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The scientific basis for modeling Northern Spotted Owl habitat: A response to Loehle, Irwin, Manly, and Merrill



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ABSTRACT

The U.S. Fish and Wildlife Service recently revised the recovery plan (USFWS, 2011) and designated Critical Habitat (USFWS, 2012a) for the Northern Spotted Owl (*Strix occidentalis caurina*). The Critical Habitat designation was based in part on a map of relative habitat suitability that was developed by USFWS (2011, 2012b) for this purpose. Loehle et al. (2015) critiqued the U.S. Fish and Wildlife Service's approach to modeling relative habitat suitability for the Northern Spotted Owl. Here, we respond to Loehle et al.'s assessment, and identify four major shortcomings within it. First, it mischaracterizes the literature on spotted owls and MaxEnt, the species distribution model used by the U.S. Fish and Wildlife Service. Second, it is predicated upon several logic errors that, when resolved, undermine Loehle et al.'s conclusions. Third, it fails to demonstrate that the nesting and roosting site location data used by the U.S. Fish and Wildlife Service is a biased sample. Lastly, Loehle et al.'s claims of significant flaws in analytical methods and ecological inference by the U.S. Fish and Wildlife Service are not convincing. We assert that the U.S. Fish and Wildlife Service's Northern Spotted Owl relative habitat suitability model was in fact scientifically rigorous, and that it met the intended goals that the U.S. Fish and Wildlife Service articulated for their models.

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1. Introduction

In a recent paper, *Range-wide analysis of northern spotted owl nesting habitat relations*, Loehle et al. (2015, hereafter L IMM) critiqued the U.S. Fish and Wildlife Service's approach to identifying Critical Habitat for the Northern Spotted Owl (*Strix occidentalis caurina*, hereafter NSO). In their evaluation, L IMM used owl location and reproduction data from two study areas to “test” the relative habitat suitability model developed by U.S. Fish and Wildlife Service (hereafter USFWS). They also compared two alternative models, MaxLike and Relative Frequency Function, to the

USFWS's MaxEnt models using the same data set that the USFWS used. Most of us worked with or for USFWS to develop and test the modeling products L IMM critiqued, so we are very familiar with how USFWS used those products. Below, we evaluate the major criticisms of the USFWS models made by L IMM, their interpretations of the published literature on NSO habitat relationships, and the defensibility of their modeling efforts.

We believe that L IMM's evaluation is flawed or misleading in several aspects: (1) it mischaracterizes the literature on both NSOs and the MaxEnt species distribution model (Phillips et al., 2006) used by the USFWS; (2) it contains logic errors; (3) it fails to demonstrate that the NSO nesting site location data is a biased sample; and (4) claims of significant flaws in analytical methods and ecological inference by the USFWS are not convincing. In

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contrast, as described below, we believe that LMM's own evaluations demonstrate that the USFWS's habitat model is *superior* to their models. In this paper we focus on the criticism of the USFWS modeling efforts and claims of false inference. We also take issue with their characterization of the reliability of the forest vegetation data (Ohmann and Gregory, 2002) used to derive habitat covariates, but this concern is addressed separately by Bell et al. (2015).

2. Mischaracterization of the literature on Northern Spotted Owls

LMM state that our understanding of NSO–habitat relationships is poorly known. We believe this is a mischaracterization and misinterpretation of the peer-reviewed literature. The NSO is one of the most well-studied bird species in the world (Gutiérrez et al., 1995; USFWS, 2011), and the published literature includes numerous studies of the owl's habitat relationships at multiple spatial scales ranging from local (e.g., nest-sites) to landscape scale studies. In several key studies, the demographic performance of NSOs (survival, reproduction, growth rate) has been related to spatial variation in habitat characteristics (e.g., Franklin et al., 2000; Dugger et al., 2005). Several comprehensive reviews (Thomas et al., 1990; Gutiérrez et al., 1995; Blakesley, 2004; USFWS, 2011) of NSO habitat selection have been published, and each review concluded that NSOs exhibit strong selection for forested habitats dominated by mature and old-growth trees at local to landscape scales.

Given the above, we disagree with LMM's statement, "One of the puzzles has been the failure of these various studies to converge on the landscape and vegetation features that can be used to predict nest site locations and demographic performance." Many studies, for example, have used species distribution models to contrast nest-site location to background available data in terms of habitat covariates measured at both local and landscape scales. In general, these models have demonstrated strong habitat differences between owl nesting and roosting sites and random or unused locations within the forested landscape. For example, in northern California Zabel et al. (2003) created predictive models for four National Forests totaling >2.3 million ha. Their best-fitting model was at the 200-ha scale and correctly classified owl-occupied sites 94% of the time using their developmental data (a randomized sample of the four National Forests), and between 85% and 92% of the time on four independent test data sets. Zabel et al.'s (2003) best model included a threshold relationship with nesting and roosting habitat (large diameter trees with large amounts of canopy cover) and a quadratic relationship with foraging habitat (smaller trees than nesting and roosting, with less canopy cover). They also reported a very strong relationship between amount of habitat (sum of probabilities from pixels) and number of owls on nine study areas ($r = 0.89$). Similarly, Meyer et al. (1998) found that differences between owl-occupied and random sites were greatest for 0.8-km circles (~200-ha, but that differences were found out to 3.4-km radii too), concluding that random owl sites contained more old-growth forest, larger average size of old-growth patches, and larger maximum size of old-growth patches than occurred in random landscape locations. The peer-reviewed literature includes dozens of studies on NSO habitat selection that demonstrate the species' selection of mature and old-growth forest patches for nesting, roosting and foraging. The strength and consistency of these habitat associations are notable given the diversity of forest types and management histories across the NSO's range. Even supposed exceptions, such as the abundance of NSO nest sites found within mid-seral stands in coastal redwood forests, are well-understood and support the

consistent pattern of a strong association with large diameter trees (Folliard et al., 2000).

The strength of the relationships between habitat covariates and NSO demography and fitness are generally less pronounced. In part, this is due to strong climatic drivers of variation in NSO reproduction and survival that often override habitat effects (Glenn et al., 2011a, 2011b), though significant interactions between habitat and climate covariates have been reported (e.g., Franklin et al., 2000). LMM noted that the amount of variance explained in owl productivity (by coarse-scale habitat covariates) ranged from less than 2% to 38% among studies and conclude that coarse-scale habitat measures have little explanatory power. Similarly, they noted that the amount of variance in apparent survival accounted for by habitat covariates varied from 14% to 54% among three studies. LMM again emphasized the low explanatory power of habitat covariates from those studies. However, for a species in decline, and with limited reproductive potential, even small magnitude changes in a vital rate can greatly compromise the species' recovery potential. For example, given the strong sensitivity of the NSO's growth rate to variation in adult survival (Noon and Biles, 1990), even very small decreases in this vital rate can lead to precipitous population declines. If habitat heterogeneity accounts for 14 to >50% of the variation in survival rates in some years and in some parts of the species range, this clearly documents the importance of habitat.

Despite the difficulties of conducting large-scale and long-term field studies on NSOs, and the imperfect vegetation covariate data, multiple studies have shown significant relationships (of varying strengths) between habitat and NSO demographic rates. For long-lived species like the NSO, the link between the behavioral and evolutionary aspects of habitat selection (i.e., the fitness consequences of selecting differing habitat types) may only need to be pronounced in some years and at some locations in the species' geographic range. We acknowledge the remaining uncertainties that exist in our understanding of NSOs and their habitat relationships, but they do not overwhelm what we know. As a result, the habitat models developed by the USFWS to inform landscape-level decisions such as the designation of Critical Habitat are justified.

3. Mischaracterization of the literature on MaxEnt

LMM question the performance of the MaxEnt species distribution model (Phillips et al., 2006) used by the USFWS for their modeling of NSO habitat. Specifically, LMM assert that MaxEnt leads to high rates of false negative (errors of omission) and false positive (errors of commission) assignments. This criticism is surprising given the many evaluations of MaxEnt performance on both real and simulated species distribution data (e.g., Elith et al., 2006; Wisz et al., 2008; Willems and Hill, 2009; Williams et al., 2009; Elith and Graham, 2009; Graham et al., 2008; Hernandez et al., 2006) and the fact that the MaxEnt model has been cited more than 3400 times in the scientific literature. Further, it has recently been shown that MaxEnt is exactly mathematically equivalent to a likelihood-based Poisson regression model (Renner and Warton, 2013; Warton and Shepherd, 2010) bringing into question the recent criticism of MaxEnt by Royle et al. (2012). According to Merow and Silander (2014), MaxEnt is now the most widely used software for conducting presence-only species distribution modeling (SDM) and a recent survey of over 300 scientists found it is currently considered to be one of the most useful SDM methods available (Ahmed et al., 2015).

LMM contrast USFWS MaxEnt model assignments of relative habitat suitability (hereafter, RHS) as a function of habitat covariates with the MaxLike model (Royle et al., 2012) implying that it

is more robust to assignment errors. LIMM regularly imply that MaxEnt is not a maximum likelihood method, and that MaxLike is. The fact is that both MaxEnt and MaxLike are maximum likelihood methods. LIMM's comparison is surprising given recent evaluations of the MaxLike model (Phillips and Elith, 2013; Merow and Silander, 2014) and the finding that MaxEnt and MaxLike have far more similarities than differences. LIMM note that they interpreted their MaxLike predictions as relative probabilities of presence. That said, the main point of MaxLike, according to its creators, Royle et al. (2012), was to "...show that occurrence probability *can* be estimated from presence-only data."

Regarding MaxEnt's use for modeling NSO habitat, LIMM suggest that Ackers et al. (2015), who compared MaxEnt-derived maps of NSO habitat using GNN (Ohmann and Gregory, 2002) to Light Detection and Ranging (Lidar) data to a photo-interpreted habitat map, support their contention that there is "ambiguity in the data and/or our ability to accurately map owl habitat". LIMM based their conclusion on what they called "weak" agreements between the Ackers et al. (2015) maps based on LIMM's comparisons of the publication's figures. Yet, Ackers et al. (2015) reported "fair" to "substantial" agreement between these same maps using state-of-the-art map comparison software (see Table 4, Fig. 4 and Section 3.3 in Ackers et al., 2015). Furthermore, Ackers et al. (2015) concluded that both the GNN and Lidar-based SDMs produced reasonable maps and area estimates for NSO habitat and that, while the GNN-based map provided a less precise spatial representation of habitat than the Lidar-based map, it produced a habitat area estimate that was similar to both the photo-interpreted and Lidar-based maps. They concluded that GNN-based maps were appropriate for large scale analyses of amounts and general spatial patterns of habitat at regional scales, which is consistent with how the USFWS used their models.

4. Interpretation of data, tests, and evaluations

LIMM further criticize the USFWS modeling efforts because of the sample of NSO nesting and roosting locations and possible sampling biases. For example, they state: "The problem is that the sample of nest sites needs to be representative of all nest sites, yet it is a small fraction of the entire region which is then an out-of-sample application of the models." We find this criticism to be unfounded. The USFWS (2011) had available to them >3700 NSO nesting and roosting locations, of which they selected 2858 (to reduce spatial autocorrelation and increase independence locations were thinned to be >3-km distant from each other). Modeled locations were based on field surveys conducted within a 6-year window (3 years on either side of the forest vegetation data base layers), and representative of the NSO's geographic range. The USFWS analyses, and those of Davis et al. (2011), represent the largest sample to date of NSO nesting and roosting locations for modeling NSO habitat relationships. In addition, this sample represented nearly the entire gradient of habitat conditions (forest types and seral stages) used by nesting and roosting NSOs, and included location data from multiple land ownerships (private and public). One possible sampling bias in the data set is that Wilderness and other protected areas where timber harvest is restricted may have been under-sampled.

LIMM also criticized the USFWS's modeling efforts for not adequately evaluating the rate of false positives. However, the presence-only data available to the USFWS did not allow for an estimate of the rate of false positives because true absence data were not available. Further, the goals of the USFWS modeling efforts were to estimate *relative* habitat suitability, not probability of occurrence which requires additional information on the species prevalence (Phillips and Elith, 2013). RHS provides an ordinal

ranking of habitat locations in terms of the habitat covariate values at a given location. The expectation is simply that areas with higher RHS are used disproportionately more by NSOs (higher densities) than areas with lower suitability. RHS model predictions do not account for dispersal limitations, congeneric competitors (e.g., Barred Owl; *Strix varia*), or populations substantially below their environmental carrying capacity. As a consequence, some unknown rate of false positives is expected from these model projections given the state of NSO populations in the Pacific Northwest—rapidly declining populations, extensive habitat fragmentation and dispersal constraints.

5. Model calibration

To reflect geographic variation in habitat associations and space-use requirements, the USFWS (2011) partitioned the range of the NSO into 11 geographic regions. The USFWS estimated whether each modeling region's model was well calibrated. A well calibrated model is one that shows a strong positive relationship between area adjusted frequencies (AAF – *sensu* Boyce et al., 2002) and RHS. Boyce et al. (2002) recommended an evaluation of the correlation between ranks of RHS scores (partitioned into bin intervals) and AAF. USFWS converted their AAF values to Strength of Selection (SOS) which allowed for areas that were selected against to not be bound between 0 and 1, whereas areas selected for could have any value above 1.0; AAF and SOS are otherwise equivalent and their rankings are identical. The USFWS (2011) did not provide these correlations directly, but instead illustrated them graphically (see Fig. C-5, USFWS, 2011). However, the results of these analyses are available. For the cross-validated data (25% of the owl locations randomly withheld 10 times), the rank correlations between SOS and RHS bins from the withheld data were >0.968 for all eleven modeling regions (mean $r = 0.993$), and >0.99 for 9 of the 11 modeling regions. USFWS (2011) was therefore justified in concluding their models were very well-calibrated.

6. Model discrimination

USFWS measured the ability of its RHS models to discriminate among used and available sites by using area under the receiver-operating characteristic curve (AUC, Fielding and Bell, 1997). For use versus available data, AUC can be interpreted as a measure of the proportion of times a random sample of a presence location has a larger RHS value than a random sample of an available location (the true state of an available location, used or not, is unknown). USFWS (2011; p. C-30) noted that "... AUC is a measure of discrimination, but that a use-versus-availability model's ability to discriminate is a function of both the animal's habitat specificity and the abundance of the animal's habitat in the region of interest." USFWS (2011) estimated the correlation between AUC values and the amount of area with RHS values >30, >40, and >50, among all 11 regions, and found strong positive correlations of 0.984, 0.982, and 0.978 for the three RHS thresholds, respectively. USFWS (2011) concluded that geographic variation in AUC values among modeling regions had "...less to do with model discrimination ability (i.e., the quality of the model) and more to do with the quantity of suitable habitat in each modeling region."

Despite the fact that the USFWS tested for, and found no evidence of, over-fitting in their models, LIMM suggest that high AUC values from some regional USFWS models may reflect over-fitting. LIMM interpret the negative relationship between regional estimates of AUC and number of NSO locations to "... suggest[s] that spurious models may be generated for smaller samples, with performance degrading linearly with sample size." USFWS

essentially found that when modeling regions were comprised of a relatively larger percentage of mid-to high-RHS habitat (mid-RHS = ~30–50, high-RHS = ~>50) AUC values were lower than when modeling regions had much less mid-to-high RHS habitat. This is likely due to the fact that when a larger proportion of any landscape has mid-to-high RHS lands, a larger percentage of available or background locations will be occupied. Thus, AUC values are lower, not because of the model's quality, but because of the amount of good habitat in the area.

7. Limm's accuracy assessment

Using the same habitat covariates as the USFWS, Limm fit 2 alternative models to compare to the MaxEnt model results. Limm did not evaluate their models with cross-validation, independent data, or (surprisingly) their own “out of sample” data from their two study areas. In Limm's Figures 2 and 4, scattergrams showing the relationship between USFWS's MaxEnt models' predictions and Limm's MaxLike predictions for two modeling regions, it is noteworthy that the MaxLike models predict a very large fraction of the two modeling regions to occur in high RHS categories, whereas USFWS's MaxEnt models estimate a much smaller fraction with high RHS values. Are these examples of false-positives in the MaxLike model output? In the absence of information on the true distribution of NSOs, all that can be inferred from these comparisons is that the models differ.

Limm calculated model accuracy as:

$$0.5 * (\% \text{occupied sites correctly predicted} \\ + \% \text{background sites correctly predicted})$$

It is not clear how this metric could be computed since the %background sites correctly predicted is unknown (one does not know if it is occupied or not). The AUC metric, computed by USFWS, is a measure of the proportion of times a random sample of a presence location has a larger RHS value than a random sample of an available location (without drawing any inference to whether the available location is used or not). AUC is a better measure, we would argue, of a model's discrimination ability; but with presence-availability data AUC needs to be interpreted in a more nuanced manner than with presence-absence data.

Limm make additional comparisons among their models and the USFWS's MaxEnt models for all 11 modeling regions. However, Limm's own results support the fact that MaxEnt models were more accurate than their alternative models in 19 of 21 direct comparisons. The USFWS (2011, 2012b) found their RHS models had good-to-excellent discrimination, were well-calibrated, and had good generality.

8. Logic errors

Limm stated “Habitat-suitability model validation may be achieved using surrogates of fitness, such as reproductive rates and survival...” Based on this premise, Limm evaluated the correlations between owl reproductive success and estimates of RHS on two relatively small study areas. It was not one of USFWS's goals to have RHS be a determinant of reproduction and to be thusly represented in the MaxEnt habitat analysis. USFWS evaluated their models using both cross-validation and independent data. Those appropriate methods were used to evaluate whether the RHS models had good discrimination ability, were well calibrated, and whether they had good generality (all goals USFWS noted). USFWS found that their models did meet those goals. USFWS did relate RHS to survival in their spatially-explicit individual-based model (IBM) for the NSO using the HexSim modeling program (see USFWS, 2011, 2012b; Schumaker et al., 2014), but at the scale

of an owl's home range. It is important to note that USFWS explicitly did not relate RHS to reproduction other than in a binary way. In the NSO HexSim model USFWS developed, reproduction was a function of owl age and whether or not the owl was a territory owner (no breeding without a territory). Limm erected a false goal for the USFWS's MaxEnt models, then attempt to show that the false goal was not met.

Limm also claim that USFWS used a threshold RHS value of 35 as a predictor of NSO site occupancy, and proceeded to test this on their two small study areas. In fact, USFWS never stated that areas with RHS > 35 should be used as a threshold for identifying likely occupied sites. Instead, USFWS used their 30-m pixel RHS maps as input to their IBM. The IBM, in turn, aggregated the RHS data at the scale of an owl territory, which were 2000–3000 times as large as an individual raster pixel. RHS values of 35 had relevance within the IBM in its determination of which areas of the landscape qualified as suitable for territory construction. But that process integrated habitat information at large spatial scales, just as actual spotted owls do. In fact, USFWS (2011) justified their use of a minimum hexagon RHS score of 35 for territory establishment based on evaluating hexagon RHS scores at >3700 owl nest sites. This is very different than suggesting, as Limm do, that RHS values of 35 represents a threshold for identifying occupied owl sites. Differences in RHS represent differences in relative density of owl locations among various RHS classes. USFWS noted that spotted owls were known to occupy low-value RHS areas, just much less than would be expected based on the areal extent of such areas. USFWS's evaluation showing that their RHS models were all well-calibrated corroborates this.

Limm stated “Our analysis...raises further questions about using MaxEnt RHS values for local management decisions.” But USFWS (2011, 2012a, 2012b) clearly developed their modeling tools for use in large-scale (not local) decision making. USFWS (2011, 2012a, 2012b) only applied their models at very large spatial scales (modeling regions and the NSO's geographic range), but in USFWS (2011) also noted that “Specifically, the modeling framework can be applied to various spotted owl management challenges, such as to: ...Provide a framework for landscape-scale planning by both Federal and non-federal land managers...” Nowhere do they suggest the models be used for local management decisions.

In their Conclusions section Limm suggest that a problem must exist if only a portion of sites occupied by NSOs are identified as high quality habitat. It is illogical to suggest, as Limm did, that a large proportion of occupied sites must be considered high quality habitat. USFWS (2011) demonstrated that NSOs showed much stronger selection for high RHS value areas than would be expected based on the extent of such areas. For a long-lived and generally site-faithful species that was listed as Threatened (in 1990) due largely to habitat loss, it is not at all surprising that some moderate or poor quality areas are occupied.

9. Conclusions

Limm conclude their article by raising concerns that the use of the USFWS model in the designation of Critical Habitat may over-protect (and thus over-regulate) large quantities of lower-quality habitat while failing to protect large quantities of high-quality habitat. In particular, they raise the concern that this may lead to increased requirements for NSO surveys on private lands, which is odd given that survey requirements are not related to Critical Habitat designation, and because private land was excluded from the final NSO Critical Habitat network (USFWS, 2012a). We have noted many ways in which Limm's analysis of the USFWS model's accuracy is misguided, but we do acknowledge that USFWS's RHS

maps, like products from any model, provide an imperfect representation of the real world (e.g., some high RHS areas likely include some locations that a real spotted owl would find unsuitable, and vice versa). Indeed, LMM note that “applying alternate statistical tools may not ameliorate these difficulties.” Having misinterpreted the detailed evaluations of calibration and discrimination as described above, LMM go on to suggest that more testing of the USFWS model is needed. They do not, however, offer any insight on how the results of that testing could be used to create a more “focused and effective” Critical Habitat network.

Decision makers, including those at regulatory agencies, do not have the luxury of waiting indefinitely for perfect information. They must use the best information that is available at the time the decision is made. USFWS (2012b) noted, “We consistently base our evaluations on the best scientific information available, while acknowledging that this information is clearly incomplete.” Decision makers must also attempt to understand the limitations and biases of the information they use, and the uncertainties with model projections, to best incorporate this understanding into the decision-making process. Aside from their misguided accuracy tests, LMM do not offer any suggestion as to how the USFWS could have created a better habitat model or used it in a more appropriate way. In fact, in developing its latest recovery plan and designating Critical Habitat for the NSO, the USFWS had access to, and made exhaustive use of a data archive that rivals that available for any species of conservation concern, worldwide. USFWS made extensive use of the peer-reviewed literature and knowledge and expertise of many scientists, including many of the best known and widely-published authors involved in the study of NSO ecology and management. Constructive criticism is essential to both the scientific and regulatory processes, and there are many issues to be resolved regarding the accurate modeling and effective conservation of habitat for declining species. LMM, unfortunately, failed to provide meaningful alternatives to or improvement of USFWS's efforts to identify Critical Habitat for the NSO.

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