5,000	Not provided
Elevation ^c	Elevation	Topographic	LANDFIRE	5,000	Not provided
Solar ^b	Solar radiation index	Climate	PRISM Climate Group	100	Not provided
MonsoonPrecip ^a	Monsoon-season precipitation	Climate	PRISM Climate Group	5,000	3,300
DegreeDays ^a	Cumulative degree-days	Climate	PRISM Climate Group	5,000	5,000
SAC	Spatial autocovariate				

^a Covariates excluded from our final model but used in Timm et al. (2016) final multi-scale model.

^b Covariates excluded from Timm et al. (2016) final multi-scale model.

^c Covariates excluded from both models.

^d Hansen et al. (2013) used in the Sacramento Mountains, a raster from Dickson et al. (2014) used in the Mogollon Plateau. Both data sources were derived from Landsat imagery at 30-m resolution.

triangulation and because MSO might be attracted from relatively long distances at night by calling surveys.

We used separate owl location data sets for training and validating the habitat model in the Sacramento Mountains. To train the habitat model, we used a data set from a demography study conducted in the Sacramento Mountains (Ganey et al. 2014) from 2002 to 2011. Surveys in this study were conducted from March through August at 1,206 fixed call stations distributed throughout the study area. This data set contained a total of 3,652 nest and roost location points from 94 owl territories. We removed points that were spatially duplicated so that there was only one point per location, as well as points within 10 km of the edge of the study area to avoid boundary problems, leaving 2,070 presence points for model training. To account for possible pseudo-replication, we used a bootstrap procedure to randomly sub-sample (without replacement) 200 presence points from the training data set and ensured a minimum distance of 500 m between points. We repeated this process to obtain 100 bootstrap training data sets. We chose a bootstrap sample size of 200 to maintain a sufficient sample-to-variable ratio in the habitat selection model and for consistency with the sample intensity in the Mogollon Rim study. Although the 500 m minimum distance was less than the average distance between owl territories, resulting in an average of roughly 2 observations per owl territory, it was the largest distance that allowed us to generate a sample size of 200.

To validate the habitat model, we used MSO survey data ($n = 326$, after removing spatial duplicates and points within 10 km of the study area boundary) collected throughout the study area by the U.S. Forest Service (USFS) during April to August from 1990 to 1993. These locations were from the same data set that Timm et al. (2016) used for model training and cross-validation. Most surveys contributing to this data set were conducted at calling stations located at 0.3–0.8 km intervals along forest roads throughout the study area. Each survey lasted 15 min or until an MSO responded. In roadless areas, surveys were conducted by calling every 30–40 s while hiking to ridgetops or canyon bottoms. Surveys were conducted on calm nights. Most locations, especially where an MSO responded, were surveyed multiple times. When an MSO responded, crews marked the location and estimated distance to the calling owl, and tried to locate the roosting/nesting owl by day. We excluded nocturnal locations in model validation, as did Timm et al. (2016). For consistency with model development, we used the same bootstrap procedure as above to create 100 validation data sets.

Pseudo-absence Locations

Because our owl location data sets contained presence-only data, it was necessary to generate pseudo-absence location points for the logistic regression models described below. We generated pseudo-absence points using the

procedure of Timm et al. (2016) to account for potential sampling bias associated with elevation and proximity to roads (Northrup et al. 2013). Briefly, we determined the elevation range (2,243–2,903 m) of owl location points using the digital elevation model (DEM) GIS layer from LANDFIRE (2001), and buffered that range by 10% of the difference between the maximum and minimum elevations to create an elevational zone (2,177–2,969 m). We used this zone to specify the constraining extent in which random points were generated. We reduced the area of this zone by removing areas that were >5 km from the convex hull (i.e. smallest enclosing area) of owl location points. We extracted the Euclidean distance from road for each owl location using a road map obtained from the Lincoln National Forest GIS database (USFS 2016) and then calculated the frequency of owl location points in each 100-m interval distance bin (i.e. 0–100 m, 100–200m, etc.). We generated 10,000 random points that essentially filled the entire elevational zone, and then randomly sampled 5,000 pseudo-absence points that matched the proportion of owl location points in each distance bin. We repeated the process and created 2 independent sets of 5,000 pseudo-absence points, one for model training and the other for model validation. We sub-sampled these pseudo-absence points using the same bootstrap procedure as before to create 100 training data sets and 100 validation data sets. While it was generally recommended to sample many more pseudo-absence points than presence points to ensure sufficient representation of available habitat (e.g., Barbet-Massin et al. 2012), our use of the bootstrap approach obviated the need to do so, as the available habitat was well represented across the bootstrap replications.

Habitat Covariates

We used the same 12 habitat covariates (5 composition, 4 topographic, and 3 climatic) that Timm et al. (2016) used for model development, all of which were hypothesized a priori to potentially be important to MSO based on previous studies. The 5 composition covariates were (1) percent canopy cover, (2) percent cover of mixed-conifer, (3) percent cover of ponderosa pine, (4) forest edge density, and (5) forest edge proximity. With the exception of the percent canopy cover layer, all covariates were developed using the same data source as Timm et al. (2016). The canopy cover raster used by Timm et al. (2016) was specifically developed for the Coconino and Apache-Sitgreaves National Forests (Dickson et al. 2014) and was unavailable for our study area. We instead used the Hansen et al. (2013) global tree cover layer because it was the best (overall accuracy >90%) freely available raster that was comparable to the raster used by Timm et al. (2016) as both data sets were derived from LANDSAT imagery and had the same spatial resolution. For the measurement of

percent cover of mixed-conifer and ponderosa pine, we created 30-m resolution binary forest maps of the respective cover type by classifying USFS-delineated forest stands to one of five cover classes (mixed-conifer, ponderosa pine, spruce-fir, pinyon-juniper, and other) based on a majority rule using the LANDFIRE Existing Vegetation Type layer (LANDFIRE 2001). To calculate forest edge density and proximity, we combined forest classes (i.e. ponderosa pine, mixed-conifer, and aspen) and created a binary forest map (i.e. forest and non-forest), and then used FRAGSTATS (McGarigal et al. 2002) to analyze the map. The 4 topographic covariates were (1) elevation, (2) slope, (3) topographic roughness index, and (4) topographic position index (Jenness et al. 2013). These covariates were derived from the LANDFIRE digital elevation model (LANDFIRE 2001). The 3 climatic covariates were (1) total monsoon season (May–August) precipitation, (2) cumulative annual degree-days (using 10 °C threshold), and (3) solar radiation index (Fu and Rich 2002). These covariates were calculated using 30-year normal (1981–2010) PRISM climate data (PRISM Climate Group 2016).

The PRISM climate data had an original resolution of 800 m; all other habitat covariate layers had an original resolution of 30 m. We resampled all layers to 30 m resolution and kept the spatial grain of the analyses constant at 30 m for all analyses.

Scaling Analysis and Covariate Selection

To identify the optimized scale and functional form (i.e. linear or quadratic) for each covariate, we calculated uniform kernel density values at each presence and pseudo-absence location, using bandwidths from 100 m to 5,000 m at 100-m intervals for a total of 50 scales. Note, because we were interested in the equivalent of Johnson's (1980) second-order selection (i.e. home range selection within the study areas), as described below, it was logical to include scales that far exceeded the average home range radius. We then conducted a single covariate logistic regression model using linear and quadratic logistic functional forms independently at each scale. We compared models using Akaike's Information Criterion corrected for small sample size (AIC_c). For each covariate, the scale and functional form of the model with the lowest AIC_c score were identified as the best scale and functional form, respectively. We repeated this procedure for each of the 100 bootstrap training data sets and selected the modal best scale and functional form of each covariate for use in the multi-scale model below. As a safeguard against multicollinearity in the multi-scale model, we computed the Pearson's correlation coefficient between each pair of covariates at their best scale and functional form. When 2 or more covariates were found to be highly correlated (i.e. $|r| \geq 0.7$), we retained the covariate with the greater

average deviance explained across bootstrap replicates and excluded the rest from subsequent analyses. Using this rule, we removed percent cover of ponderosa pine, topographic roughness index, elevation, monsoon season precipitation, and cumulative degree-days from the models. Variance inflation factors (VIFs) were <3 for all remaining covariates in the full multi-scale and single-scale models (i.e. containing all remaining covariates) for each bootstrap replicate.

Multi-scale Modeling

To model MSO nesting and roosting habitat suitability within the Sacramento Mountains study area, we developed a point Resource Selection Function (RSF) by conducting an all-subsets multiple logistic regression analysis with the retained covariates (each at its optimized-scale and functional form) from the univariate scaling analysis. We used logistic regression to estimate the RSF as it approximated the use–availability point process model (Johnson et al. 2006, Warton and Shepherd 2010, Aarts et al. 2012) and allowed us to easily obtain inference on selection or avoidance of covariates and generate predictive maps (Northrup et al. 2013). Because all of our covariates were hypothesized a priori to be potentially important to MSO based on previous studies, we considered the all-subsets modeling approach the best way to represent our uncertainty in the parsimonious combination of variables that would best describe MSO habitat selection in the study area. In addition, because we considered each nest/roost as the potential center of a home range and the pseudo-absence points were drawn randomly from the entire study area, as described above, we considered this point RSF as somewhat analogous to Johnson's (1980) second-order home range selection. However, because we were obligated to use point locations rather than delineated home ranges as the observation unit, it was impossible to decouple true second-order selection from potential third-order (i.e. within home range) selection. Therefore, we recognized that the multi-scale model represented a hybrid of sorts in which the optimized scale of each covariate may have reflected, to varying degrees, second- and/or third-order selection.

We corrected for residual spatial autocorrelation by adding an exponential spatial autocovariate term (SAC) into the models (Timm et al. 2016). To determine model(s) that best described the MSO distribution, we ranked all candidate models using AIC_c and Akaike's model weights. We considered models with $\Delta AIC_c \leq 2$ to represent competing models (Burnham and Anderson 2003). We averaged the estimates of each covariate from the suite of competing models based on AIC_c weights (w_i). We repeated this process on all 100 bootstrap replicates. We generated a bootstrap distribution for each parameter in

the model and calculated the mean and 95% quantile interval (nonparametric analog to a confidence interval). We used the mean of each parameter distribution to build the final model.

Single-scale Modeling

We developed single-scale models using the covariates and methods described above, but holding scale constant across all covariates. We developed models across all scales from 100 m to 5,000 m at intervals of 100 m for a total of 50 scales. We calculated model-averaged deviance explained at each scale across bootstrap replicates, and selected the scale with the greatest deviance explained as the optimized scale for the single-scale model.

Model Performance and Comparison

To compare the explanatory power of the multi-scale and single-scale models, we used the proportion of deviance explained. We used variance decomposition (`varpart` {`vegan`}) in R (Oksanen et al. 2013) to assess the amount of variance explained independently and jointly by each of the 3 covariate groups (i.e. topographic, landscape composition, and climate). We compared the parameter estimates and the 95% confidence intervals, as well as variable importance for each covariate (defined as the sum of model weights across all models containing that covariate) with the results from Timm et al. (2016). To further inspect the importance of each covariate, we sequentially removed each covariate (with replacement) and evaluated the reduction in model deviance explained. We divided that reduction by the total model deviance explained to obtain the percent drop in deviance explained for each covariate.

To compare the predictive performance of the multi-scale and single-scale models, we evaluated and calculated the percent correctly classified (PCC), sensitivity, specificity, Kappa statistics (κ), and area under the curve (AUC) using an independent owl location data set (see Owl Locations). We used the `optimal.thresholds` function from the `Presence/Absence` package (`optimal.thresholds` {`PresenceAbsence`}) in R (Freeman and Moisen 2008) to determine the cutoff point for assessing PCC, sensitivity, specificity, and κ . Because these statistics were calculated using presence–available data, the absolute values were not meaningful; instead, we used these statistics solely to compare models.

We created maps of the predicted relative probability of occurrence of MSO for the entire Sacramento Mountains study area using the parameter estimates from the multi-scale model, the top single-scale model, and the multi-scale model from Timm et al. (2016). We calculated the area-adjusted frequencies (AAF) by breaking the predicted RSF scores into 10 equal-sized bins (i.e. 0–0.1, 0.1–0.3, etc.) and dividing the propor-

tion of observations in each bin by the proportion of the landscape in the same bin (Boyce et al. 2002). We used the Spearman's nonparametric test to estimate the rank-order correlation between the AAF and bins. We evaluated the correlation between the multi-scale and the top single-scale derived predictive maps through a pixel-by-pixel comparison using the complement of the absolute difference between the 2 maps. At any given pixel, this gave us a value that ranged from 0 to 1, in which a greater value indicated stronger correlation and vice versa.

Multi-scale Spatial Distribution Analysis

To evaluate the spatial relationship between predicted habitat suitability and MSO nest/roost distribution in the Sacramento Mountains, we computed Moran's I correlograms (Legendre and Legendre 1998) for suitable habitat and owl locations separately and compared their patterns. MSO locations comprised a point feature layer that was directly useful here. We converted the habitat suitability surface to a point feature layer by creating 5,000 random points such that their distribution was proportionate to the predicted habitat suitability. We calculated point densities at each of the habitat points and owl points within a uniform circular window with a radius of 100 m to 5,000 m in 100-m increments for a total of 50 scales. At each scale, we computed the correlograms of the MSO point density and the habitat point density across lag distances (i.e. the range over which spatial autocorrelation is measured) of up to 10 km. We used the correlog function from the *ncf* package (`correlog {ncf}`) in R to compute the correlograms. We plotted the correlograms of all 50 scales together as a surface using scales, lag distance, and Moran's I values as the axes. The correlogram depicts the strength of spatial autocorrelation across a range of lag distances. If the distribution of MSO and habitat suitability were highly associated, their Moran's I correlograms would show similar patterns across lag distances. In contrast, dissimilar patterns would indicate that MSO distribution could be limited by factors other than habitat, assuming that the habitat model provided good predictions. In this context, a periodic pattern to the MSO correlogram could indicate that owl distribution was limited by territoriality with the spatial lag between peaks in the correlogram associated with mean distance between territory centers.

To estimate spacing of MSO nest sites in the Sacramento Mountains, we measured the Euclidean nearest-neighbor distance between known nest sites (i.e. the shortest straight-line distance from a nest site to another nest site; $n = 61$), and calculated the mean and the coefficient of variation across these nest sites. Note, because field crews were unable to locate all existing nest

sites, this estimate only represented the best estimate given the data that we had.

RESULTS

Multi-scale Model

The final multi-scale model consisted of 7 covariates (excluding intercept, quadratic terms, and SAC; Figure 2), and explained an average deviance of 0.27 across all bootstrap replicates. Percent canopy cover, percent mixed-conifer, and slope were positively related to MSO habitat selection, whereas forest edge proximity, solar radiation index, and topographic position index were negatively related to MSO habitat selection (Table 2). Forest edge density and slope had negative quadratic coefficients, suggesting a concave downward relationship with MSO habitat selection. Percent canopy cover was the most important covariate in the model, and showed the greatest drop in model deviance explained when removed from the model. Percent mixed-conifer and slope were the next most important covariates, while all other covariates had low variable importance and drop in deviance explained when removed from the model.

In the Mogollon Plateau, the final model contained 8 covariates (excluding quadratic terms and SAC), and had a 0.64 deviance explained. Canopy cover and slope were the most important covariates in the model, followed by monsoon-season precipitation, topographic position index, and percent cover of ponderosa pine (Table 2). Other covariates, including forest edge density, percent cover of mixed-conifer, and cumulative annual degree-days had low variable importance. Data on drop in deviance explained for covariates dropped from the model were not available for the Mogollon Rim model.

Optimized Scale and Covariates

The univariate scaling analysis revealed variation in optimized scale among covariates and between study areas (Table 1). Composition covariates showed a broad range of optimized scales in both the Sacramento Mountains (100–5,000 m) and the Mogollon Plateau (400–5,000 m). Percent canopy cover was related to MSO habitat at a fine scale in the Sacramento Mountains (100 m), but at a broader scale in the Mogollon Plateau (2,700 m). Species composition covariates such as percent cover of ponderosa pine and mixed-conifer were related at broader scales in the Sacramento Mountains (3,600 m and 5,000 m, respectively), whereas the scales of these same covariates contrasted more strongly with each other (5,000 m and 500 m, respectively) in the Mogollon Plateau. Forest edge density and proximity were related to the relative likelihood of MSO occurrence at broad scales in the Sacramento Mountains (3,700 m and 4,000 m, respective-

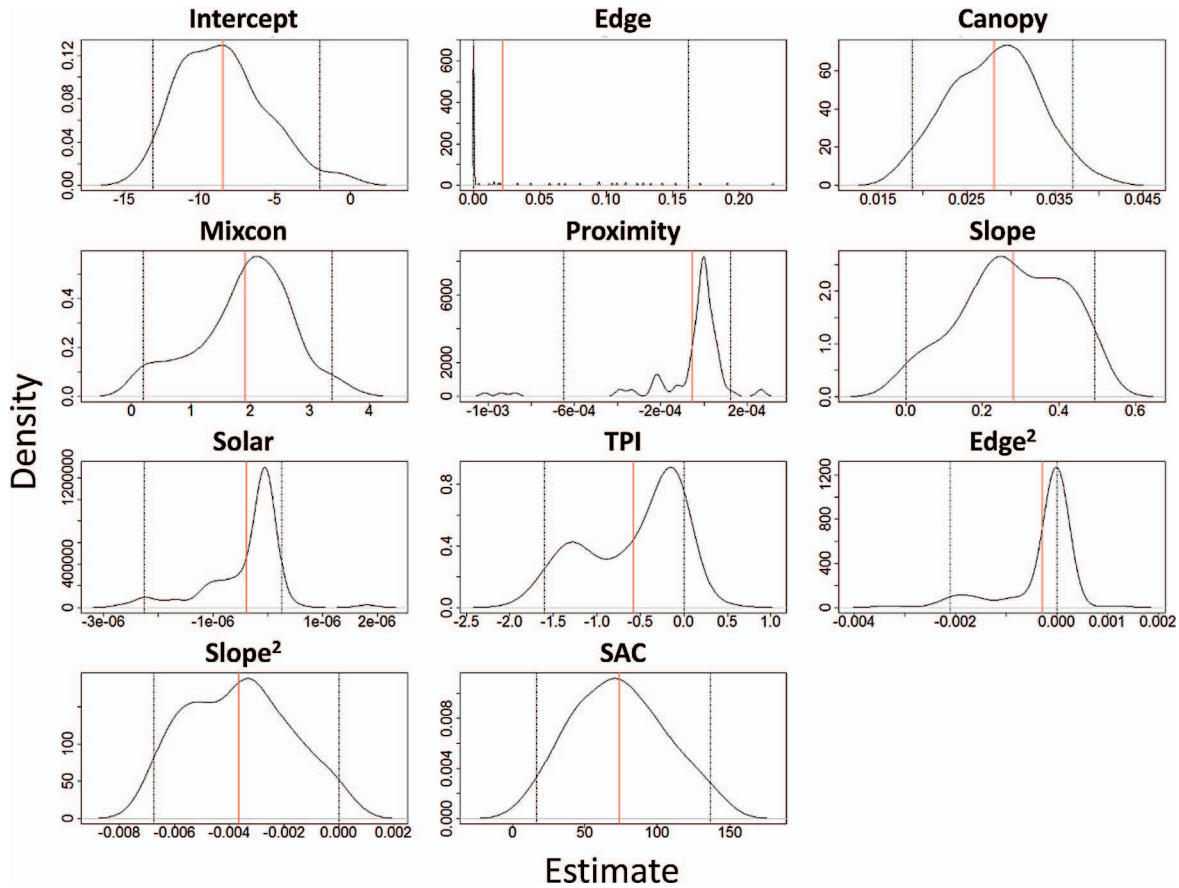


FIGURE 2. Bootstrap distribution of each parameter in the multi-scale model. Red line represents the mean. Dotted lines represent the 95% quantile interval (i.e. nonparametric analog to confidence interval). The mean of each parameter distribution was used to build the final multi-scale model. See Table 1 for explanation of parameters.

ly). In contrast, forest edge density was related at a fine scale in the Mogollon Plateau (400 m).

The optimized scale for topographic covariates varied more in the Sacramento Mountains (300–5,000 m) than in the Mogollon Plateau (400–500 m). In the Sacramento Mountains, topographic position index and slope were optimized at fine scales (300 m and 500 m, respectively), whereas topographic roughness index and elevation were both optimized at the broadest scale measured (5,000 m). In the Mogollon Plateau, slope and topographic position index were optimized at fine scales (400 m and 500 m).

Climate covariates were mostly related to the relative likelihood of MSO occurrence at broad scales in both study areas. In the Sacramento Plateau, monsoon-season precipitation and cumulative degree-days were best measured at broad scales (5,000 m), whereas solar radiation index showed a fine-scale relationship (100 m). In the Mogollon Plateau, monsoon-season precipitation and cumulative degree-days were also optimized at broader scales (3,300 m and 5,000 m, respectively).

Single-scale Model

The optimized scale for the single-scale model in the Sacramento Mountains was at 200 m with an average deviance explained of 0.26. The average deviance explained of single-scale models across all scales was 0.22. The optimized single-scale model contained the same covariates as the multi-scale top models (Figure 3; see also Figure 2). Except for forest edge proximity, signs of parameter estimates were identical between the single- and multi-scale models (Table 2). Like the multi-scale model, percent canopy cover was the most important covariate in the best single-scale model followed by slope. All other covariates had low variable importance and drop in deviance explained when removed from the model.

In the Mogollon Plateau, the best single-scale model (400 m scale) included the same covariates as the multi-scale model and had a deviance explained of 0.62 (see Timm et al. 2016). The averaged deviance explained of all single-scale models was 0.55 in the Mogollon Plateau. Slope was the only covariate with a variable importance of 1.00. Canopy cover, percent cover of ponderosa pine,

Table 2. Model-averaged parameter coefficients, 95% confidence intervals (CI), variable importance (Vi), and percent of model deviance explained (% model D²) for the multi-scale model and the top single-scale model (200-m radius) developed for MSO habitat in the Sacramento Mountains, and the multi-scale model developed for the Mogollon Plateau (Timm et al. 2016). Quadratic terms used in the models are denoted by superscripted "2". Values for the Sacramento Mountains were averages from 100 bootstrap replications. See Table 1 for explanation of parameters.

Parameter	Sacramento Mountains			Sacramento Mountains			Mogollon Plateau	
	Multi-scale model			Single-scale model			Multi-scale model	
	Model-averaged estimate (CI)	Vi	% model D ²	Model-averaged estimate (CI)	Vi	% model D ²	Model-averaged estimate (CI)	Vi
Intercept	-8.46 (-1.31 to -2.03)	1.00	-	-6.79 (-1.02 to -2.35)	1.00	-	1.72 (3.71 to 7.99)	1.00
Canopy	2.81 (1.88 to 3.70)	1.00	18.0%	3.63 (2.79 to 4.55)	1.00	24.6%	4.86 (1.81 to 1.30)	1.00
Edge	2.22 (0.00 to 1.62)	0.14	0.7%	5.24 (0.00 to 2.80)	0.27	1.3%	8.32 (4.20 to 1.65)	0.30
Edge ²	-2.91 (-2.10 to 0.00)	-	-	-3.60 (-2.49 to 0.00)	-	-	Excluded	-
Mixcon	1.91 (1.94 to 3.37)	0.90	4.9%	4.73 (0.00 to 1.20)	0.65	2.3%	1.10 (5.93 to 2.03)	0.27
PonderosaPine	Excluded	-	-	Excluded	-	-	2.54 (9.96 to 6.35)	0.72
Proximity	-5.44 (-6.47 to 1.21)	0.20	0.3%	4.60 (-3.67 to 2.88)	0.30	0.7%	Excluded	-
Slope	2.80 (0.00 to 4.94)	0.85	5.3%	1.64 (0.00 to 3.22)	0.75	5.5%	3.44 (2.91 to 4.07)	1.00
Slope ²	-3.65 (-6.75 to 0.00)	-	-	-2.13 (-4.19 to 0.00)	-	-	9.00 (1.74 to 4.61)	1.00
Solar	-3.94 (-2.26 to 2.48)	0.32	0.6%	-5.26 (-1.37 to 7.18)	0.20	0.3%	Excluded	-
TPI	-5.81 (-1.60 to 0.00)	0.55	1.8%	-4.24 (-1.12 to 3.74)	0.62	2.3%	1.22 (6.82 to 2.18)	0.79
TPI ²	Excluded	-	-	Excluded	-	-	1.00 (7.66 to 2.37)	0.79
MonsoonPrecip	Excluded	-	-	Excluded	-	-	2.00 (1.76 to 2.06)	0.90
MonsoonPrecip ²	Excluded	-	-	Excluded	-	-	1.50 (2.40 to 9.43)	0.90
DegreeDays	Excluded	-	-	Excluded	-	-	1.36 (7.54 to 2.46)	0.20
DegreeDays ²	Excluded	-	-	Excluded	-	-	6.00 (2.74 to 1.33)	0.20
SAC	7.36 (1.67 to 1.37)	1.00	-	1.11 (6.89 to 1.59)	1.00	-	1.37 (5.95 to 3.14)	1.00

topographic position index, and monsoon-season precipitation were also important, with variable importance of 0.97, 0.88, 0.83, and 0.66, respectively. Other covariates had variable importance of <0.48.

Model Performance and Comparison

The multi-scale model outperformed the single-scale model in terms of model explanatory power with greater deviance explained across all scales in the Sacramento Mountains (Figure 4). This also was the case in the Mogollon Plateau (see Timm et al. 2016).

The multi-scale model showed nearly identical predictive performance to the top single-scale model in PCC, sensitivity, specificity, κ , and AUC (Table 3). Although the absolute values of these statistics were not meaningful given our presence-available study design, the relative values provided useful comparative indices. The multi-scale and the single-scale models both correctly classified 68% of validation points and had κ of 0.36. Both models had higher sensitivity (0.70–0.74) than specificity (0.62–0.67), displaying higher accuracy in predicting the relative likelihood of suitable habitat than available habitat, which was expected because we had pseudo-absence points instead of true absence points. AUC for the multi-scale and the single-scale models were both 0.73. AAF and binned RSF scores were significantly correlated for both models (Figure 5).

The Mogollon Plateau's multi-scale model performed more poorly in predicting owl locations in the Sacramento Mountains than our multi-scale and top single-scale models, correctly classifying only 59% of validation points and having lower κ (0.18), AUC (0.60; Table 3), and sensitivity (0.48) statistics (also evident in Figure 6C). Conversely, specificity was higher (0.70), which was likely a result of over-classification of "non-suitable" habitat. AAF was not significantly correlated with the binned RSF scores (Figure 5).

Variance decomposition results showed nearly the same results between the optimized single and multi-scale models in the Sacramento Mountains, with composition covariates explaining considerably greater variance compared to the other 2 types of covariates in both models. Composition covariates also explained far more of the variance in the Sacramento Mountains than in the Mogollon Plateau, where the best multi-scale model was largely driven by topographic covariates (Figure 7). In addition, there was much less confounding in the variance explained by the 3 factors in the Sacramento Mountains (i.e. relatively little "joint" variance explained by combinations of factors) compared to the Mogollon Plateau, where there was considerable confounding among factors.

The predictive maps created by the single-scale and the multi-scale models were highly correlated in the Sacramento Mountains, with most of the study area having a correlation value of >0.8 (Figure 8).

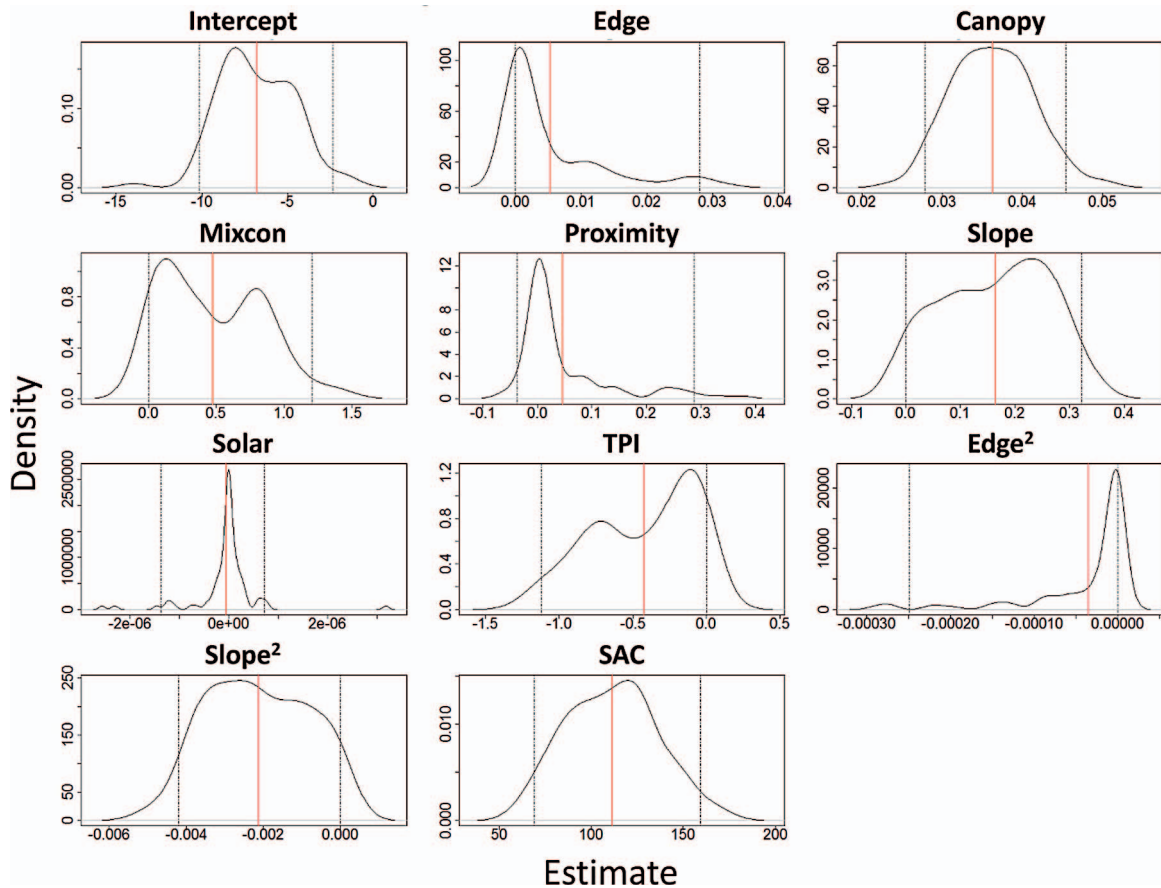


FIGURE 3. Bootstrap distribution of each parameter in the top single-scale model (200-m radius). Red line represents the mean. Dotted lines represent the 95% quantile interval (i.e. nonparametric analog to confidence interval). The mean of each parameter distribution was used to build the final single-scale model. See Table 1 for explanation of parameters.

Multi-scale Spatial Distribution Analysis

Moran's I correlogram surfaces showed strongly dissimilar patterns of spatial autocorrelation between MSO points and habitat points at all scales in the Sacramento Mountains study area (Figure 9A, 9B). Across all scales, habitat points displayed a gradient-like pattern of autocorrelation that gradually decreased across lag distance, indicating a smooth decline in similarity of habitat suitability as distance increases (Cushman 2010). In contrast, MSO points showed a periodic pattern of autocorrelation at all scales; in particular, with peaks at roughly 500 m and 2,000 m (Figure 9C–F).

The mean Euclidean nearest neighbor distance of MSO nest sites was 1,879.45 m with a coefficient of variation of 39.04%.

DISCUSSION

Scale is a fundamental concept in ecology, but most habitat selection studies, with notable exceptions, have not used scale optimization frameworks to address the issue

(McGarigal et al. 2016). Habitat selection modeling has often focused on identifying the most important habitat variables in relation to species occurrence. However, even with the appropriate variables, using unoptimized scales may lead to weak or incorrect depiction of relationships (DeCesare et al. 2012, Shirk et al. 2012, Sánchez et al. 2014, Zeller et al. 2014, Vergara et al. 2016). Moreover, factors that affect these relationships could be nonstationary across different landscapes (Shirk et al. 2014). In this paper, we demonstrated an optimized multi-scale modeling framework for analyzing habitat selection and showed how it could better our understanding of spatial nonstationarity in habitat selection.

The Advantages of Scale Optimization Framework

Consistent with our first hypothesis, the optimized multi-scale model outperformed all single-scale models in deviance explained (Figure 4), strengthening the perspective that a multi-scale framework is useful for rigorously quantifying habitat relationships (McGarigal et al. 2016). However, the improvement of the multi-scale model over

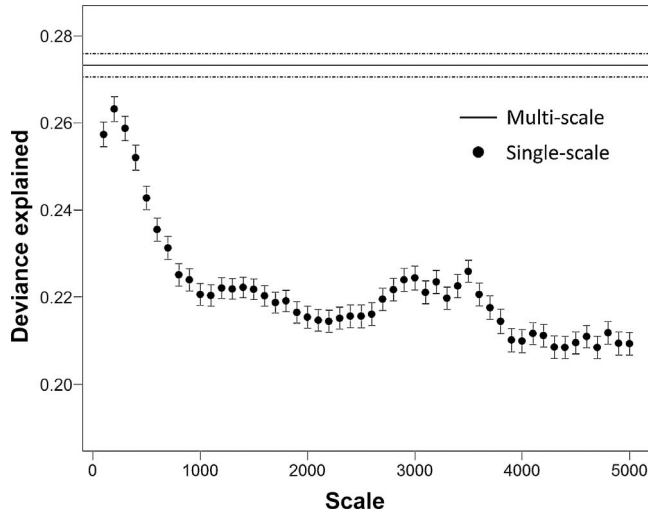


FIGURE 4. Model-averaged proportion of deviance explained by the optimized multi-scale model of MSO habitat (solid horizontal line) and by single-scale models ranging from 100 m to 5,000 m in 100-m increments (black markers) in the Sacramento Mountains study area. Values represent averages of 100 bootstrap replications. Dotted lines and error bars represent 95% confidence interval.

the top single-scale model was relatively minor, as indicated by all of the performance statistics (Table 3) and the similarity of the predicted surfaces (Figures 6A, 6B, 8). The advantage of the multi-scale modeling approach in our case study was mainly in the interpretation of the model. First, we observed that the top suite of multi-scale and single-scale models yielded different sets of covariates, even with the same bootstrapped samples, and thus provided a different characterization of suitable MSO habitat (Table 4). For example, percent cover of mixed-conifer appeared in the top-suite of multi-scale models in most bootstrap replicates (variable importance = 0.90), but appeared less in the top single-scale models among the

same bootstrap replicates (variable importance = 0.65). In this case, using the best related scale provided greater sensitivity for characterizing the importance of mixed-conifer stands to the owl.

Second, the scaling analysis also provided a statistical approach to quantify and evaluate the specific scale of selection for each covariate. For example, we found that MSO were associated with some habitat covariates at the finest scales but others at very broad scales (Table 1). In the Sacramento Mountains model, canopy cover was optimized at 100 m scale, whereas forest edge density was optimized at 3,700 m scale, both with positive coefficients. This implied that the MSO selected higher canopy cover at nest/roost sites, but around that nest/roost core might prefer forest landscapes featuring openings. Overall, our results suggested that MSO selected home ranges at broad scales in high-elevation forests dominated by mixed-conifer forest, and within those forests they selected areas with high canopy cover on lower slopes and in canyon bottoms, but avoided openings and meadows at fine spatial scales. Although these multi-scale habitat relationships were generally recognized in previous MSO literature, Timm et al. (2016) and this study are the only studies we know of that explicitly and statistically examined multiple scales for each covariate.

Nonstationarity in Habitat Selection

The scale-optimized framework combined with the replicated study areas allowed us to identify and quantify nonstationarity in habitat selection. Consistent with our second hypothesis, we documented considerable nonstationarity in habitat selection between these 2 study areas. For example, the Mogollon Plateau model did a relatively poor job of predicting MSO nest/roost sites in the Sacramento Mountains study area compared to its performance in the Mogollon Plateau study area (Table 3 and Figures 5, 6C), indicating that the factors affecting

TABLE 3. Comparative model performance for an optimized multi-scale model and the top single-scale model (200-m radius) developed for MSO habitat in the Sacramento Mountains study area, and the multi-scale model developed for the Mogollon Plateau study area (Timm et al. 2016) but applied to the Sacramento Mountains. All models were validated using independent MSO survey data collected from 1990 to 1993 in the Sacramento Mountains. Sensitivity is the number of correctly predicted present locations divided by the total number of present locations (true positive fraction). Specificity is the number of correctly predicted pseudo-absent locations divided by the total number of pseudo-absent locations (true negative fraction). κ represent the percent improvement over random classification. Area under the curve (AUC) is a threshold independent measure of model performance, with larger values indicating better model performance. Values are averages (\pm standard errors) of 100 bootstrap replications.

Model	Threshold	PCC	Sensitivity	Specificity	κ	AUC
Multi-scale model (Sacramento Mountains)	0.3	0.68 \pm 0.002	0.74 \pm 0.002	0.62 \pm 0.003	0.36 \pm 0.004	0.73 \pm 0.002
Top single-scale model (Sacramento Mountains)	0.3	0.68 \pm 0.002	0.70 \pm 0.002	0.67 \pm 0.003	0.36 \pm 0.004	0.73 \pm 0.002
Multi-scale model (Mogollon Plateau)	0.3	0.59 \pm 0.002	0.48 \pm 0.002	0.70 \pm 0.004	0.18 \pm 0.004	0.60 \pm 0.002

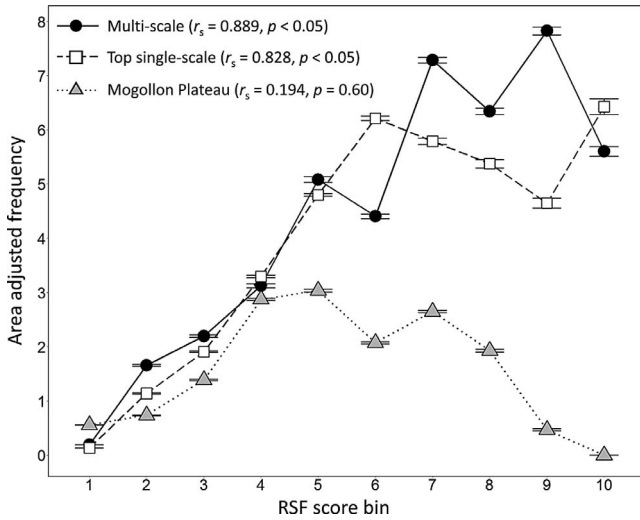


FIGURE 5. Area-adjusted frequencies (AAF) of the multi-scale model, the top single-scale model, and the Mogollon Plateau multi-scale model by resource selection function (RSF) score bins. Error bars represent 95% confidence interval. Spearman's correlation and p values are shown in parentheses in the legend. AAF was significantly correlated with RSF bin for both the single- and multi-scale models developed for the Sacramento Mountains, but not for the multi-scale model developed for the Mogollon Plateau.

habitat selection differed between study areas. Moreover, although we and Timm et al. (2016) both demonstrated scale-dependent MSO–habitat relationships, the scales selected for each covariate varied considerably between the 2 study areas (Table 1). Both studies showed similar scales for topographic and climatic covariates, but differed

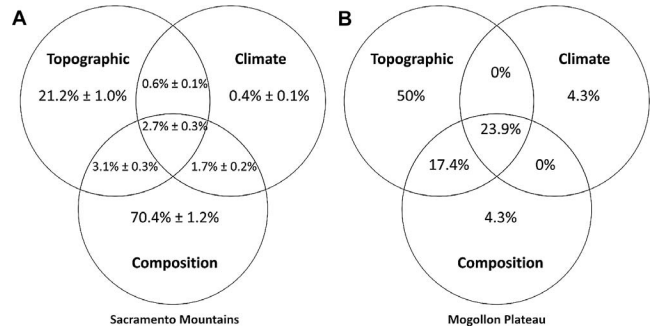


FIGURE 7. Model-averaged variance decomposition showing proportions of variance explained (\pm standard error) by topographic, climate, and composition covariates in multi-scale MSO habitat models developed for (A) the Sacramento Mountains study area and (B) the Mogollon Plateau study area (Timm et al. 2016). Areas of overlap between circles represent shared variance between covariates.

markedly for composition covariates. For example, percent canopy cover was selected at a much finer scale in the Sacramento Mountains than in the Mogollon Plateau (100 m and 2,700 m, respectively), whereas percent cover of mixed-conifer was selected at a much broader scale (5,000 m and 500 m, respectively). While we are uncertain as to what factors might be causing these differences, these findings suggest that the spatial scales of habitat covariates which the MSO responded to were likely nonstationary and could potentially be influenced by local adaptation to spatial environmental variation across different landscapes.

The differences in the variance decomposition between study areas further illustrated nonstationarity in habitat

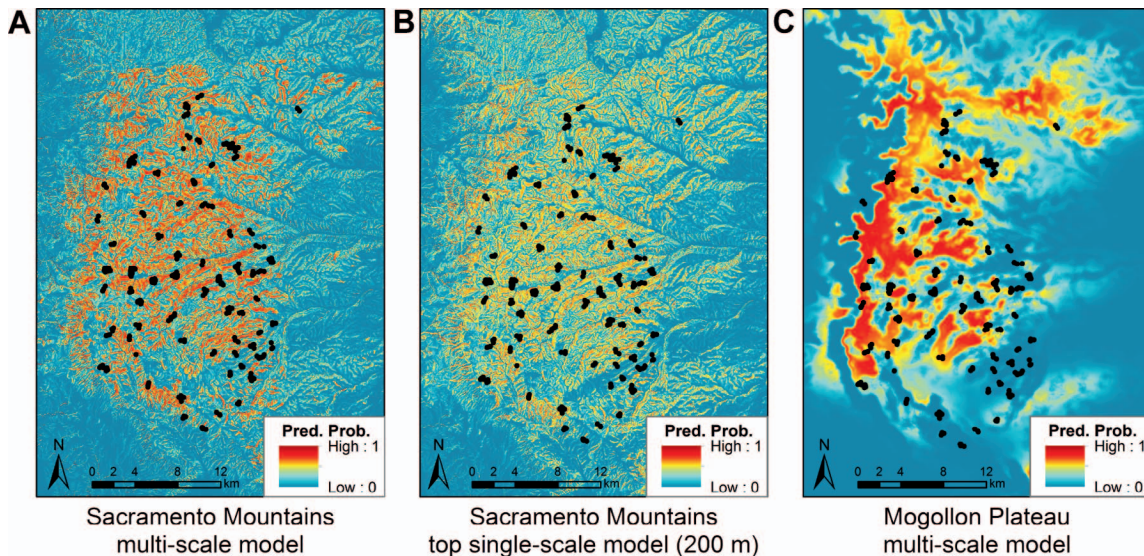


FIGURE 6. MSO nesting and roosting habitat suitability surface in the Sacramento Mountains study area predicted by (A) the multi-scale model, (B) the top single-scale model (200-m radius), and (C) the Mogollon Plateau multi-scale model. Black markers represent MSO locations from the entire validation dataset. Maps are on the same scale.

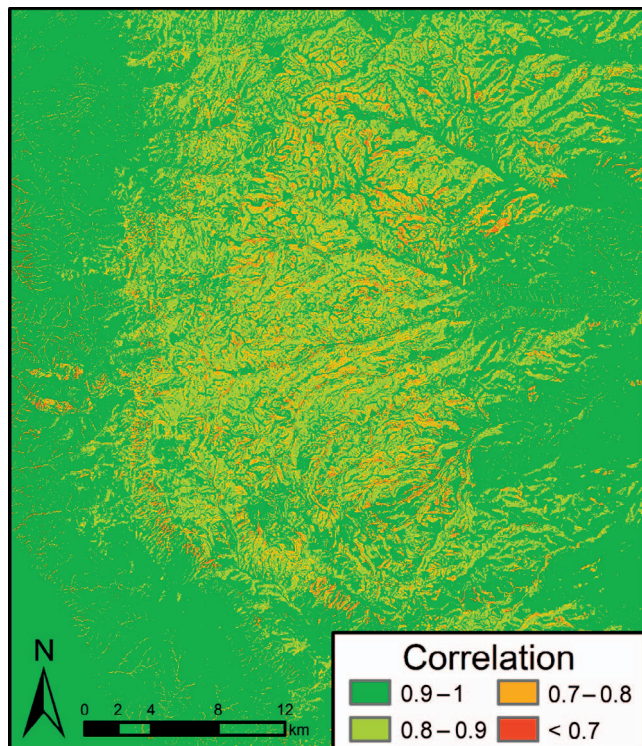


FIGURE 8. Pixel-by-pixel comparison between the multi-scale and the single-scale models' predictive maps. Correlation was calculated by $1 -$ the absolute difference between the multi-scale and the top single-scale maps. Higher value indicates stronger correlation.

selection. Landscape composition was a better predictor of owl occurrence than either topography or climate in the Sacramento Mountains, whereas topography was the best predictor in the Mogollon Plateau (Figure 7). We hypothesized this relationship because the distribution of suitable forested habitat in the Sacramento Mountains was not related to topography as it was on the Mogollon Plateau, where suitable habitats were restricted primarily to cinder cones and canyons. Moreover, consistent with our third hypothesis, the Sacramento Mountains model explained less variance than the Mogollon Plateau model. In the Mogollon Plateau, suitable forested habitats were relatively rare, patchy, and constrained by topography, which created large differences in the ecological characteristics between used and available sites, resulting in a model with high deviance explained ($D^2 = 0.64$; Timm et al. 2016). Unlike the Mogollon Plateau, forested habitats typical for nesting and roosting in the Sacramento Mountains were relatively abundant, well distributed, and not limited by topography. This resulted in a more homogeneous landscape with extensive mixed-conifer forests with high canopy cover and relatively lower contrast between the ecological characteristics of used

and available locations, and thus lower deviance explained ($D^2 = 0.27$). Such differences likely played a major role in determining the nonstationarity of habitat covariates in the multi-scale and top single-scale models.

Scale-explicit Spatial Distribution Analysis Revealed Potential Territorial Behavior

This was the first study that we were aware of that evaluated spatial autocorrelation of species and habitat distribution in a scale-explicit manner. The dissimilar patterns of spatial autocorrelation between suitable habitat and MSO distribution indicated that MSO density was likely influenced by factors in addition to, or other than, habitat (Figure 9). We suspect that the MSO distribution pattern was at least partly limited by territorial behavior and intraspecific competition for resources linked to space, resulting in fairly even spacing between MSO sites (Figure 6). The correlograms consistently showed 2 peaks of autocorrelation at ~ 500 m and $\sim 2,000$ m lag distances across all scales (Figure 9). We think that the first peak represented the spatial clustering of points used by each MSO individual or pair, and the distance between the 2 peaks (i.e. $\sim 1,500$ m) likely reflected the approximate averaged distance separating owl territories (mean Euclidean nearest neighbor distance = 1,879.45 m). A 940-m radius (i.e. the approximate half-distance between pairs) circular area encompasses 277 ha, which is comparable to both the breeding season home range size in mixed-conifer forests in this study area (i.e. 228 ± 37 ha) (Ganey et al. 2005) and the minimum area (243 ha) for Protected Activity Centers (PACs) recommended in the recovery plan (USFWS 2012). The fact that the MSO distribution is spatially periodic at a lag distance approximating the distance between territory centers and not following the spatial pattern of habitat availability suggests that in the Sacramento Mountains study area MSO population may be near carrying capacity in at least some areas, with most suitable territories occupied in a relatively uniform spatial pattern.

Consistency with Previous Work in Describing MSO Habitat

Nesting and roosting habitat characterized in this study was mostly consistent with current literature on MSO habitat selection. We observed strong selection for high canopy cover around nest/roost sites at relatively fine scales (Table 1) consistent with several previous studies (Ganey and Balda 1989, Seamans and Gutiérrez 1995, Peery et al. 1999, May and Gutiérrez 2002, May et al. 2004, Ganey et al. 2013, Timm et al. 2016). MSO's strong preference for high canopy cover around nest/roost sites may be linked to thermoregulation (Ganey 2004), protection from predators (Ganey et al. 1997), and nest structure availability (Seamans and Gutiérrez 1995). In addition, we

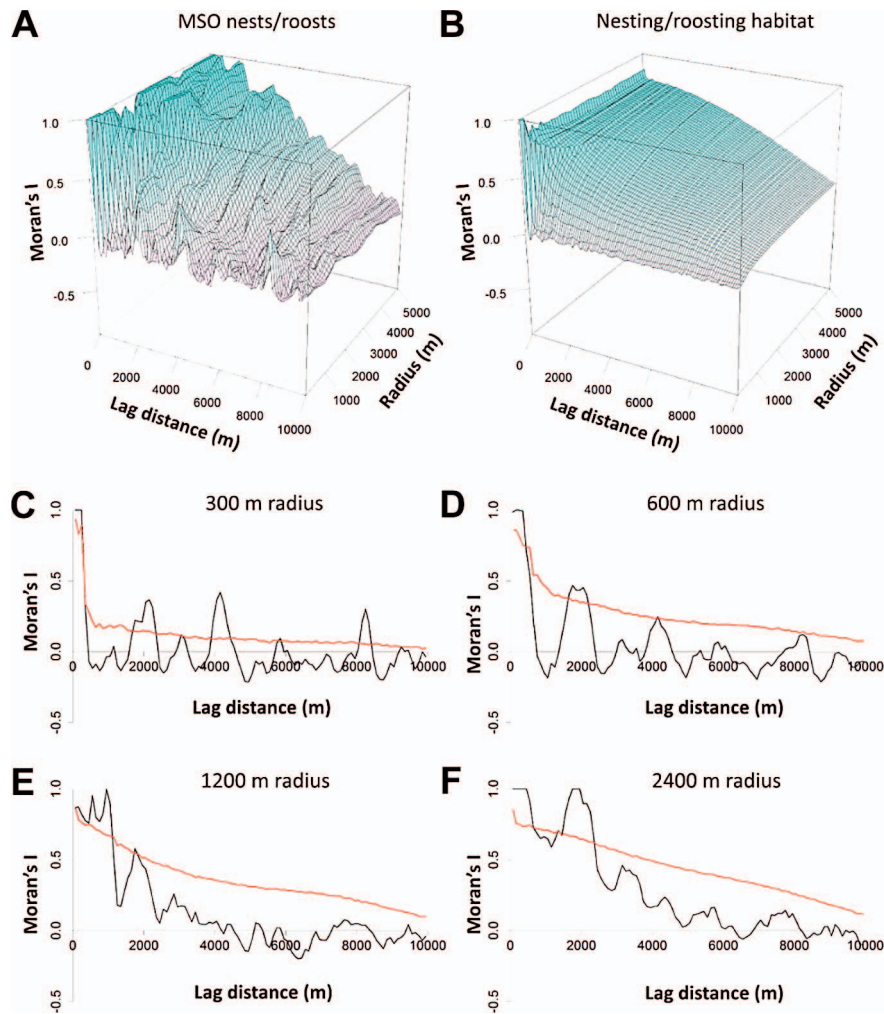


FIGURE 9. Moran's I correlogram surfaces of (A) MSO distribution and (B) nesting and roosting habitat in the Sacramento Mountains study area. Radius refers to the scale or size of moving window for calculating density distribution. Panels (C), (D), (E), and (F) are correlograms at 400 m, 800 m, 1,200 m, and 2,400 m scales, respectively. Black curves show values for MSO nests/roosts, whereas red curves show values for predicted habitat. Moran's I value near 0 indicates weak spatial autocorrelation (random spatial distribution), near +1 indicates positive autocorrelation (spatial clustering), and near -1 indicates negative autocorrelation (spatial dispersion).

TABLE 4. An example of the top suite of multi-scale and single-scale (200 m) logistic regression models for predicting probability of MSO occurrence in the Sacramento Mountains study area. Models at both scales were based on an identical bootstrap process, and ranked by Akaike's information criterion scores corrected for small sample size (AIC_c). Proportion of deviance explained (D^2), change in AIC_c (ΔAIC_c), and AIC_c weights (w_i) of each model are provided. Models with $\Delta AIC_c \leq 2$ are included.

Scale	Model	D^2	AIC_c	ΔAIC_c	w_i
Multi-scale	Canopy+Mixcon+Slope+Slope ² +SAC	0.30	398.98	0.00	0.34
	Canopy+Mixcon+Proximity+Slope+Slope ² +SAC	0.30	400.49	1.50	0.16
	Canopy+Mixcon+TPI+Slope+Slope ² +SAC	0.30	400.60	1.59	0.16
Single-scale (200 m)	Canopy+Slope+Slope ² +SAC	0.29	403.56	0.00	0.09
	Canopy+Edge+Edge ² +Slope+Slope ² +SAC	0.30	403.71	0.15	0.08
	Canopy+Edge+Edge ² +Mixcon+Slope+Slope ² +SAC	0.30	404.13	0.57	0.07
	Canopy+Proximity+Slope+Slope ² +SAC	0.29	404.21	0.65	0.07
	Canopy+Slope+Slope ² +TPI+SAC	0.29	404.21	0.66	0.07
	Canopy+Mixcon+Slope+Slope ² +SAC	0.29	404.92	1.37	0.05
	Canopy+Proximity+Slope+Slope ² +TPI+SAC	0.30	405.32	1.77	0.04
	Canopy+Edge+Edge ² +Slope+Slope ² +TPI+SAC	0.30	405.44	1.89	0.04
	Canopy+Mixcon+Proximity+Slope+Slope ² +SAC	0.30	405.50	1.94	0.04

observed a concave downward relationship between forest edge density and MSO habitat selection, the same pattern previously reported in a study of Northern Spotted Owl (*S. o. caurina*; Comfort et al. 2016). Similarly, consistent with others, we observed negative coefficients for topographic position index, indicating selection for nesting and roosting in drainage bottoms or on lower slopes (Seamans and Gutiérrez 1995, May et al. 2004, Ganey et al. 2013). The MSO is considered heat intolerant (Ganey et al. 1993, Weathers et al. 2001); nesting/roosting in drainage bottoms and on lower slopes likely provides a cooler microclimate that minimizes heat stress. These sites also may be better suited to grow the large trees typically associated with Spotted Owl nest sites (Seamans and Gutiérrez 1995, May et al. 2004, Ganey et al. 2013).

We observed strong selection for high percent cover of mixed-conifer forest (Table 2) consistent with several previous studies (Ganey and Balda 1989, Seamans and Gutiérrez 1995, Peery et al. 1999, May and Gutiérrez 2002, Ganey et al. 2013). However, Timm et al. (2016) reported relatively low effect size and importance of percent mixed-conifer in northern Arizona, and suggested that the MSO in their study area might be utilizing pine–oak stands as an alternative to mixed-conifer forest (Ganey et al. 1999).

Lastly, the 2 MSO populations we examined showed large differences in the importance of topographical variables in predicting habitat suitability. In the Sacramento Mountains study area, topography appears to be less important than vegetation. Here, the topography is dominated by montane terrain in which the suitable habitat is relatively widespread and primarily associated with occurrence of mixed-conifer forests with high canopy cover. In contrast, topography dominated the Mogollon Plateau model, with suitable habitat typically associated with canyons and isolated mountain peaks. This difference in the relative effects of topography on the relative likelihood of MSO occurrence in these 2 study areas is of particular importance. A large portion of the MSO range is characterized by canyons, and MSO inhabiting these areas likely have habitat relationships that are different from those inhabiting contiguous forest (Rinkevich and Gutiérrez 1996, Willey and van Riper 2007, Bowden et al. 2015). Previous habitat models for MSO inhabiting canyonlands also identified topography as the best predictor of owl occurrence, with vegetation indices and geologic layers also providing some information (Willey and Zambon 2014). Unlike forested habitats, the rocky canyonlands are less susceptible to fire and might function as crucial fire refugia for the MSO as the risk of stand-replacing fire increases in forested habitats (Jenness et al. 2004).

Management Implications

Differences in habitat selection between the 2 MSO populations suggest that effective MSO conservation may require different habitat management strategies in differ-

ent landscapes. In the Mogollon Plateau, in addition to the scattered mixed-conifer forest, ponderosa pine stands may be providing important suitable habitat for the MSO, especially where Gambel oaks comprise the understory (Ganey et al. 1999). In this area, managers should consider conserving both mixed-conifer and pine–oak stands, especially where they occur in relatively steep and narrow canyons. In contrast, in the Sacramento Mountains, ponderosa pine stands were less diagnostic of suitable MSO nest/roost sites, and conserving mixed-conifer stands should remain the highest priority.

Conclusion

Habitat selection models can be used to identify important locations for prioritizing conservation efforts, but projecting a habitat model from one area to another can lead to prediction errors because of nonstationarity of species–environment relationships. We provided a methodology for evaluating potential nonstationary species–habitat relationships at multiple scales, and demonstrated that it was possible and important to identify this nonstationarity when considering habitat requirements in the case of the MSO. We found that both spatial scales and the factors important to predicting species distributions can vary between different landscapes, suggesting the importance of meta-replication and scale optimization analyses, especially across wide geographical areas.

Conservation recommendations across the range of the MSO would greatly benefit from broader replicated studies focusing on MSO habitat selection in more canyon-dominated ecosystems. Optimized multi-scale models broadened our understanding of Spotted Owl–habitat relationships in the study areas we evaluated. Applying these same analyses in other terrain types would help to provide a unifying evaluation of habitat selection across the range of the MSO. In the meantime, given the differences we observed between 2 MSO populations within forested habitat, we recommend that managers develop and use information specific to different populations and ecological settings to guide management and conservation planning.

ACKNOWLEDGMENTS

We thank the many dedicated field personnel who helped locate owls within the Sacramento Mountains and Mogollon Plateau study areas. We especially thank J. P. Ward, Jr., for his assistance in implementing the Sacramento Mountains study, and Sacramento Mountains field crew leaders D. Apprill, R. Jonnes, S. Kyle, and T. Rawlinson. Personnel on the Sacramento Ranger District, Lincoln National Forest provided operational support during the Sacramento Mountains study. We thank S. Hedwall for comments on earlier drafts. We also thank R. J. Gutiérrez and two anonymous reviewers for providing comprehensive reviews and comments.

Funding statement: Primary funding was provided by the Southwestern Region, USFS, with secondary funding from the Lincoln National Forest and Rocky Mountain Research Station, USFS.

Ethics statement: This study complies with all federal and state regulations regarding the ethical treatment of research subject.

Author contributions: SAC conceived the idea and supervised the research. HYW formulated hypotheses, developed the methods, conducted the modeling, analyzed the data, and was lead in writing the paper. VL assisted in conducting the modeling. BCT and KM developed the methods, and the latter helped write the paper. JLG contributed data and funding, and helped with data interpretation and writing.

LITERATURE CITED

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