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RESEARCH ARTICLE

Estimating density of a territorial species in a dynamic landscape

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Abstract
Context Conservation planning for at-risk species requires understanding of where species are likely to occur, how many individuals are likely to be supported on a given landscape, and the ability to monitor those changes through time.
Objectives We developed a distribution model for northern spotted owls that incorporates both habitat suitability and probability of territory occupancy while accounting for interspecies competition.
Methods We developed range-wide habitat suitability maps for two time periods (1993 and 2012) for northern spotted owls that accounted for regional differences in habitat use and home range size. We used these maps for a long-term demographic monitoring study area to assess habitat change and estimate the number of potential territories based on available habitat for both time periods. We adjusted the number of potential territories using known occupancy rates to estimate owl densities for both time periods. We evaluated our range-wide habitat suitability model using independent survey data.
Results Our range-wide habitat maps predicted areas suitable for territorial spotted owl presence well. On the demographic study area, the amount of habitat declined 19.7% between 1993 and 2012, while our estimate of the habitat-based carrying capacity declined from 150 to 146 territories. Estimated number of occupied territories declined from 94 to 57.
Conclusions Conservation and recovery of at-risk species depends on understanding how habitat changes over time in response to factors such as wildfire, climate change, biological invasions, and interspecies competition, and how these changes influence species distribution. We demonstrate a

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model-based approach that provides an effective planning tool.

Keywords Habitat modeling · Carrying capacity · Occupancy rates · Territory density · Northern spotted owl

Introduction

Critical to the conservation of at-risk wildlife species is a fundamental understanding of their current and former spatial distribution. This is a challenge because a species' distribution across space and time is influenced by abiotic and biotic elements that interact and change in complex ways. For example, a species' distribution is directly linked to required habitat, which is itself distributed based on biotic and abiotic components of the ecosystem (Hirzel et al. 2006; Requena-Mullor et al. 2014). Numerous factors can alter the distribution of habitat over space and time. For the distribution of forest dependent species, habitat loss, habitat fragmentation, and changes in forest composition resulting from timber harvest may be compounded by effects of climate change, wildfire, and/or biological invasions (Carroll et al. 2010a, b; Dugger et al. 2016).

Advancements in remote sensing and machine-learning technology are increasing the ability to predict and monitor species distributions across landscapes (Pimm et al. 2015). For example, species distribution models are numerical models used both for describing species distribution patterns and making predictions. These models assess a suite of components influencing spatial distribution and can be used to evaluate species-habitat relationships, effects of disturbance, evaluate an area's suitability for the species, and predict a species' presence or relative density (Elith and Leathwick 2009). These models are sometimes called habitat selection or ecological niche models, and are now a valuable tool for effective conservation planning and for assessing impacts of land management actions (Hirzel et al. 2006; Merow et al. 2014a; Ahmed et al. 2015).

For many species, occupancy modeling has become the preferred method for evaluating the dynamics of species distributions because heterogeneity in occupancy and detectability are modeled directly for each species (MacKenzie et al. 2006). However, conservation planning can be improved with more understanding than just species distribution and detection probability. Abundance and density are also critical parameters of interest for management and conservation of wildlife populations. Occupancy and abundance are interrelated, but in most circumstances occupancy alone is a poor surrogate for abundance because the relationship between these metrics is species- and site-specific (Gaston 1999). Further, abundance and occupancy are often nonlinear due to individual behavioral responses to heterogeneously aggregated resources, competitors, conspecifics, and predation risk (Gaston 1999; Yackulic et al. 2014).

In the United States of America, Section 7 of the Endangered Species Act (ESA) requires federal agencies to consult with the US Fish and Wildlife Service (USFWS) and/or National Marine Fisheries Service (NMFS) when engaged in activities that can potentially harm an ESA-listed species or its federally designated critical habitat. Additionally, the National Environmental Policy Act (NEPA) requires entities to complete Environmental Assessments or Environmental Impact Statements to determine and disclose the likely environmental impact of proposed activities. Having knowledge about listed species' densities and distributions on landscapes of interest enables managers to better address the intent of both ESA and NEPA. Although conservation planning relies on understanding a species' abundance it is frequently an ambiguous quantity and difficult to estimate (Tingley et al. 2015). Wildlife densities are often estimated using various types of mark–resight studies or surveys at a range of geographic scales. For closed populations, mark–resight methods provide reliable estimations of population size, but demand significant effort to mark and resight individuals within a population (Pierce et al. 2012). Additionally, there is often a scaling mismatch because most surveys or studies that inform conservation planning are conducted at a different scale than the project area where environmental impacts may occur (Johnson et al. 2004; Elith and Leathwick 2009). Abundance rarely scales directly with occupancy or density because species are not homogenously distributed in space or time (Brown et al. 1995; Mehlman 1997).

Here we illustrate the use of a landscape-scale model to predict the distribution and density of a territorial species using the northern spotted owl (*Strix* *occidentalis caurina*) (hereafter, spotted owl) as our example. In 1990, the spotted owl was listed as threatened under the ESA, primarily as a result of harvesting of late-successional forest in western North America from southern British Columbia to northern California (USFWS 1990; Gutiérrez et al. 1995). Spotted owls are highly reliant on mature and late-successional forest for multiple life-history requirements. Adult spotted owls are territorial, maintain large home ranges (Forsman et al. 2005; Price et al. 2015), relatively long-lived, and have high site fidelity (Forsman et al. 1984). To meet requirements of the ESA and National Forest Management Act/Federal Land Policy and Management Act, federal agencies adopted the Northwest Forest Plan (NWFP) (United States Department of Agriculture [USDA] and United States Department of Interior [USDI] 1994) as a conservation strategy for the subspecies that occurs in the Pacific Northwest. Although a range of habitat conservation measures were implemented under the NWFP, two decades of monitoring and research have documented continued declines in spotted owl populations (Forsman et al. 2011; Dugger et al. 2016). In recent decades, barred owls (*Strix varia*) have expanded into the range of the spotted owl, and accelerated range-wide declines in spotted owl populations are directly associated with increased barred owl populations (Dugger et al. 2011, 2016; Wiens et al. 2014).

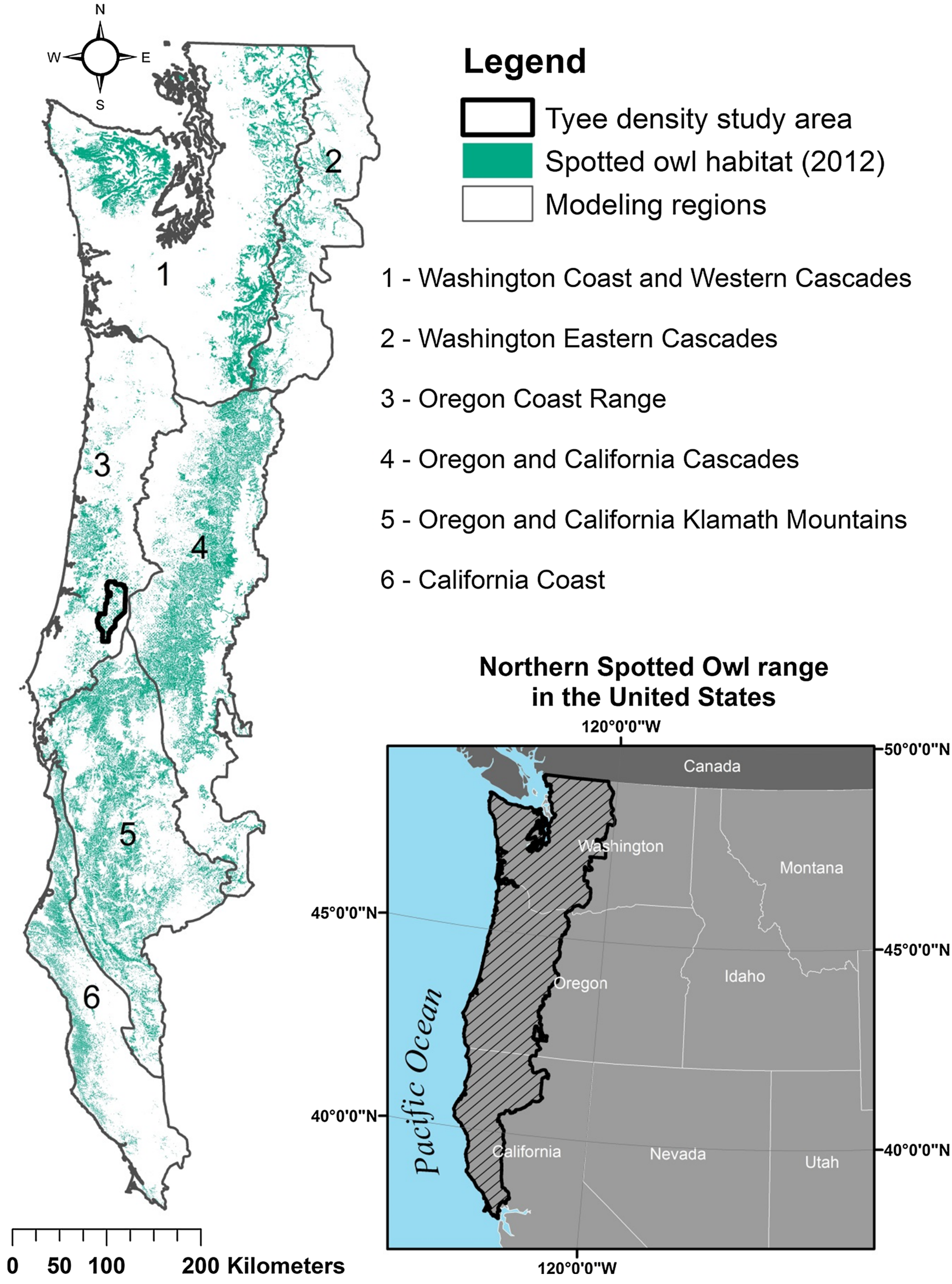
Despite being a highly-studied wildlife species, only a few range-wide evaluations of spotted owl habitat association (Carroll and Johnson 2008) and habitat distribution (Davis et al. 2011, 2016; USFWS 2011b) have been conducted. While federal agencies have used species distribution models to develop spotted owl habitat maps for broad scale monitoring purposes (Davis et al. 2011), a territory density model for estimating spotted owl territory densities for large unsurveyed landscapes has not yet been developed. Land management agencies have typically followed an auditory survey protocol (USFWS 2011a) to identify areas occupied by spotted owls for project planning efforts. The feasibility of using these methods is limited because surveys are expensive, time consuming to conduct, and of limited temporal duration and use.

As an alternative to using project level surveys to inform management decisions and conservation efforts, we developed a relative habitat suitability model for spotted owls and estimated potential densities at the landscape scale. We incorporated additional factors such as interspecies competition and changes in habitat and fire risk resulting from climate change. Our objectives were to: (1) develop a range-wide relative habitat suitability model using forest vegetation, topographic, and climate data, and (2) develop a territory density model for predicting distribution and density of spotted owls based on ecological factors and their territorial behavior. We used those models to assess habitat change and associated spotted owl densities by evaluating changes in forest conditions between 1993 and 2012. We selected these dates to coincide with pre- and post-range expansion of the barred owl. We evaluated our relative habitat suitability models using independently-collected survey data for spotted owls, and evaluated our territory density model using monitoring data from a territorial density study area. We present this approach for estimating potential distribution of spotted owls and demonstrate that such models provide a valuable tool for evaluating effects of land management actions, wildfire, interspecies competition, and climate change on conservation and recovery of at-risk species.

Study area

Our study covered the geographic range of the northern spotted owl in the United States, including portions of California, Oregon, and Washington, which contains approximately 183,100 km^2 of forest land (USFWS 2012). We divided the study area into six modeling regions (Fig. 1) based on the regional distribution of major forest types (Franklin and Dyrness 1988) and further refined for use in the NWFP area (Thomas et al. 1990; FEMAT 1993; USDA and USDI 1994). The modeling regions differed in forest composition, topography, climate, disturbance regimes, spotted owl prey base, and space use patterns by spotted owls (Davis et al. 2011).

Vegetation throughout the study area was predominately coniferous forests, but age and species composition of forests varied widely within and among modeling regions, depending upon elevation, latitude, climate, and disturbance (fire and timber harvest) history. All model regions were characterized by mixtures of mature forest ($\geq$80 years old) interspersed


N
W
E
S
Legend
Tyee density study area
Spotted owl habitat (2012)
Modeling regions
1 - Washington Coast and Western Cascades
2 - Washington Eastern Cascades
3 - Oregon Coast Range
4 - Oregon and California Cascades
5 - Oregon and California Klamath Mountains
6 - California Coast
1
2
3
4
5
6
0 50 100 200 Kilometers
Northern Spotted Owl range
in the United States
120°0'0"W
50°0'0"N
45°0'0"N
40°0'0"N
Canada
Washington
Montana
Oregon
Idaho
California
Nevada
Utah
Pacific Ocean

◀ **Fig. 1** Study area map showing the six modeling regions used to develop relative habitat suitability models across the range of the northern spotted owl in the United States and location of the Tyee demographic study area in central Oregon, USA

with regenerating young forests. Areas in the central or eastern Cascades were characterized by warm, dry summers and cool winters, with most precipitation occurring as snow during winter months. In coastal forests, climate was maritime with most precipitation falling as rain during winter months, although snow was present at higher elevations. In the Klamath region of southern Oregon and Northern California, summers were warmer and drier than more coastal areas. Mean annual precipitation ranged from approximately 120 cm per year in southwest Oregon to over 350 cm per year on the Olympic Peninsula.

Our territory density model was tested on the Tyee Density Study Area (1026 km^2) located on the eastern slope of the Oregon Coast Range near Roseburg, Oregon (Fig. 1). The Tyee study area is an area used to study the long-term trends in spotted owl population, including demographics and density (Lint et al. 1999; Dugger et al. 2016). This area was characterized by intervening Sections (2.59 km^2) managed by the USDI Bureau of Land Management (BLM) and private land owners that have created a checkerboard pattern of older, unharvested forests and younger forests of various ages that had been previously harvested for timber resources (Reid et al. 1996).

Methods

The conceptual framework for our model was based on extensive research on spotted owls conducted over the past two decades that provided comprehensive information on habitat selection, home range size (Forsman et al. 1984; Carey et al. 1990; Glenn et al. 2004; Schilling et al. 2013), demography (Anthony et al. 2006; Forsman et al. 2011), and site occupancy rates (Dugger et al. 2011, 2016). Additionally, there have been several range wide modeling efforts to describe the distribution of forest cover type selected by spotted owls for nesting and roosting (Lint 2005; Davis et al. 2011, 2016). In those efforts habitat was described as the forest cover type primarily used for nesting and roosting, but that cover type is only one of several components of spotted owl habitat. Ultimately, habitat includes all the elements (biotic and abiotic) that determine where the species occurs and thus it is important for conservation efforts to be able to adequately map habitat, not just cover types (Hall et al. 1997; USFWS 2012; Bamford and Calver 2014; Mathewson and Morrison 2015). Here we use the term nesting/roosting to describe a forest cover type and the term relative habitat suitability to describe the combination of forest cover used for nesting and roosting, and other abiotic and biotic variables.

We used a 5-step process to develop our territory density model: (1) we developed relative habitat suitability models and maps for 1993 and 2012; (2) we evaluated the models and evaluated the predictive quality of the maps; (3) we estimated the territorial carrying capacity based on the amount and distribution of modeled habitat, and known spacing of spotted owl territories; (4) we estimated actual occupied territory density by adjusting the territorial carrying capacity with empirically-derived occupancy rates; and (5) we evaluated density estimates using data from the Tyee study area.

Habitat modeling and mapping

We used program MaxEnt version 3.3.3k (Phillips et al. 2006) to produce relative habitat suitability models and maps for the six modeling regions. MaxEnt estimates relative environmental suitability for species presence by using a machine learning process to develop algorithms that model the most uniform distribution (maximum entropy) of averaged environmental conditions at known species locations compared to a large randomly generated sample of available locations from within the modeling region (Phillips et al. 2006; Phillips and Dudik 2008). MaxEnt is the most widely used software for conducting presence-only species distribution modeling (Merow et al. 2014a; Ahmed et al. 2015), but caution has been advised in the use of presence-only models because key assumptions must be met (Royle et al. 2012; Yackulic et al. 2013). We used these methods because we were confident that we met those sampling assumptions of minimal sampling bias and high probability of detecting nesting spotted owls when they were present. Furthermore, when proper procedures are followed presence-only models provide reliable distribution models (Merow et al.

2013, 2014a; Phillips and Elith 2013; Ahmed et al. 2015). In order to develop a reliable spotted owl distribution model, we evaluated sources of training and testing data, applied model calibration procedures, and conducted critical examinations of modeled relationships between species occurrence and environmental covariates. In addition, we have provided information including response curves, model performance metrics, and other information to fully evaluate our results.

Owl presence data for model training and testing was based on 2809 nest or day roost locations from 1993 that were compiled for NWFP monitoring efforts (Davis et al. 2016). These data were compiled from standardized survey protocols developed to identify spotted owl territorial sites in forested landscapes (USFWS 1992, 2011a). Surveys were conducted across large forested landscapes; however, sampling effort was not uniform across all areas. In order to address and correct sampling bias (Phillips et al. 2009; Fourcade et al. 2014) we reduced the geographically clumped nature of these data by using only one location per spotted owl territory following methods of Davis et al. (2016). For each modeling region we developed baseline models that represented the relative habitat suitability for territorial spotted owl occupancy for 1993, a year when barred owl presence was not very high and interspecific competitive effects were deemed minimal to habitat selection by spotted owls (Dugger et al. 2016). We then projected those model algorithms to 2012 environmental conditions to generate a 2012 relative habitat suitability model.

Informed by existing studies and modeling efforts, we identified 9 environmental predictor variables for inclusion in the model that have demonstrated support for influencing spotted owl habitat selection and site occupancy (Table 1). Amount and spatial arrangement of nesting/roosting cover are known to influence owl space use and fitness, thus four of our variables quantified amount and configuration of nesting/roosting cover at the nest patch (200 m radius) and territory scale (600–1900 m radii). The remaining 5 variables were abiotic: elevation, topographic position, average minimum January temperature, average maximum August temperature, and average annual precipitation (Table 1). The suite of variables was the same for all modeling regions, but relationships with spotted owl presence varied across regions.

Although MaxEnt produces valid model predictions with highly correlated variables (Elith et al. 2011), interpretation of response curves for highly correlated variables can be problematic (Phillips and Dudik 2008). Therefore, we calculated variance inflation factors (VIF) for each variable to inform our interpretation of modeled response curves during the model evaluation procedure. Variables with a VIF $\geq$10 indicate excessive multi-collinearity (Marquardt 1970; Mendenhall and Sincich 2003; Kutner et al. 2004; O'Brien 2007) and therefore we did not interpret response functions for variables with VIF $\geq$10. We restricted response curves to linear, quadratic, and product functions to produce models that were not overly complex (Merow et al. 2014b).

We calibrated models using a bootstrapping technique with stepwise adjustments of a regularization multiplier, which is an algorithm coefficient used to reduce model complexity and overfitting (Phillips et al. 2006). The regularization multiplier is based on a combination of likelihood with a complexity penalty, making it conceptually similar to information theory approaches (Burnham and Anderson 2002; Merow et al. 2014a). We ran a series of ten replicates using 75% of the territorial spotted owl presence data to train the model and 25% to test the model's prediction for regularization multiplier settings from 0.5 to 5.0, adjusted at 0.5 increments for each of the six modeling regions. For each of these series, we examined the training and test gains which can indicate model overfitting. We also examined the test area under the receiver operating curve (AUC) statistic, which is often used to evaluate model accuracy and fit (Fielding and Bell 1997). We examined each model's performance based on the continuous Boyce index (CBI), which was designed specifically for testing habitat models produced from presence-only data (Boyce et al. 2002; Hirzel et al. 2006). The CBI is based on the Spearman rank correlation coefficient (R_s) of the ratio of the proportion of presence locations (P) to the proportion of modeling region available (E) for species occurrence from low to high relative habitat suitability. A good model is indicated by an increasing P/E ratio as the relative habitat suitability prediction increases (Hirzel et al. 2006). We created binary relative habitat suitability maps of spotted owl habitat (P/E >1) and non-habitat (P/E $\leq$1) for territorial spotted owls. From each series we selected the model

Table 1 Description of environmental predictor variables used to develop map of relative habitat suitability for northern spotted owls in Washington, Oregon, and northern California, USA

Predictor variable	Description	Units	Importance for northern spotted owls	Source
NR_{patch}	Percent nesting/roosting cover within a 200 m radius moving window (nest patch)	% area	Spotted owls are associated with greater amounts of nesting/roosting cover than available at nest patch scale	Franklin et al. (2000); Dugger et al. (2005); Davis et al. (2016)
$NR_{territory}$	Percent nesting/roosting cover within a 600–1900 m radius (territory) moving window (depending on modeling region)	% area	Spotted owls associated with greater amounts of nesting/roosting cover than available at the territory scale	Davis et al. (2016)
FRAG	Percent highly fragmented nesting/roosting cover within a territory radius moving window	% area	Spotted owls are associated with less fragmented habitat conditions particularly in northern OR and WA	Davis et al. (2016); Franklin et al. (2000)
$DIST_{interior}$	Euclidean distance to the nearest interior portion of a patch of nesting/roosting cover (>100 m from patch edge)	km	Spotted owls are associated with greater amounts of interior habitat	Franklin et al. (2000); Zabel et al. (2003); Davis et al. (2016)
TPI	Topographic position index, calculated as the difference between a cell's elevation and the mean elevation of cells within a 450-m-radius window	index	Spotted owl nest sites are often located at mid- and lower-slope sites	Ohmann and Gregory (2002); Stralberg et al. (2009)
ELEV	Elevation above sea level	m	Spotted owls are associated with mid-slope positions	USGS Digital Elevation Models (DEM)
PRECIP	Average annual precipitation (1981–2010)	mm	Cold, wet winters and nesting seasons negatively affect survival and reproduction	PRISM climate 30-year normals (http://www.prism.oregonstate.edu/normals/) (Franklin et al. 2000; Olson et al. 2004)
$TEMP_{max}$	Average monthly maximum temperature for August (1981–2010)	°C × 100	Hot summer conditions negatively affect vital rates in some regions	PRISM climate 30-year normals (http://www.prism.oregonstate.edu/normals/) (Glenn et al. 2010)
$TEMP_{min}$	Average monthly minimum temperature for December (1981–2010)	°C × 100	Cold, wet winters and nesting seasons negatively affect survival and reproduction	PRISM climate 30-year normals (http://www.prism.oregonstate.edu/normals/) (Franklin et al. 2000; Olson et al. 2004; Glenn et al. 2010)

that achieved similar training and test gains, while maximizing test AUC and CBI statistics.

Habitat model evaluation and validation

Although we did not use a model selection approach because we included only variables with documented support for influencing spotted owl habitat selection and site occupancy, we reviewed predictor variable response functions (VIF <10) and permutation importance indices to determine if model variables were consistent with published accounts of spotted owl ecology and retained those variables that were consistent. Permutation importance index is a measure of variable contribution to the model based on random permutations of that variable among the training and background points. Its value represents the percentage decrease in training AUC and large values indicate that the model relies heavily on the variable.

We evaluated the 2012 range-wide relative habitat suitability map using 815 independently collected territorial spotted owl pair locations from federal and state land management and regulatory agency surveys from 2012 thru 2014. These survey data were compiled from the USDA Forest Service, USDI Bureau of Land Management, California Department of Game and Fish, and the Washington Department of Natural Resources. These location data were overlaid on the 2012 relative habitat suitability map and we calculated the CBI across the entire spectrum of habitat predictions as well as the percentage of locations ≤100 m (average spatial accuracy of the agency survey data) from spotted owl habitat on the 2012 relative habitat suitability map.

Territorial carrying capacity estimation

We used the binary relative habitat suitability maps to estimate habitat-based carrying capacity ($TERR_{hab}$) for the Tyee study area, where individually-marked owls, demographic rates, and density have been monitored over the last 2 decades (Reid et al. 1996). We used a binary map in order to provide a broadly applicable methodology for estimating territory density. For spotted owls, a binary map provides a habitat footprint where owls are most likely to establish territories. In an intensive survey effort, Dugger et al. (2016) delineated 156 territories, which we considered an accurate representation of the known density for that landscape. We used the median nearest neighbor distance (2113 m) between delineated territory centers for the study area to estimate the number of potential territories for the landscape based on available habitat in 1993 and 2012. We generated a maximum number of random points (20 iterations for 1993 and 2012) within the binary relative habitat suitability maps using nearest neighbor as the constraint parameter to prevent random points from being generated closer than the median nearest neighbor distance (Geospatial Environmental Modeling (GME) software (Beyer 2012). For each iteration, we input a large sample size parameter that we knew exceeded the density of the study area and after 1,000,000 attempts GME output the maximum number of points within binary relative habitat suitability footprint.

Occupied territory density estimation and validation

We estimated the number of territories that would likely be occupied ($TERR_{occ}$) using annual occupancy rate (ψ) information from Dugger et al. (2016) as follows:

$$TERR_{occ} = TERR_{hab} \times \psi. \quad (1)$$

We calculated $TERR_{occ}$ as a range using the mean and confidence limits of ψ for 1993 and 2012 (Dugger et al. 2016). We evaluated our 1993 estimate of $TERR_{hab}$ at the Tyee study area by comparing our estimate to the number of known territories ($n = 156$) that were established from Dugger et al. (2016). We compared our $TERR_{occ}$ estimates to survey data from the annual demographic surveys conducted in the study area for both time periods.

Results

Our relative habitat suitability models performed well in predicting known territorial owl pair locations, with mean AUCs for each modeling region ranging from 0.81 to 0.91 (Table 2). Mean bootstrapped Spearman rank test statistics of the relationship of relative habitat suitability to P/E ratios (CBI index) ranged from 0.66 to 0.96. The models performed well in all modeling regions as reflected by AUC values ≥0.81 in all regions (Table 2). The test of the range-wide 2012 relative habitat suitability map using independent survey data showed that the model was well-calibrated in all regions with higher densities of owls in areas with higher relative habitat suitability ($R_s = 0.998$) (Fig. 2). Ninety percent of the independent test locations were on or within 100 m of mapped spotted owl habitat.

Almost all environment variables had VIFs <10 (range 1.1–12.0) and those with VIFs ≥10 were abiotic (Table 3). Therefore, we did not interpret the response functions for the abiotic variables. In addition, abiotic variables generally had lower model permutation importance than the nesting/roosting variables; however, importance varied considerably (8.6–41.5) across modeling regions (Table 4). Abiotic variables contributed more in the drier and southern portions of the spotted owl range. The strongest abiotic variable was the topographic position index, which indicated lower slope positions may be important in those areas. We only examined response functions for biotic covariates because they had high collinearity and low model importance.

Nesting/roosting cover-type predictor variables provided more explanatory information in our models than abiotic variables with total mean permutation

Table 2 Summary of model calibration statistics by model region for the northern spotted owl relative habitat suitability model for Washington, Oregon, and northern California, USA

Model region	RM[a]	Training sample	Test sample	Training gain	Test gain	AUC[b]	CBI (R_s)[c]	P/E = 1[d]
Washington Coast and Western Cascades	0.5	250	83	1.51 (±0.04)	1.46 (±0.07)	0.91 (±0.01)	0.89 (±0.08)	0.21 (±0.04)
Washington Eastern Cascades	3.5	87	28	1.09 (±0.05)	1.20 (±0.05)	0.89 (±0.01)	0.66 (±0.10)	0.36 (±0.05)
Oregon Coast Range	4.5	247	82	1.49 (±0.06)	1.52 (±0.11)	0.91 (±0.08)	0.94 (±0.03)	0.24 (±0.04)
Oregon and California Cascades	1.5	595	198	0.77 (±0.03)	0.76 (±0.04)	0.83 (±0.08)	0.94 (±0.06)	0.32 (±0.05)
Oregon and California Klamath Mountains	5.0	756	251	0.62 (±0.03)	0.68 (±0.03)	0.81 (±0.01)	0.96 (±0.04)	0.39 (±0.02)
California Coast	0.5	174	58	0.96 (±0.05)	0.98 (±0.06)	0.85 (±0.01)	0.91 (±0.05)	0.38 (±0.05)

[a] Regularization multiplier

[b] Test area under the receiver operating curve

[c] Continuous Boyce index

[d] Ratio of presence locations to the proportion of modeling region available

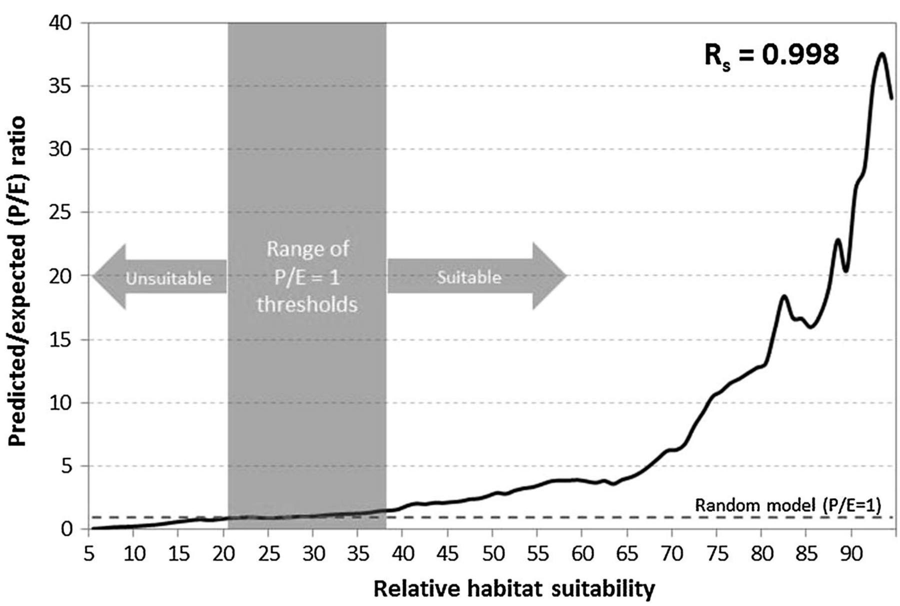


Fig. 2 Predicted versus expected (P/E) curve and continuous Boyce index (CBI) based on Spearman rank (R_s) analysis for 2012 spotted owl habitat map evaluation using independent agency survey data. The x-axis is truncated from 5 to 95 because we used a 10-interval moving average

importance ranging from 58.5–91.3% (80.8% in the Tyee study area) (Table 4). The response curves (averaged across all modeling regions) for the amount of nesting/roosting cover at the nest patch-scale (200 m radius) showed a logistic relationship where relative habitat suitability increased as the percentage of nesting/roosting cover increased (Fig. 3). At the larger territory-scale, the general relationship between amount of nesting/roosting cover and relative habitat suitability followed a more bell-shaped curve (skewed to the right), indicating that there is a threshold (~70–80%) where there was no longer a positive relationship between nesting/roosting cover and relative habitat suitability. Likewise, the relationship between the amount of highly fragmented nesting/roosting cover and relative habitat suitability from

Table 3 Variance inflation factors (VIFs) for environmental predictor variables for the northern spotted owl relative habitat suitability model for Washington, Oregon, and northern California, USA

Predictor variable	Washington Coast and Western Cascades	Washington Eastern Cascades	Oregon Coast Range	Oregon and California Cascades	Oregon and California Klamath mountains	California Coast
NR_{patch}	2.8	2.2	2.2	2.6	2.8	6.2
$NR_{territory}$	3.6	3.1	3.2	3.4	3.3	7.1
$DIST_{interior}$	1.7	1.8	1.6	1.9	1.8	1.8
FRAG	1.7	1.8	2.0	1.4	1.3	1.4
TPI	1.2	1.2	1.1	1.1	1.1	1.1
ELEV	10.0	12.0	1.6	4.1	2.8	1.8
PRECIP	1.4	2.5	1.5	2.5	1.3	1.4
$TEMP_{max}$	2.1	12.1	1.7	2.4	2.0	2.6
$TEMP_{min}$	7.0	2.2	1.5	4.8	1.9	1.8

A VIF $\geq$10 indicates high collinearity with other variables. See Table 1 for variable descriptions

Table 4 Mean environmental predictor variable permutation importance values (±95% confidence intervals) for the northern spotted owl relative habitat suitability model for Washington, Oregon, and northern California, USA

Predictor variable	Washington Coast and Western Cascades	Washington Eastern Cascades	Oregon Coast Range	Oregon and California Cascades	Oregon and California Klamath mountains	California Coast
Biotic						
NR_{patch}	24.4 (±7.0)	28.1 (±10.8)	60.1 (±4.1)	66.7 (±5.9)	63.8 (±1.6)	48.3 (±3.9)
$NR_{territory}$	6.8 (±1.7)	1.9 (±0.9)	3.2 (±1.1)	6.8 (±0.6)	2.7 (±0.6)	3.6 (±1.0)
FRAG	3.2 (±0.8)	6.0 (±3.5)	13.5 (±4.0)	3.9 (±2.1)	4.3 (±1.1)	2.7 (±1.5)
$DIST_{interior}$	46.3 (±10.4)	48.0 (±11.6)	4.0 (±1.7)	13.9 (±1.7)	3.5 (±1.7)	3.9 (±1.7)
Mean total	80.8	84.0	80.8	91.3	74.2	58.5
Abiotic						
TPI	1.4 (±0.3)	4.3 (±1.5)	0.9 (±0.3)	3.2 (±0.5)	8.7 (±1.5)	21.4 (±2.9)
ELEV	8.9 (±2.2)	2.1 (±1.3)	4.7 (±1.3)	1.1 (±0.4)	2.4 (±0.9)	4.8 (±1.6)
PRECIP	6.3 (±1.2)	1.9 (±0.7)	3.6 (±0.9)	0.7 (±0.3)	12.9 (±1.2)	4.2 (±0.9)
$TEMP_{max}$	1.1 (±0.3)	1.3 (±1.1)	4.9 (±1.1)	0.6 (±0.3)	0.4 (±0.2)	2.3 (±0.7)
$TEMP_{min}$	1.5 (±0.5)	6.4 (±2.3)	5.1 (±1.3)	3.3 (±0.8)	1.3 (±0.4)	9.0 (±1.8)
Mean total	19.2	16.0	19.2	8.7	25.8	41.5

See Table 1 for variable descriptions

territorial use followed a bell-shaped curve (skewed to the left), indicating selection for approximately 20% of non-nesting/roosting vegetative cover (Fig. 3). Relative habitat suitability for territorial use generally decreased exponentially with increasing distance for larger nesting/roosting patches and was close to zero past about 7 km, indicating a preference for large patches of nesting/roosting cover for territorial use.

Changes in spotted owl nesting/roosting habitat and territory density, 1993–2012

Within the Tyee study area, nesting/roosting forest cover decreased from 20,206 ha to 16,734 ha (−17.2%) due primarily to timber harvesting on private lands (Davis et al. 2016). Proportionally, spotted owl habitat, identified on our binary relative habitat suitability map, decreased from 37,144 ha to 29,822 ha (−19.7%; Fig. 4). We estimated 154 possible territories in the Tyee study area in 1993 based on available habitat ($TERR_{hab}$; Table 5), which was very close to the actual number of known territories (n = 156) that were delineated by Dugger et al. (2016). For 2012, we estimated 148 possible territories, which was a 4% decrease from 1993 (Table 5). Dugger et al. (2016) estimated significantly lower occupancy rates in 2012 compared to 1993, which they attributed primarily to negative effects of barred owls and also to reductions in habitat. Consequently, our estimates of number of likely occupied territories decreased 39% from 94 likely occupied territories in 1993 to 57 likely occupied territories in 2012 (Table 5).

Discussion

The ability to adequately predict territorial species distributions and densities across landscapes and through time is important for implementing effective conservation strategies as well as monitoring the success of those strategies in a spatially extensive and cost–effective manner. We presented one example using existing spotted owl data and research from several sources. Our training and primary testing location data were available from an extensive demographic monitoring program with numerous strategically located long-term study areas across the spotted owl's range (Lint et al. 1999; Dugger et al. 2016). We relied on several radio-telemetry studies that identified home range sizes and territory spacing patterns throughout the

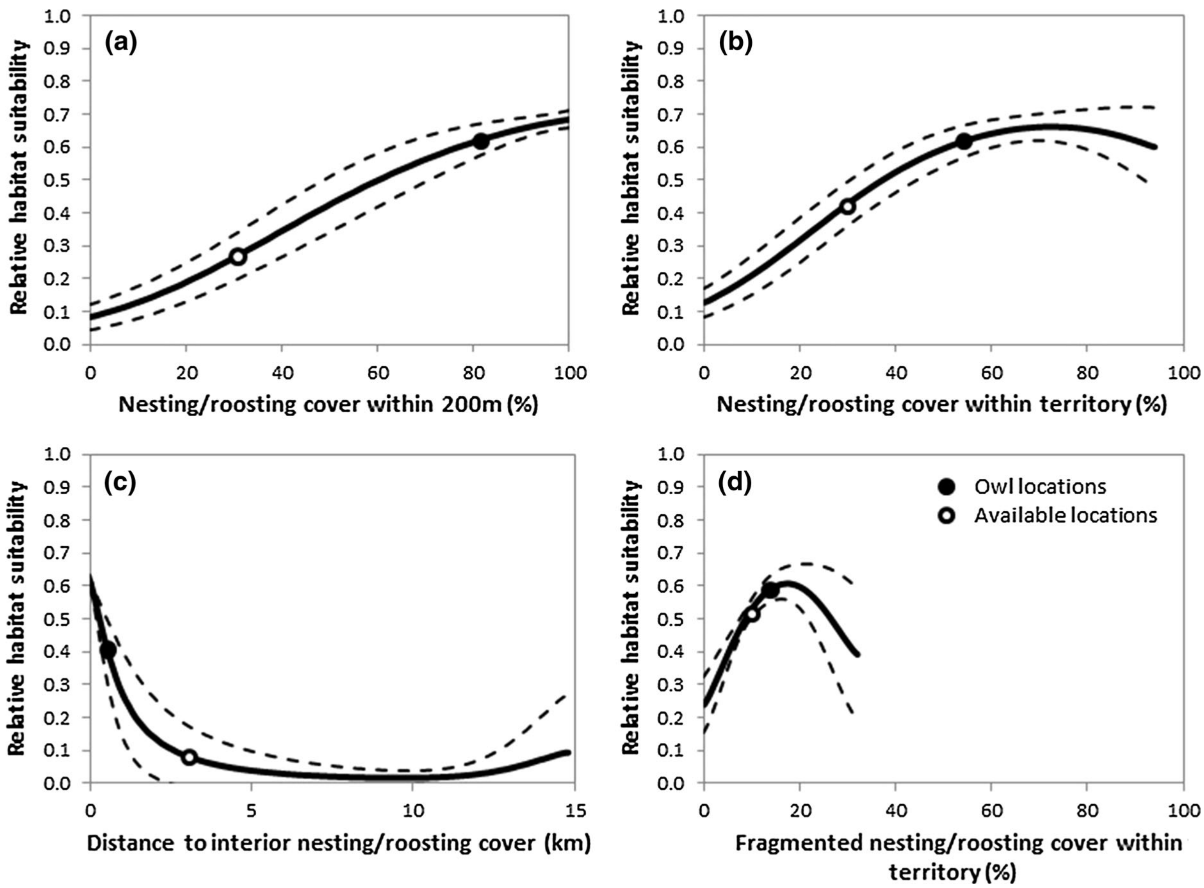


Fig. 3 Northern spotted owl relative habitat suitability response functions based on nesting/roosting cover averaged across modeling regions. The black line represents the mean and the dashed line represents 95% confidence intervals. The dots represent the average conditions at known spotted owl locations and available locations. The fragmentation curve was clamped to the maximum variable value used in the modeling process

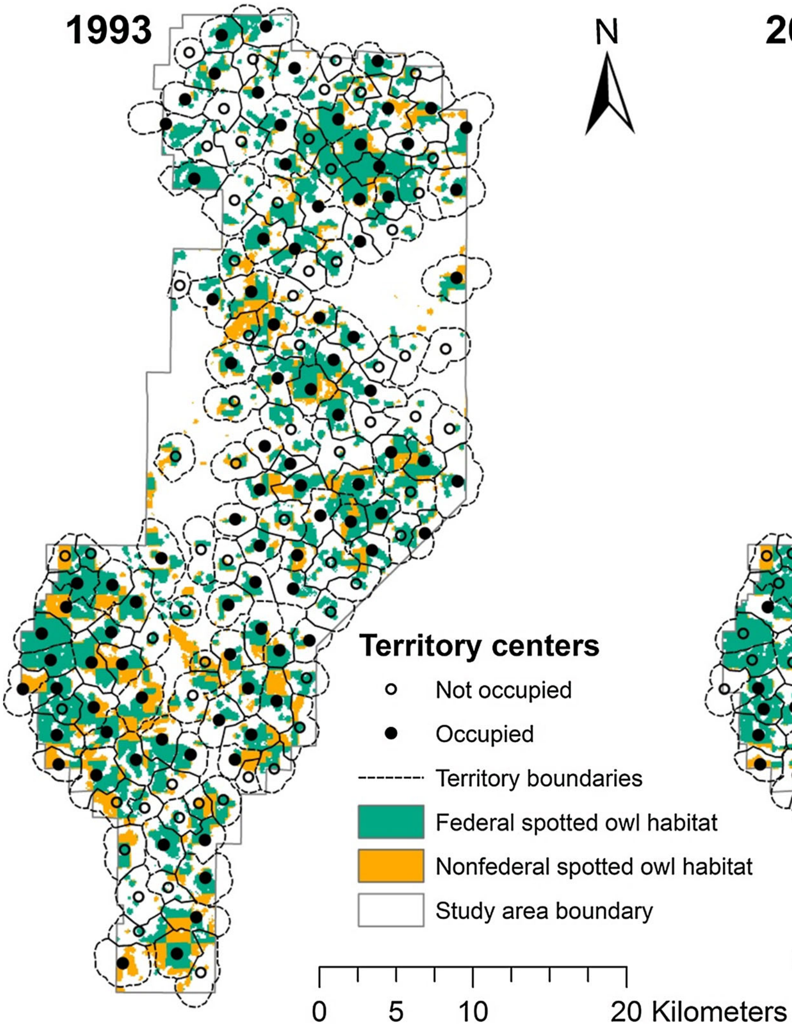


Fig. 4 Northern spotted owl habitat maps for the Tyee density study area in 1993 and 2012, showing known territory occupancy status from monitoring surveys in 1993 and 2012

Table 5 Territory density estimates for northern spotted owls in 1993 and 2012 on the Tyee density study area, Oregon

Year	Estimated habitat-based carrying capacity			Estimated occupancy rate[a]			Estimated occupied territories			Surveyed occupied territories
	LCL	MEAN	UCL	LCL	MEAN	UCL	LCL	MEAN	UCL	
1993	153	154	156	0.477	0.609	0.726	73	94	113	92
2012	146	148	150	0.285	0.384	0.495	42	57	74	69

[a] Dugger et al. (2016, Table 8)

range of the spotted owl. For further validation of our model, independent spotted owl locations were available because surveys for the species were required for timber sale planning activities across most federal lands since the early 1990s. Additionally, occupancy rates estimated by Dugger et al. (2016) provided detailed information on the impacts of barred owls and loss of habitat on density of spotted owls.

In comparison with another recent spotted owl habitat mapping effort (USFWS 2012), our model provided similar estimates of amount and distribution of spotted owl habitat. Our map estimated that approximately 22% of the forest-capable land within the range of the northern spotted owl was comprised of nesting/roosting habitat in 1993. A relative habitat suitability map developed for the purpose of designating critical habitat (USFWS 2012) estimated that approximately 30% of the forest-capable landscape was spotted owl habitat based on 1996 imagery. The slightly different objectives of these map products influenced the estimates of amount of habitat available throughout the range of the spotted owl derived from each. The objective of our model was to identify nesting/roosting habitat for estimating spotted owl territorial density while the relative habitat suitability model produced by USFWS (2012) sought to reliably identify areas that could have supported northern spotted owl territories at the time of ESA listing (1990). Consequently, minor differences in distribution and amount of habitat mapped should be expected when comparing map products created for slightly different purposes. Nevertheless, amount and distribution of habitat from our model was highly correlated with USFWS (2012) estimates at both the range-wide and study area scales.

Our approach incorporated regional variation in habitat associations and occupancy rates to develop a territory density model that could be applied to large landscapes across the range of this subspecies. These models could be developed for a wide range of species that exhibit territorial behavior and where data are available for mapping distribution and territory spacing. By integrating models with empirical data, this approach can provide more effective conservation planning tools than either technique by itself. Although we had extensive demographic data for spotted owls, similar territory density models can be effective for species that are monitored less intensively if the ecology of the species is sufficiently understood to parameterize the model. We also demonstrated that this approach has utility for assessing the effect of habitat change on territory densities over time.

Spatial models for estimating carrying capacity, abundance, or density have been used for other at-risk species including black-backed woodpeckers (*Picoides arcticus*) (Tingley et al. 2015), greater sandhill cranes (*Grus canadensis tabida*) (Downs et al. 2008), European badger (*Meles meles*) (Requena-Mullor et al. 2014), bats (*Myotis* spp.) (Pauli et al. 2015), brown bears (*Ursus arctos*) (Güthlin et al. 2011), sea birds (Clarke et al. 2003), and cetaceans (Braithwaite et al. 2012; Forney et al. 2012). Each of these models were tailored to address the biology of the species of interest, specific research objectives, and types of data available for model development; however, there are commonalities among them.

We offer suggestions for essential components needed for the development of models that provide effective, useful tools for estimating the distribution and density of territorial species for conservation and land management planning purposes. First, an adequate understanding the species' spatial ecology is needed, including how individuals are distributed across landscapes. For species lacking scientific study, strategic surveys and focused research may provide sufficient data to build and validate distribution models. Second, it remains important to model distribution at the appropriate spatial scale and resolution for the species of interest and to quantify interactions between vegetation and climate (Downs et al. 2008; Forney et al. 2012; Garden et al. 2015). Remotely-sensed vegetation and terrain data, and spatially- and temporally-explicit weather and climate data are widely available, but care should be taken to use appropriately-scaled spatial data for biotic and abiotic factors that characterize habitat across the landscape. As with all species distribution models, inference should only be drawn from within the geographic area and range of covariates used for model development (Tingley et al. 2015). Third, incorporating an estimate of occupancy rates will improve predictive capability of the model because probability of occurrence based on available habitat is often non-linearly correlated with species abundance, species rarely occupy all available habitat, and the presence of a competitor can decrease the target species' site occupancy (Bradley 2015; Lesmeister et al. 2015; Tingley et al. 2015). Without occupancy estimates available, surveys may be needed to provide detection and non-detection data from sites that accurately represent the spatial and temporal variation in environmental conditions throughout the modeling extent (MacKenzie et al. 2006). Finally, our procedure reinforced the need to directly address uncertainty, assess accuracy of environmental predictor variables, and to account for variation in habitat suitability at a scale relevant to the species of interest (Murphy and Noon 1992; Noon and McKelvey 1996; Glenn and

Ripple 2004). Model replication and validation procedures that produce predictions with variance estimates are useful and informative, especially when the level of uncertainty of the model is incorporated into the decision-making process. All models can be improved as understanding of species' ecology develops and as better environmental predictor variables become available. We recommend that users continue to refine their territory density models as the ecology of the species under study is better known. For spotted owls, this may include refining the territory density model if barred owl impacts on spotted owls change, or incorporating advances in remotely-sensed vegetation data into the relative habitat suitability map.

In addition to providing estimates of density and distribution, the modeling approach we present provides a tool for evaluating a range of different stressors on animal density and distribution that can provide useful insights into ecological effects of habitat configuration across landscapes. On the Tyee study area, the amount of habitat declined 19.7% between 1993 and 2012; however, the habitat-based carrying capacity declined only 4%. Our results revealed a non-linear relationship between available habitat and predicted carrying capacity that may reflect a reduction in habitat that was influenced by land management practices that increased habitat fragmentation, particularly on private lands. Across the range of the spotted owl, federal lands have long served as the primary focus for conservation of habitat and spotted owls, but the distribution and disturbance of habitat across all land ownerships influences landscape-scale occupancy rates and territory densities. Future modeling efforts that incorporate a continuous habitat suitability-based prediction for the probability of supporting a territory may provide more refined territory density estimates. For example, areas with large blocks of highly suitable habitat may support higher densities of spotted owls than areas with more fragmented and less suitable habitat. Such an analysis may reveal interesting insights regarding how spatial patterns of change in habitat across multiple ownerships influence densities of spotted owls.

Conservation implications

Wildlife and their habitat play a critical role in the provision of many ecosystem services relied upon by humans. In recognition of these values, wildlife conservation is an important policy and financial issue globally. Wildlife conservation is most effective when properly funded and economical, but spending dedicated to wildlife conservation has trended downward over the past several decades. A common goal in most conservation strategies is to minimize the cost of achieving goals related to species protections and population-level performance measures. Ultimately, cost-effective conservation leads to higher levels and more effective conservation in the face of limited funding. Unfortunately, population-level estimates of across large landscapes is an enormous technical and financial challenge.

For the past several decades, conservation planning and management for spotted owls has often been limited by the expense of surveying large landscapes to determine the status of the population within the planning area. Recent advances in methods and accumulation of ecological knowledge present opportunities to produce reliable and cost-effective estimates of the population that are critical for making management decisions. Our approach for estimating territory density provides a more economical and effective alternative for informing conservation efforts where surveys have not been conducted, are outdated, or may be impractical. For example, the Tyee study area encompassed an area of comparable size to most federal planning areas, and our modeling approach provided accurate estimates for both the maximum number of possible territories and the estimated number of occupied territories at time periods approximately two decades apart. For species with large home ranges, such as the spotted owl, this method is likely most appropriate at approximately 243 km^2 or larger. Our methods are appropriate for estimating territory densities across landscapes, but it was not designed to make predictions about the location of individual territory centers.

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