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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 LIMM) 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, LIMM 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 LIMM critiqued, so we are very familiar with how USFWS used those products. Below, we evaluate the major criticisms of the USFWS models made by LIMM, their interpretations of the published literature on NSO habitat relationships, and the defensibility of their modeling efforts.

We believe that LIMM'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 LIMM'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

LIMM 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 LIMM'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). LIMM 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. LIMM 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

LIMM question the performance of the MaxEnt species distribution model (Phillips et al., 2006) used by the USFWS for their modeling of NSO habitat. Specifically, LIMM 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).

LIMM 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

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