

Using Ecological-Niche Modeling to Predict Barred Owl Invasions with Implications for Spotted Owl Conservation

A. TOWNSEND PETERSON* AND C. RICHARD ROBINS

Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045, U.S.A.

Abstract: The Spotted Owl (*Strix occidentalis*) is the focus of intense concern as a species threatened by the destruction and fragmentation of primary forest in the Pacific Northwest (U.S.A.). Aside from habitat concerns, an additional peril exists for the species: the larger and more aggressive Barred Owl (*S. varia*) is invading the Pacific Northwest and has the potential to overrun much of the range of the endangered species. We evaluated the dimensions of this potential invasion by using ecological niche models based on point-occurrence data. With these tools, we developed models with significant predictions for the native distributions of both Spotted and Barred owls (tested via independent occurrence data) and for the invasive range of Barred Owls. Overlap between the models for the two species suggests that most of the northern portion of the Spotted Owl's distribution (south to about lat. 38°N) is vulnerable to Barred Owl invasion. We present an example of the potential effects of species invasions on endangered species conservation.

Uso de Modelos de Nicho-Ecológico para Predecir Invasiones de *Strix varia* y Sus Implicaciones para la Conservación de *Strix occidentalis*

Resumen: El búho manchado (*Strix occidentalis*) es de gran interés como especie amenazada por la destrucción y fragmentación del bosque primario del Pacífico noroccidental (E.U.A.). Además de la preocupación por el hábitat, existe una amenaza adicional para la especie. El búho *S. varia*, más grande y agresivo, está invadiendo el Pacífico Noroccidental y podría invadir gran parte de la distribución de la especie en peligro. Evaluamos la importancia de esta posible invasión utilizando modelos de nicho ecológico basados en datos puntuales de presencia. Con estas herramientas, desarrollamos modelos que permitían hacer predicciones significativas de las distribuciones nativas de ambas especies de búho (corroboradas con datos independientes de presencia) y para el área de invasión de *Strix varia*. La superposición de modelos para las dos especies sugiere que la mayor parte de la porción norte de la distribución de búho manchado (hacia el sur hasta 38° latitud N) es vulnerable a la invasión de *Strix varia*. Este estudio representa un ejemplo del efecto potencial de invasiones de especies sobre la conservación de especies en peligro.

Introduction

The Northern Spotted Owl (*Strix occidentalis caurina*) is ecologically restricted to old-growth forests, ranging from the Pacific Northwest south to northern California (U.S.A.). Related forms include the California Spotted Owl (*S. o. occidentalis*), which ranges south in montane

areas to southern California, and the Mexican Spotted Owl (*S. o. lucida*), which ranges from the mountains of extreme southern Utah and Colorado south through the mountains of northern and central Mexico (Gutierrez et al. 1995). Given widespread habitat destruction across much of its geographic distribution and consequent population declines (Gutierrez et al. 1995), the Northern Spotted Owl was placed on the U.S. Endangered Species List in 1990 with threatened species status, which afforded it new measures of protection, including redesign of timber concessions on public lands (Forest

*email town@ukans.edu

Paper submitted May 16, 2002; revised manuscript accepted September 19, 2002.

and Rangeland Ecosystem Science Center 2002). With the species' high-profile status and abundant population and demographic data, it has also become a touchstone for many theoretical treatments in conservation biology (Murphy & Noon 1992; Lamberson et al. 1994; Andersen & Mahato 1995).

Recently, however, an additional peril for the Northern Spotted Owl has appeared. Its eastern North American congener, the Barred Owl (*Strix varia*), has been extending its range westward since the 1960s, jumping over much of the Great Plains, Rocky Mountains, and Intermontane Region to arrive in the Pacific Northwest (Sauer et al. 2001). Where Barred Owls have arrived in areas inhabited by Spotted Owls, owing to the former's more aggressive nature, the latter has generally been displaced (Root & Weckstein 1994). Hence, the Spotted Owl may be in danger in portions of its distribution accessible to Barred Owls even when habitat fragmentation is not a factor.

New high-end computational tools make it possible to predict potential species invasions via modeling of ecological niches, based on primary point-occurrence data (Peterson & Vieglais 2001). We applied these methods to the Barred Owl's invasion of the Pacific Northwest. We present ecological niche models and distributional predictions for Barred and Spotted (Northern and California subspecies) owls, allowing identification of portions of the range of the Spotted Owl that Barred Owls are able to invade. The combination of two factors—habitat fragmentation and invasive species—presents a bleak picture for Northern Spotted Owls, and our analysis suggests possible adjustments in strategies for their conservation. Our methodology, modeling potential geographic distributions of invasive species as possible competitors of native species, offers important new analytical capacities to conservation biology.

Methods

We based our ecological niche models on 1218 unique occurrence points for Barred Owls and 24 unique occurrence points for Spotted Owls from the U.S. Breeding Bird Survey (BBS) (Sauer et al. 2001). Northern and California Spotted owls were analyzed together in light of the continuity of their geographic distributions (B. R. Noon, personal communication). We used a sample of 31 Barred Owl and 9 Spotted Owl specimen records drawn from The Species Analyst, an Internet-based distributed biodiversity information network (Vieglais 2000) (Fig. 1), as an independent test of model predictivity for the native distributional area of each species. We used 35 Pacific Northwest occurrences of Barred Owls in the BBS data as a test of the predictive nature of the invasion scenarios developed for the species, based on its ecological characteristics in its native distribution.

Ecological niches were modeled with the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Noble 1992; Stockwell 1999; Stockwell & Peters 1999). In general, the procedure focuses on modeling ecological niches, the conjunction of ecological conditions within which a species is able to maintain populations without immigration (Grinnell 1917). Specifically, GARP relates ecological characteristics of known occurrence points to those of points randomly sampled from the rest of the study region, developing a series of decision rules that best summarize those factors associated with the species' presence (Peterson et al. 2002a).

Occurrence points are divided evenly into training and test data sets. GARP applies an iterative process of rule selection, evaluation, testing, and incorporation or rejection. In particular, it chooses a method from a set of possibilities (e.g., logistic regression, bioclimatic rules) applied to the training data, and a rule is developed or evolved. Predictive accuracy is then evaluated based on 1250 points resampled from the test data and 1250 points sampled randomly from the study region as a whole. Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, and crossing over. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence.

All our modeling was carried out on a desktop implementation of GARP now available for the public to download (Scachetti-Pereira 2002). This implementation offers much-improved flexibility in choice of predictive environmental and ecological geographic information system data coverage. In this case, we used 11 data layers summarizing elevation; slope; aspect (U.S. Geological Survey 2001); aspects of climate including diurnal temperature range; frost days; mean annual precipitation; solar radiation; maximum, minimum, and mean annual temperatures; vapor pressure; and wet days (annual means 1960–1990) (Intergovernmental Panel on Climate Change 2001); and aspects of land cover, including the University of Maryland's land-use and land-cover classification and tree-cover summary (National Aeronautic and Space Administration 2002) for an area consisting of most of North America (north to central Canada). All input environmental data were resolved to a 10×10 km grid, although the native resolution of the topographic data is finer (1×1 km) and that of the climatic data is coarser (30×30 km). The predictive abilities of GARP have been tested and proven under diverse circumstances (e.g., Peterson et al. 2002a, 2002b; Stockwell & Peterson 2002a, 2002b).

To optimize model performance, we developed 100 replicate models of ecological niches of each species based on random 50/50 splits of available occurrence points. Unlike previous applications, which either used

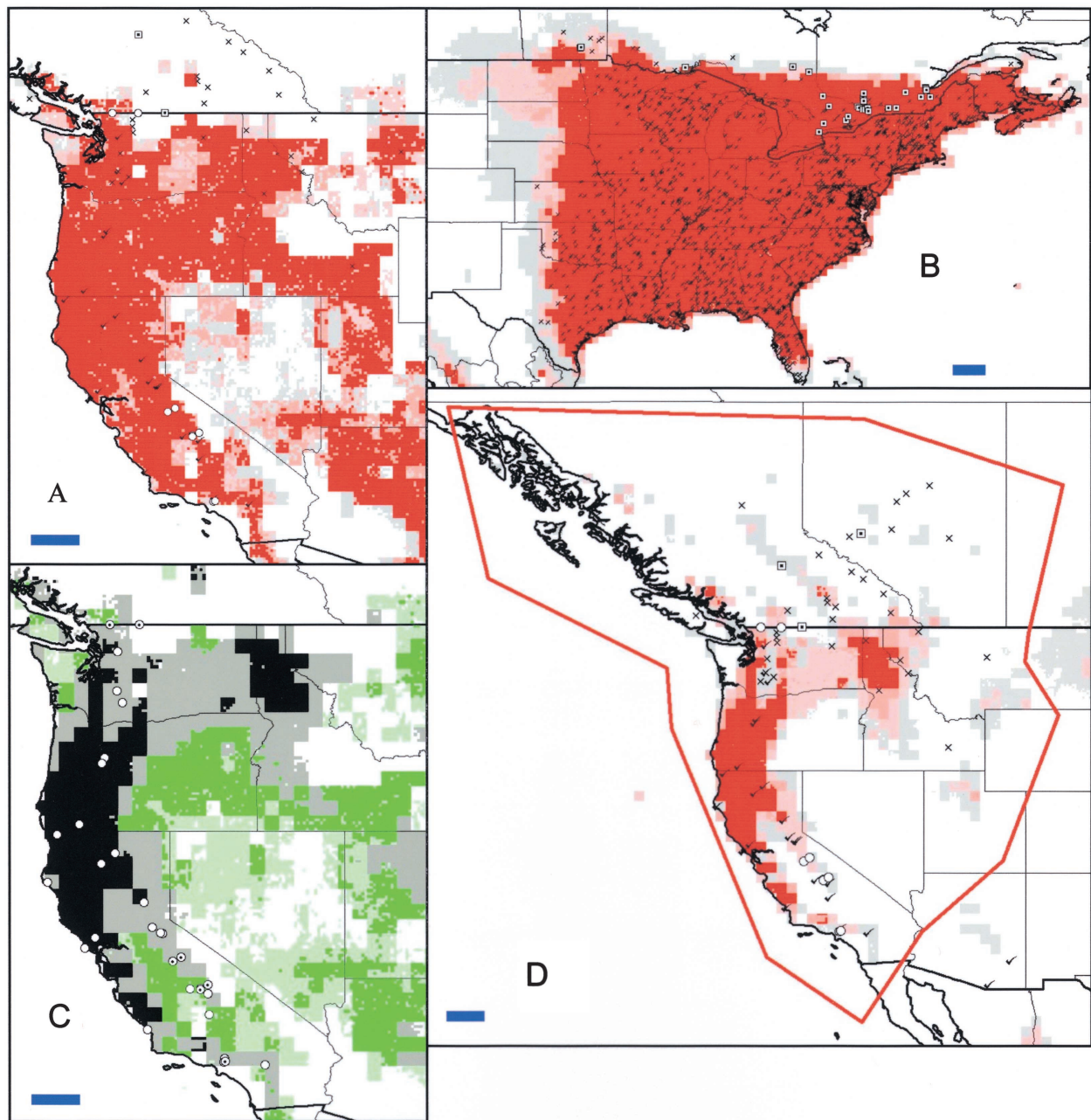


Figure 1. Results of modeling of *Strix* owls in North America: (a) Spotted Owl native distribution, (b) Barred Owl native distribution, (c) potential invasion of Barred Owls into the Pacific Northwest, and (d) test of invaded distribution for Barred Owls in the Pacific Northwest. For a, b, and d, white, no prediction; light gray, 1–5 best-subsets models agree; pink, 6–9 best-subsets models agree; and red, all 10 best-subsets models agree. For c, light green (Spotted Owls) and light gray (Barred Owls) indicate areas predicted by any of the best-subsets models, and green (Spotted Owls) and black (Barred Owls) indicate areas predicted by all of the best-subsets models. The red line in d indicates the area of analysis for the invaded range of Barred Owls. In general, U.S. Breeding Bird Survey data are plotted as checks (✓) for Spotted Owls and Xs for Barred Owls, and museum specimen localities are plotted as open circles for Spotted Owls and dotted squares for Barred Owls. The thick blue line segments denote a 200-km scale on each map panel.

single models to predict species' distributions (Peterson 2001; Peterson et al. 2002a) or summed multiple models to incorporate model-to-model variation (Peterson & Vieglais 2001), we used a new procedure (Anderson et

al. 2003) for choosing best subsets of models. The procedure is based on the observations that (1) models vary in quality, (2) variation among models involves an inverse relationship between errors of omission (leaving

out true distributional area) and commission (including areas not actually inhabited), and (3) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points and moderate area predicted (an axis related directly to commission error). The relative position of the points representing each model relative to the two error axes provides an assessment of the relative accuracy of each model. To choose best subsets of models, we (1) eliminated all models that had nonzero omission error based on independent test points, (2) calculated the average area predicted present among these zero-omission points, and (3) identified models that were within 1% of the overall average.

Projection of the rule sets for these models onto maps of North America provided distributional predictions. Model quality was tested via the independent sets of points (museum specimen records). We used a chi-square test (or Fisher's exact test when expected frequencies were too low) to compare observed success in predicting the distribution of test points with that expected under a random model (the product of proportional area and number of test occurrence points). For native-range predictions, we used areas across all of North America in which all best-subsets models coincided for testing model quality. For predictions of Barred Owl invaded range, for which relatively small areas represented full model agreement, we used areas in the Pacific Northwest predicted present by any best-subsets model.

Results

The ecological niche model predicted potential distributional areas for Barred Owls broadly across eastern North America (Fig. 1b), and in the Pacific Northwest (Fig. 1d). In all, 24 of 28 (85.7%) independent test points from museum specimen records were successfully predicted. Given 27.2% of the area of analysis predicted present, seven to eight points would have been successfully predicted at random, indicating significant predictive ability of the niche model ($\chi^2 = 48.4$, $p = 3.4 \times 10^{-12}$). In general, the distributional prediction developed from these models (Fig. 1b) reflected well the known distribution of the species. Similarly, the model for Spotted Owls (Fig. 1a) correctly predicted seven of nine independent test points, when only one to two would have been expected at random (Fisher's exact test, $p = 0.028$). Although this model was somewhat overpredicted in eastern Washington and Oregon, it nevertheless included much of the range of the species.

A formal test of the predictive nature of the ecological niche model for Barred Owls on their invaded range in the Pacific Northwest was provided by the 35 independent BBS occurrence points in the region for the species (Fig.

1d). Of these, 18 were correctly predicted, when only 6 or 7 would have been expected at chance ($\chi^2 = 23.2$, $p = 1.4 \times 10^{-6}$). Hence, the ecological niche model developed on the native range of the Barred Owl had highly significant predictive ability even on the invaded range of the species in the Pacific Northwest. Potential distributional areas of Barred and Spotted Owls coincided throughout much of the Pacific Northwest (Fig. 1c), and Barred Owls have the potential to invade as far south as 38° N latitude.

Discussion

The endangered Northern Spotted Owl and the invasive Barred Owl illustrate the interactions that occur among species when they meet under novel circumstances: Spotted Owls and Barred Owls have a mosaic distribution in southern Mexico without apparent negative interactions (Gutierrez et al. 1995; American Ornithologists' Union 1998). The new area of contact in the Pacific Northwest, however, presents a situation in which the rapidly invading Barred Owl appears capable of overrunning much of the distribution of the Northern Spotted Owl subspecies, leaving the California subspecies relatively untouched. The two species can also hybridize successfully, producing viable, fertile young (R. H. Lamberson, personal communication). The western populations (Northern and California spotted owls), and possibly even the Northern Spotted Owl itself, may be sufficiently distinct to warrant recognition as full phylogenetic species distinct from the Mexican Spotted Owl (Barrowclough & Gutierrez 1990; Barrowclough et al. 1999).

Given these results, measures of protection for the Northern Spotted Owl should be extended from simply ameliorating the effects of habitat fragmentation to combating invasive species as well. In this example, differences in local habitat use may help to some degree. Spotted Owls may occur in more continuous native forest, whereas Barred Owls appear to be focused in more secondary habitats (Gremel 2000). Nevertheless, this double challenge of preserving habitat and eradicating or controlling an invasive species will require careful attention from land managers in the region. The analytical procedures we used should prove of broad utility in conservation applications, given the ability to anticipate problems with nonnative and invasive species among native elements of biodiversity.

Acknowledgments

We thank K. Dvornich for providing useful data and information and D. H. Clayton for review of an early version of the manuscript. B. R. Noon and R. H. Lamberson provided insightful reviews of the first submitted ver-

sion of the manuscript. Information used in this paper was supplied by the U.S. Breeding Bird Survey, the Museum of Vertebrate Zoology of the University of California at Berkeley, Cornell University Museum of Zoology, and The University of Kansas Natural History Museum. This research was supported by the National Science Foundation.

Literature Cited

- American Ornithologists' Union (AOU). 1998. Check-list of North American birds. 8th edition. AOU, Washington, D.C.
- Andersen, M. C., and D. Mahato. 1995. Demographic models and reserve designs for the California Spotted Owl. *Ecological Applications* **5**:639–647.
- Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Using error distributions to select best subsets of predictive models of species' distributions. *Ecological Modelling* **162**:211–232.
- Barrowclough, G. F., and R. J. Gutierrez. 1990. Genetic variation and differentiation in the Spotted Owl (*Strix occidentalis*). *Auk* **107**:737–744.
- Barrowclough, G. F., R. J. Gutierrez, and J. G. Groth. 1999. Genetic structure of Spotted Owl populations based on mitochondrial DNA sequences. *Evolution* **53**:919–931.
- Forest and Rangeland Ecosystem Science Center (FRESC). 2002. Identification and evaluation of Northern Spotted Owl habitat in managed forests of southwest Oregon and the development of silvicultural systems for managing such habitat. U.S. Geological Survey, FRESC, Corvallis, Oregon. Available from http://xorn.wr.usgs.gov/fresc/administrative/detail.php?projectID=44&cat=App_Sci_Info (accessed August 2002).
- Gremel, S. 2000. Barred Owl displaces Northern Spotted Owl at Olympic. U.S. National Park Service, Washington, D.C. Available from http://www.aqd.nps.gov/pubs/yir/yir2000/pages/02_nps_science/02_03_gremel.html (accessed August 2002).
- Grinnell, J. 1917. Field tests of theories concerning distributional control. *The American Naturalist* **51**:115–128.
- Gutierrez, R. J., A. B. Franklin, and W. S. Lahaye. 1995. Spotted Owl, *Strix occidentalis*. *Birds of North America* **179**:1–28.
- Intergovernmental Panel on Climate Change (IPCC). 2001. Climate data archive. IPCC, Geneva, Switzerland. Available from <http://www.ipcc.ch/> (accessed August 2002).
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology* **8**:185–195.
- Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. *Ecological Applications* **2**:3–17.
- National Aeronautic and Space Administration (NASA). 2002. Land cover land use program. NASA, Washington, D.C. Available from <http://lcluc.gsfc.nasa.gov/> (accessed August 2002).
- Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. *Condor* **103**:599–605.
- Peterson, A. T., and D. A. Vieglais. 2001. Predicting species invasions using ecological niche modeling. *BioScience* **51**:363–371.
- Peterson, A. T., L. G. Ball, and K. C. Cohoon. 2002a. Predicting distributions of tropical birds. *Ibis* **144**:e27–e32.
- Peterson, A. T., D. R. B. Stockwell, and D. A. Kluza. 2002b. Distributional prediction based on ecological niche modeling of primary occurrence data. Pages 617–623 in J. M. Scott, P. J. Heglund, and M. L. Morrison, editors. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Washington, D.C.
- Root, T. L., and J. D. Weckstein. 1994. Changes in distribution patterns of select wintering North American birds from 1901 to 1989. *Studies in Avian Biology* **15**:191–201.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2001. The North American Breeding Bird Survey, results and analysis 1966–2000. Version 2001.2. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD. Available from <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html> (accessed August 2002).
- Scachetti-Pereira, R. 2002. Desktop GARP. University of Kansas Natural History Museum, Lawrence. Available from <http://www.lifemapper.org/desktopgarp/> (accessed August 2002).
- Stockwell, D. R. B. 1999. Genetic algorithms II. Pages 123–144 in A. H. Fielding, editor. *Machine learning methods for ecological applications*. Kluwer Academic Publishers, Boston.
- Stockwell, D. R. B., and I. R. Noble. 1992. Induction of sets of rules from animal distribution data: a robust and informative method of analysis. *Mathematics and Computers in Simulation* **33**:385–390.
- Stockwell, D. R. B., and D. P. Peters. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Information Systems* **13**:143–158.
- Stockwell, D. R. B., and A. T. Peterson. 2002a. Controlling bias in biodiversity data. Pages 537–546 in J. M. Scott, P. J. Heglund, and M. L. Morrison, editors. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Washington, D.C.
- Stockwell, D. R. B., and A. T. Peterson. 2002b. Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**:1–13.
- U.S. Geological Survey (USGS). 2001. HYDRO1k elevation derivative database. USGS, Washington, D.C. Available from <http://edcdaac.usgs.gov/gtopo30/hydro/> (accessed August 2002).
- Vieglais, D. A. 2000. The species analyst. University of Kansas Natural History Museum, Lawrence. Available from <http://speciesanalyst.net/> (accessed August 2002).

