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Range-wide analysis of northern spotted owl nesting habitat relations

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ABSTRACT

Recently the US Fish and Wildlife Service, as part of a critical habitat analysis for the northern spotted owl (*Strix occidentalis caurina*), developed habitat suitability models based on thousands of owl nest sites distributed across 11 regions using the MaxEnt tool. Because these models formed the basis for critical habitat designations on millions of hectares of land, we undertook an independent evaluation of the FWS effort. We evaluated the accuracy of vegetation data used as input to develop the models, conducted out of sample analyses, correlated model output with owl reproductive success in two study areas, and developed alternate models using two different statistical methods. Vegetation data appeared accurate for only a few variables, and accuracy varied among model regions. Out of sample testing gave a high rate of classification errors and owl productivity was not correlated with MaxEnt model output in two study areas. Alternate statistical methods produced reasonable models with fewer variables. Critically, neither the models compared across regions nor the regions analyzed with different tools led to comparable use of variables. Thus biological interpretation of owl habitat selection models seemed ambiguous. In addition, for MaxEnt and one of the other tools, a highly significant trend by regression was found showing decreasing model accuracy as number of training nest sites increased. Together, these two results suggest that the generated models may be spurious to some unknown degree, perhaps because the underlying vegetation data, also derived from a model, are not sufficiently accurate to support the analysis and/or because the owls themselves affect habitat suitability by consuming their prey base. We suggest that the USFWS exercise caution in using MaxEnt models as a basis for regulatory purposes such as consultation, estimating likelihood of occupancy by owls, or evaluation of site-specific recovery actions.

1. Introduction

The northern spotted owl (NSO) (*Strix occidentalis caurina*) is a species of great conservation concern. Although large investments in protection and changes of forest management on millions of hectares have occurred since 1990, this species continues to decline (USFWS, 2011). A better understanding of the habitat needs of this species might lead to more effective conservation. A recent critical habitat analysis by the United States Fish and Wildlife Service (USFWS, 2011, hereafter FWS) includes a range-wide analysis of owl nest site data using statistical models. The potential and limitations of this analysis are evaluated in the current study and supplemented with analyses using alternate statistical tools.

Many analyses of NSO habitat have been conducted using various types of data at different scales. 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. Although numerous studies have repeatedly demonstrated the importance of vegetative structures found most often in late-seral and old-growth forests to nest-site and foraging habitat selection (e.g., Thomas et al., 1990; Blakesley, 2004; FWS, 2011), empirical attempts to link various definitions of habitat to indicators of population performance and distribution of northern spotted owls have met with limited and varying success. These attempts generally used circles, often of varying radius, as proxies for core areas or annual home ranges, and coarse-scale definitions of habitat as proxies for prey availability, habitat structure and composition based on radio-tracking studies indicating strong association with old-growth forest (e.g., Forsman et al., 1984). In addition, various covariates such as fragmentation indices, linear habitat edge, weather, or elevation

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have been employed. Circle sizes in these studies varied from 28 ha (McComb et al., 2002) to 158 ha (Franklin et al., 2000), 200 ha (Irwin et al., 2004), 400 ha (Bart and Forsman, 1992), and 3632 ha (Meyer et al., 1998). The amount of variance in owl productivity accounted for by coarse-scaled habitat covariates has ranged from less than 2% (Olson et al., 2004), to 11% (Irwin et al., 2004) to 38% (Franklin et al., 2000). In Franklin et al. (2000) and Olson et al. (2004), owl productivity (unexpectedly) declined with increases in mid- and late-seral forest and increased with the amount of edge between early seral and nonforest class and other classes combined. The amount of variance in apparent survival accounted for by the habitat covariates in studies where survival could be estimated has ranged from 14% (Olson et al., 2004) to 44% (Dugger et al., 2005), to 54% (Franklin et al., 2000). Forsman et al. (2011) found that suitable habitat (as estimated from a presence-only model in Davis and Lint, 2005) was correlated with juvenile recruitment rate at the study-area level for 5 owl populations in Oregon, although the relationship was negative for the Klamath area in Oregon. Dugger and Davis (2011) therefore concluded that statistical relations between population performance indicators for northern spotted owls and (coarse-scale) measures of suitable habitat were weak. For similar reasons, Gosselin (2009) asserted that the "habitat issue" for northern spotted owls remains unresolved. Other investigators have noted that coarse-scale habitat measures of habitat have not accounted for much variation in population performance measures of bird species in general (Cushman et al., 2008), possibly because such proxy-on-proxy metrics are at least two steps removed from reality (Noon et al., 2009).

The FWS (USFWS, 2011) effort has the potential to resolve the difficulties noted above by including a larger suite of covariates, including certain habitat-structural details and abiotic features believed to influence owl demography, such as climatic factors (Glenn et al., 2010). Complete and consistent map coverage of habitat data was achieved by FWS across most of the US range of the owl. In addition, the database of owl nest site occurrences is the largest ever assembled. The revised recovery plan for the NSO (USFWS, 2011) utilizes a full geographic coverage of abiotic (topographic and climatic variables) and vegetation data across the range of the owl. Vegetation layers were imputed to the entire range of the owl using a gradient nearest neighbor (GNN) technique based on linking standardized USDA Forest Service Forest Inventory and Analysis (FIA) data with satellite imagery (Ohmann and Gregory, 2002). Imputed vegetation data such as basal area and trees per acre were combined into multiple indices of nesting/roosting (nr) and foraging (f) habitat using literature review and expert opinion. These were combined at each 30 m pixel as the sum of values over the surrounding 200 ha. These nr and f variables were not necessarily exactly the same for each region. In addition, climate and topographic variables were included, giving about 31 descriptors for each pixel (see Appendix A).

The FWS applied the MaxEnt algorithm (Phillips and Dudik, 2008; Phillips et al., 2006; Phillips and Elith, 2013) for the 11 ecological regions to model NSO distributions based upon GNN data from 1996 (1994 in California) and owl nest site data from this same period to avoid barred owl effects, climatic information, and a digital elevation model. A companion model known as Land Trendr (Kennedy et al., 2007, 2010) was used to estimate changes in vegetation conditions that occurred between 1996 and 2006 (2007 in California). The MaxEnt tool was used to develop a habitat model by first including the best nr and f variables and then adding other variables. Eleven physiographic provinces were defined (see Appendix A) and models developed for each. MaxEnt output (relative habitat suitability or RHS) was used to define habitat quality. Various tests of model quality were performed (discussed below).

The FWS accepted GNN data as sufficiently accurate for modeling purposes based upon GNN variables that were moderately correlated with ground-truthed data from FIA plots (Pearson correlation coefficients >0.7), variables that were weakly correlated (Pearson correlation coefficients 0.3–0.5), and still others that had Kappa coefficients as low as 0.2–0.3, but were included in modeling because they were considered likely to influence distributions of spotted owls (USFWS, 2011:C-17).

The Service did not assess the accuracy of GNN input data, but informally compared the distribution of GNN variables at a large sample of spotted owl nest sites and foraging locations to published estimates of those variables at the same scales. The Service also received comparisons of GNN maps to a number of local plot-based vegetation maps prepared by various field personnel. The database only includes data that can be detected with remote sensing data plus some variables imputed based on available inventory plots. Thus certain structural characteristics potentially important to owls, such as downed wood and midstory vegetation, are not in the database.

While the FWS maintains that the primary purpose of MaxEnt modeling was to make predictions rather than to obtain biological insights, the models were based first on biological indices of nesting-roosting and foraging habitat and can thus be examined for biological insights. In addition, model predictions will be used for biological interpretations of habitat. For example, the FWS noted (USFWS, 2011:C-32) that the models can be used for predicting the likelihood of owl occupancy, for consultation and evaluation of the efficacy of recovery actions, and for determining the effects of northern barred owls (*Strix varia*) on spotted owl demography (USFWS, 2011:C-42). The FWS also used output of MaxEnt to parameterize a spatially explicit population simulation model, by assuming that a gradient of low, moderate and high relative habitat suitability values corresponds to a similar gradient of survival rates. These results were then used in a spatial model (Zonation) to identify patches of connected critical habitat. Thus the designation of critical habitat in this case depends on the output of MaxEnt being biologically meaningful since it is assumed that high RHS values will correspond to positive population performance.

There is a vast literature on the use of habitat models such as produced by MaxEnt for predicting geographic distributions and understanding wildlife habitat relations (e.g., Guisan and Zimmermann, 2000; Moisen and Frescino, 2002; Elith et al., 2006). While many studies support the utility of MaxEnt (Elith et al., 2006; Phillips et al., 2006; Phillips and Dudik, 2008; Phillips and Elith, 2013), others such as Torres et al. (2012) and Royle et al. (2012) have found MaxEnt may make poor predictions, may be based on unjustified assumptions (Haegeman and Etienne, 2010), and may use arbitrary parameters and data adjustments. Anderson et al. (2001) also caution that any statistical tool characterized by many variables, screening (keeping only some variables), and a stepwise regression approach can result in "good" models even based on random data (see also Freedman, 1983; Stauffer et al., 1985; Flack and Chang, 1987). This caution dates back to the late 1800s (discussed by Aldrich, 1995) and applies to all applications of this approach (e.g., the stock market, Ferson et al., 2003). 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.

In the case of the NSO, the need for predicting habitat distribution is critical because the species continues to decline in spite of attempts to conserve what was believed at the time of listing under the US Endangered Species Act in 1990 to be critical habitat and because locating this species in the field after the invasion by competing northern barred owls (*Strix varia*) is both uncertain (Wiens et al., 2014) and expensive. Furthermore, a better