From:	Renee Cormier <rcormier@pointblue.org>
Sent:	Wednesday, April 30, 2014 5:03 PM
To:	Wildlife Management
Cc:	Ellie Cohen; Diana Humple
Subject:	Nothern Spotted Owl
Attachments:	PointBlue_comments_NSO_status_review.pdf; Jennings_etal_2011.pdf; Stralberg_etal_2009.pdf; PointBlue_MMWD_MCOSD_SPOW_report_2013.pdf

Dear Neil Clipperton,

Thank you for the opportunity to provide data and information about NSO in California for their Status Review. I have attached a letter with information on our NSO monitoring project in Marin County, a report from 2013 surveys, and two manuscripts (Jennings et al. 2011, and Stralberg et al. 2009).

Please let me know if you would like additional information, or if you have any questions.

Sincerely,

Renée Cormier

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April 30, 2014

California Department of Fish and Wildlife
Nongame Wildlife Program
Attn: Neil Clipperton
1812 9th Street
Sacramento, California 95811

RE: Comments for the status review of the Northern Spotted Owl (*Strix occidentalis caurina*).

Dear Neil Clipperton,

This letter is to provide information for the status review of the NSO pursuant to the Fish and Game Code section 2074.4 to solicit data and comments on the petitioned action. I have reviewed the report titled "Evaluation of the petition from the Environmental Protection Information Center to list the Northern Spotted Owl (*Strix occidentalis caurina*) as threatened or endangered under the California Endangered Species Act" (CDFW 2013).

Point Blue Conservation Science (formerly PRBO Conservation Science) is a non-profit conservation organization with the mission to advance conservation of birds, other wildlife, and ecosystems through science, partnerships, and outreach. We have been studying the Northern Spotted Owl (NSO; *Strix occidentalis caurina*) in Marin County since 1997.

We encourage the CDFW to review our recent report and two peer-reviewed manuscripts concerning NSO in Marin County (copies included with this letter). The report is our 2013 annual report from NSO monitoring on Marin Municipal Water District and Marin County Open Space District lands (Cormier 2013). We have been monitoring NSO on these public lands, and adjacent areas with the objectives of monitoring long-term trends, and helping to ensure that disturbance to nesting owls is avoided. We have annual reports from our surveys since monitoring efforts began; please feel free to contact me if earlier reports would be useful. The first manuscript provides results from modeling spatial predictions of nest-site occurrence in Marin County (Stralberg et al. 2009) and the second describes the status and distribution of the Barred Owl (*S. varia*) in Marin County (Jennings et al. 2011).

Finally, all of our data are submitted annually to the California Natural Diversity Database managed by your agency. Please do not hesitate to contact me if you need additional information about these data.

Thank you for the opportunity to provide information for the status review.

Sincerely,

Renée Cormier
415.868.0655 ext. 316
rcormier@pointblue.org

cc: Ellie Cohen, President and CEO, Point Blue Conservation Science

Citations

California Department of Fish and Wildlife. 2013. Evaluation of the petition from the Environmental Protection Information Center to list the Northern Spotted Owl (*Strix occidentalis caurina*) as threatened or endangered under the California Endangered Species Act. Report to the Fish and Game Commission.

Cormier, R. L. 2013. Northern Spotted Owl monitoring on Marin County Open Space District and Marin Municipal Water District Lands in Marin County, CA – 2013 Report. Point Blue Conservation Science, unpublished report.

Jennings, S., R. L. Cormier, T. Gardali, D. Press, W. W. Merkle. 2011. Status and distribution of the Barred Owl in Marin County, California. Western Birds 42: 103-110.

Stralberg, D., K. E. Fehring, L. A. Pomara, N. Nur, D. B. Adams, D. Hatch, G. R. Geupel, S. Allen. 2009. Modeling nest-site occurrence for the Northern Spotted Owl at its southern range limit in central California. Landscape and Urban Planning 90: 76-85.

STATUS AND DISTRIBUTION OF THE BARRED OWL IN MARIN COUNTY, CALIFORNIA

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ABSTRACT: Marin County, California, is the southern limit of the range of the Northern Spotted Owl (*Strix occidentalis caurina*), listed as threatened by the U.S. Fish and Wildlife Service. The density of the Marin population of the Northern Spotted Owl is unusually high, the population breeds in unique habitat associations, and it is genetically isolated from other Spotted Owl populations. Unlike elsewhere in the Northern Spotted Owl's range, habitat loss to logging is not an issue in Marin County. The Barred Owl (*Strix varia*) has been detected in Marin County only since 2002 and may pose a threat to the Northern Spotted Owl through competition and/or interbreeding. We amassed information on the distribution and abundance of the Barred Owl in Marin County via published literature, by consulting local birders, and primarily through data we obtained during our monitoring of the Northern Spotted Owl in Marin County. Monitoring, continuous since 1996, provides an opportunity for an evaluation of the effect of the Barred Owl invasion on the Northern Spotted Owl there. We estimate the county's current population of the Barred Owl at four to seven individuals, including one territorial pair and a single territorial male. We documented two nestings, with four young fledged. Two pairs of the Northern Spotted Owl have been displaced from territories. These results are of concern for an otherwise stable population of the Northern Spotted Owl.

The Barred Owl (*Strix varia*) began expanding its range from eastern North America into western provinces and states in the late 1800s, arriving in the northern portion of range of the Northern Spotted Owl (*Strix occidentalis caurina*) by 1950 (Livesey 2009). The Barred Owl has subsequently expanded west and south through British Columbia, Washington, Oregon, and northern California, to occupy the Northern Spotted Owl's entire range (Gutiérrez et al. 2007).

A growing body of theoretical and empirical work predicts and documents the effects of the Barred Owl on both the Northern and California (*S. o. occidentalis*) Spotted Owls. Displacement and direct competition for food and space are thought to be the largest threats to the Northern Spotted Owl (Kelly et al. 2003, Crozier et al. 2006, Gutierrez et al. 2007). The Barred Owl also interbreeds with (Hamer et al. 1994, Haig et al. 2004, Kelly and Forsman 2004), and possibly preys upon, both the Northern and California Spotted Owls (Leskiw and Gutiérrez 1998). In much of its range the Northern Spotted Owl continues to decline despite federal protection, and the Barred Owl was identified as a major threat in the 2010 draft revised recovery plan for the Northern Spotted Owl (USFWS 2010).

Across most of its range, the Northern Spotted Owl inhabits mature, relatively undisturbed coniferous forests with a closed canopy (Gutierrez et al. 1995). In contrast, where the two species are sympatric, the Barred Owl uses a wider range of habitat types including regenerated coniferous and deciduous forests, areas of lower elevation and flatter topography, and areas of human use and occupation (Hamer et al. 2007, Livesey 2007, Livesey and Flemming 2007). This broader niche may facilitate the Barred Owl outcompeting the Spotted (Livesey and Flemming 2007). Interestingly, in Marin County the Northern Spotted Owl occupies not only mature coniferous forest but second- and third-growth coniferous and broadleaf forests and areas along the urban–wildland interface (Stralberg et al. 2009). While the size of Marin County's Spotted Owl population is not known, surveys of much of the suitable habitat on public land, completed in 1999 before the Barred Owl's arrival, revealed the Spotted Owl at 83 distinct sites, with 53 of these occupied by pairs (Press et al. 2011).

We describe the Barred Owl's colonization of Marin County, estimate its population size, report known attempts at breeding, describe interactions between the Barred and Spotted Owls, and discuss the Barred Owl's invasion in the context of the unique attributes and threats to the Marin population of the Northern Spotted Owl.

METHODS

Data for this study were gained primarily through the detection of Barred Owls during monitoring of the Spotted Owl on land managed by the federal and county governments. Widespread monitoring in Marin County by the National Park Service and PRBO Conservation Science began in 1996, though some limited surveys began in 1993. Inventories (1996–1999 and 2006) and demographic monitoring (1999–present) followed standard protocols (USFWS 1992), modified to minimize the practice of calling and feeding mice to owls while increasing visual searching, in order to reduce the owls' habituation to people (Press et al. 2010). Mimicking owl calls with the human voice or playing calls with electronic devices are widely used for locating Spotted Owls, and live mice are often presented to Spotted Owls to determine the birds' nesting status or nest location (USFWS 1992).

We obtained additional data from local experts Ryan DiGaudio, Jules Evens, Keith Hansen, Steve N. G. Howell, Dave MacKenzie, W. David Shuford, and Rich Stallcup. Additionally, we searched the North Bay Birds e-mail list-serve (http://groups.yahoo.com/group/northbaybirds), eBird (www.ebird.org), *North American Birds* since 1994, and Christmas Bird Count data since 2001 for Barred Owl observations.

We evaluated the observations to determine the birds' sex, age, and numbers. We identified the birds' sex by voice whenever possible. Individuals observed visually were often distinguished as adult or subadult (1 to 2 years old) by the shape and color of the tips of the central rectrices (Moen et al. 1991, Pyle 1997). We estimated the population's upper limit by tallying the number of locations where Barred Owls were detected in a given year and adding individuals where appropriate when multiple birds were observed together. We estimated the lower limit by evaluating the geography, habitat, and distance between locations of detection to consider if observations at different locations may have represented the same individual.

We used GPS receivers to record locations of Barred Owls detected during Spotted Owl monitoring. For Barred Owls for which the observer provided no coordinates, we mapped the location in ArcView 3.2 from the observer's description of the site.

RESULTS

Barred Owls were detected on at least 107 occasions between April 2002 and August 2010, primarily in the southern and western portions of Marin County (Figure 1). Of these detections, 67 were the result of Spotted Owl monitoring, 10 were from the list-serve, 4 were from eBird, 23 were from direct communication with local birders, and 3 were our observations made outside Spotted Owl monitoring. Additional observations, for which specific dates were not recorded, were made in Muir Woods National Monument, Olema Valley, and to a lesser extent near Point Reyes Station. We did not map observations lacking dates, but because Barred Owls were observed frequently in these areas, these individuals are likely represented by the other detections on the map.

Barred Owls have been observed at Muir Woods every year since the county's first record there in 2002, and they have been observed yearly since 2004 in the southern Olema Valley. Barred Owls were detected near Point Reyes Station in 2003, 2005, and yearly from 2008 to 2010, and in Mill Valley in 2009 and 2010. They have also been detected at several other locations across the southern and western parts of the county (Figure 1), though never in consecutive years. All of these locations, except Point Reyes Station, are also occupied by Spotted Owls.

A male and female Barred Owl were detected together in 2005 in Olema Valley, without evidence of nesting. In 2006 a male and female were detected in Muir Woods, again with no evidence of nesting. In 2007, a pair and two fledglings were found together in Muir Woods, but the nest was not located. In 2008, a nest was found in Muir Woods, both parents were confirmed as Barred Owls, and two young fledged. In 2008, a subadult Barred Owl was detected in Muir Woods, and in 2009 one was found in Mill Valley, 1.2 km from Muir Woods.

We estimate that as of August 2010 there were between four and seven Barred Owls within Marin County (Figure 2), including a territorial pair at Muir Woods, a territorial male in Olema Valley, one to two individuals around Point Reyes Station, and one or two in Mill Valley, though there may be some overlap between this site and Muir Woods.

In Marin County, more individual Barred Owls have been identified as males than as females, and only one pair has been found in any year, possibly implying a male-biased population. In many sightings, however, the bird's sex was not determined (see below regarding limitations of our data), so the true sex ratio of the population is not known. Barred Owls were classed as subadult on only two occasions, and these may represent different detections of the same bird. In spite of the number of birds of unknown age, the Marin Barred Owl population appears to be composed primarily of adults.

Hybrid Barred × Spotted Owls have not been conclusively identified in Marin County. But Jules Evens and Rich Stallcup (pers. comm.) reported

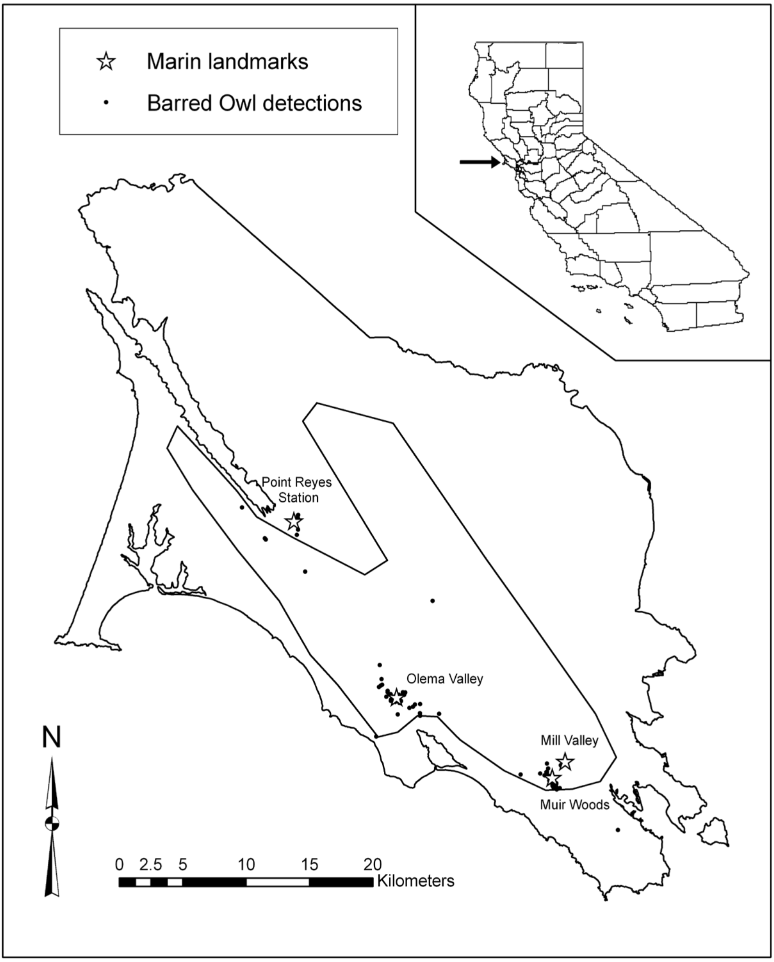

Figure 1. Locations in Marin County, California, of 89 Barred Owl observations (circles) for which specific dates and locations were recorded, 2002–2010. Stars mark the locations of landmarks referred to in the text, and the study area outline shows land covered by surveys monitoring the Northern Spotted Owl.

hearing calls intermediate between those of the Spotted and Barred near Point Reyes Station in the falls of 2005, 2006, 2007, and 2010. For example, Stallcup reported hearing a call that started with the first three notes of the Spotted Owl's standard four-note call but then proceeded into the caterwauling ending characteristic of the Barred Owl. Evens noted that he could not confidently identify the owl as Barred, but he was sure it was not a pure Spotted. Via the list-serve, Ken Burton also reported an unidentifi-

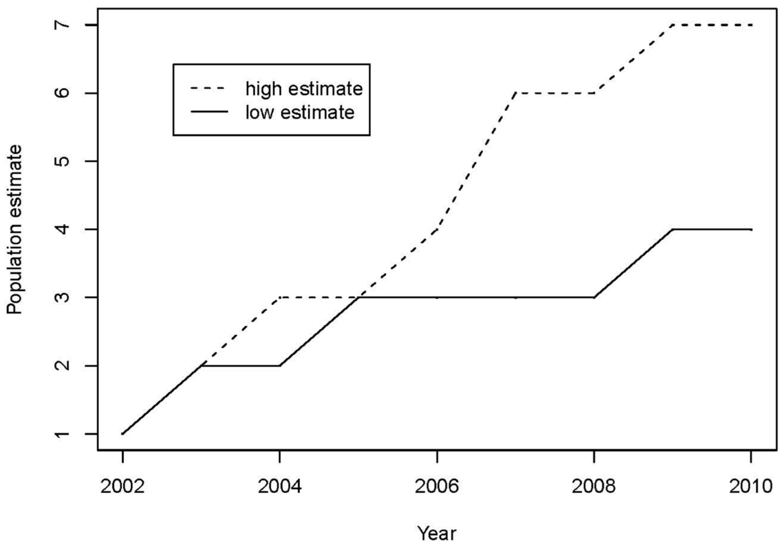

Figure 2. Estimates of the population of the Barred Owl in Marin County, California, 2002–2010. Dashed line, maximum number estimated; solid line, minimum number estimated.

able call of *Strix* in Mill Valley. In all these cases, the owl making the calls was not seen.

On multiple occasions Barred and Spotted Owls were heard calling in the same vicinity, but the extent of interaction is not known. On three daytime surveys, we and other biologists observed notable interactions between the two species: (1) both members of a pair of Spotted Owls charged and dove at a Barred Owl, (2) a Barred Owl chased a female Spotted Owl, and (3) an aerial "clash" between a Barred and a Spotted Owl.

In Muir Woods Barred Owls were observed foraging during daylight hours, hunting for crayfish (*Pacifastacus* spp.) in a stream on multiple occasions and foraging while walking on the ground.

DISCUSSION

The Barred Owl population in Marin County is currently small but well established, and it has continued to grow steadily since the species was first detected in 2002. Two home ranges have been established, one in Muir Woods and one in Olema Valley. In 2007 and 2008, Barred Owls successfully fledged two young each year from nests in Muir Woods. The 2007 Barred Owl nest is of particular interest because in that year only two of 37 monitored Spotted Owl pairs attempted nesting. Barred Owls may nest more often and produce more offspring per nesting attempt than the Northern Spotted Owl (Livesey and Fleming 2007, Wiens et al. 2009).

Hybridization between the two species in Marin County appears to be low or none; no mixed pairs have been observed, and no hybrids have been confirmed. Hamer et al. (1994) predicted hybridization to be more likely in the early stages of Barred Owl invasion, because there are few Barred Owls to make single-species pairs, but they also noted that isolating mechanisms between the two species are likely to keep hybridization to a minimum.

Our estimate of the Barred Owl's population in Marin County is conservative. The Barred Owl may not be sampled adequately by Spotted Owl monitoring (Livesey and Fleming 2007). Additionally, while most of the habitat suitable for the Spotted Owl on public land in Marin County is well covered through demographic monitoring, the Barred Owl has been detected in other habitats within the county, such as riparian. Last, little is known about the Barred Owl's occurrence on private lands. Uneven detectability and spatial distribution by sex or age class may have influenced our estimates of population size. However, given the extent and effort of Spotted Owl monitoring and of general bird watching in Marin County, we feel confident that the majority of Barred Owls present have been detected.

The presence and increasing abundance of Barred Owls at the southern limit of the Northern Spotted Owl's range in Marin County is troubling. The Marin County population of the Northern Spotted Owl may be an especially important one because it is geographically and genetically isolated from both the Northern Spotted Owl farther north in northern California and from the California Spotted Owl in the Sierra Nevada and in southern California (Barrowclough et al. 2005). Additionally, in Marin the population density of breeding Northern Spotted Owls is higher than elsewhere, the population's fecundity is consistently high, and the population uses a wider variety of habitats than does the Northern Spotted Owl in other areas (Anthony et al. 2006, Stralberg et al. 2009). Finally, the traditional threat of habitat loss and degradation due to logging is nonexistent in Marin County, and the existing pressures there (e.g., recreation, noise disturbance, urban encroachment, rodenticide use, increased risk of human-caused wildfire) have not been severe enough to cause population declines. The Marin population appears to be stable (Stralberg et al. 2009, Jensen et al. 2010).

Our early observations suggest that the Barred Owl may be affecting the Northern Spotted Owl in Marin County in ways similar to those reported elsewhere, including displacement and potential suppression of the Spotted Owl's response to mimicked calls (Kelly et al. 2003). In Muir Woods a single pair of Barred Owls now occupies the core area where two pairs of the Spotted held territories prior to the arrival of the Barred. Both pairs of the Spotted appear to have relocated to nearby areas. Additionally, the Spotted Owls have become more difficult to detect in Muir Woods and Olema Valley since the Barred Owl's arrival. In Marin, Barred Owls have been observed exploiting a diet (including crayfish) more diverse than the Spotted's, and the nesting in 2007 suggests higher fecundity. Both of these factors are thought to facilitate the Barred Owl outcompeting the Spotted (Livesey and Flemming 2007). Currently, Barred Owls occupy a small number of Spotted Owl territories and to date appear to affect individuals rather than the entire Marin population of the Spotted Owl.

The effect of the Barred Owl on the Northern Spotted Owl in Marin County is cause for concern. We recommend continued monitoring of the Spotted Owl throughout Marin County, the addition of surveys designed to improve detection of the Barred Owl, and that citizen scientists report Barred Owls sightings vigilantly.

ACKNOWLEDGMENTS

We thank the biologists who have studied the Spotted Owl in Marin County, especially Katie Fehring, Dawn Adams, Heather Jensen, and Mia Monroe. We also thank the Marin Municipal Water District, the Marin County Open Space District, Canon USA, Inc., Expedition into the Parks, the National Park Service, the National Park Foundation, Golden Gate National Parks Conservancy, Point Reyes National Seashore Association, and the David and Vicki Cox Foundation for funding Spotted Owl research. Ryan DiGaudio, Jules Evens, Keith Hanson, Steve N.G. Howell, Rick Johnson, Dave MacKenzie, W. David Shuford, Rich Stallcup, Francis Taroc, and Jim White contributed data. We thank the contributors to, moderators of, and editors of the North Bay Birds list serve, eBird, and *North American Birds* for maintaining records of Barred Owls observed outside of Spotted Owl monitoring.

Dave MacKenzie, Libby Porzig, and Dave Quady provided helpful comments on earlier drafts of the manuscript. This is PRBO contribution number 1811.

LITERATURE CITED

Anthony, R. G., Forsman, E. D., Franklin, A. B., Anderson, D. A., Burnham, K. P., White, G. C., Schwartz, C. J., Nichols, J. D., Hines, J. E., Olson, G. S., Achers, S. H., Andrews, L. S., Biswell, B. L., Carlson, P. C., Diller, L. V., Dugger, K. M., Fehring, K. E., Fleming, T. L., Gerhardt, R. P., Gremel, S. A., Gutiérrez, R. J., Happe, P. J., Herter, D. R., Higley, J. M., Horn, R. B., Irwin, L. L., Loschl, P. J., Reid, J. A., and Sovern, S. G. 2006. Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildlife Monogr. 163.

Barrowclough, G. F., Groth, J. G., Mertz, L. A., and Gutiérrez, R. J. 2005. Genetic structure, introgression, and a narrow hybrid zone between Northern and California Spotted Owls (*Strix occidentalis*). Molec. Ecol. 14:1109–1120.

Crozier, M. L., Seamans, M. E., Gutiérrez, R. J., Loschl, P. J., Horn, R. B., Sovern, S. G., and Forsman, E. D. 2006. Does the presence of Barred Owls suppress the calling behavior of Spotted Owls? Condor 108:760–769.

Gutiérrez, R. J., Franklin, A. B., and LaHaye, W. S. 1995. Spotted Owl (*Strix occidentalis*), in The Birds of North America (A. Poole and F. Gill, eds.), no. 179. Acad. Nat. Sci., Philadelphia.

Gutiérrez, R. J., Cody, M., Courtney, S., and Franklin, A. B. 2007. The invasion of Barred Owls and its potential effect on the Spotted Owl: a conservation conundrum. Biol. Invasions 9:181–196.

Hamer, T. E., Forsman, E. D., Fuchs, A. D. and Walters, M. L. 1994. Hybridization between Barred and Spotted Owls. Auk 111:487–492.

Hamer, T. E., Hays, D. L., Senger, C. M., and Forsman, E. D. 2001. Diets of Northern Barred Owls and Northern Spotted Owls in an area of sympatry. J. Raptor Res. 35:221–227.

Haig, S. M., Mullins T. D., Forsman, E. D., Trail, P.W., and Wennerberg, L. 2004. Genetic identification of Spotted Owls, Barred Owls, and their hybrids: Legal implications of hybrid identity. Cons. Biol. 18:1347–1357.

Kelly, E. G., Forsman, E. D., and Anthony, R. G. 2003. Are Barred Owls displacing Spotted Owls? Condor 105:45–53.

Jensen, H. J., Merkle, W. W., and Press, D. 2010. Monitoring Northern Spotted Owls on federal lands in Marin County, California: 2008 annual report. Natural Resources Technical Report NPS/SFAN/NRTR—2010/312. National Park Service, Fort Collins, CO (download from http://science.nature.nps.gov/im/units/sfan/vital_signs/Spotted_Owl/birds.cfm).

Kelly, E. G., and Forsman, E. D. 2004. Recent records of hybridization between Barred Owls (*Strix varia*) and Northern Spotted Owls (*S. occidentalis caurina*). Auk 121:806–810.

Leskiw, T., and Gutiérrez, R. J. 1998. Possible predation of a Spotted Owl by a Barred Owl. W. Birds 29:225-226.

Livesey, K. B., and Fleming, T. L. 2007. Effects of Barred Owls on Spotted Owls: The need for more than incidental detections and correlational analysis. J. Raptor Res. 41:319–325.

Livesey, K. B. 2009. Range expansion of Barred Owls, part I: Chronology and distribution. Am. Midland Nat. 161:49–56.

Moen, T. A., Franklin, A. B., and Gutiérrez, R. J. 1991. Age determination of subadult Northern Spotted Owls in northwest California. Wildlife Soc. Bull. 19:489–493.

Press, D., Adams, D., Jensen, H., Fehring, K., Merkle, W., Koenen, M., and Starcevich, L. A. 2010. San Francisco Bay area network Northern Spotted Owl monitoring protocol, version 6.4. Natural Resource Report NPS/SFAN/NRR—2010/245. National Park Service, Fort Collins, CO.

Press, D., Merkle, W. W., and Jensen, H. J. 2011. Monitoring Northern Spotted Owls on federal lands in Marin County, California: 2009 annual report. Natural Resources Technical Report NPS/SFAN/NRTR—2011/423. National Park Service, Fort Collins, CO.

Pyle, P. 1997. Identification Guide to North American Birds, part 1. Slate Creek Press, Bolinas, CA.

Stralberg, D., Fehring, K. E., Pomara, L. Y., Nur, N., Adams, D. B., Hatch, D., Geupel, G. R., and Allen, S. 2009. Modeling nest-site occurrence for the Northern Spotted Owl at its southern range limit in central California. Landscape and Urban Planning 90:76–85.

USFWS. 1992. Protocol for surveying proposed management activities that may impact Northern Spotted Owls. 7 March 1991, revised 17 March 1992; www.fws.gov/oregonfwo/species/data/northernspottedowl/Documents/1992Mar17NSOSurveyProtocol.pdf

USFWS. 2010. Draft revised recovery plan for the Northern Spotted Owl, *Strix occidentalis caurina*. U.S. Fish and Wildlife Service, Portland, OR (download from www.fws.gov/species/nso).

Wiens, J. D., Graham, S. A., Anthony, R.G., Forsman, E. D., and Fuller, M. R. 2009. Competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls in western Oregon: 2009 progress report. U.S. Geological Survey, Reston, VA (order from www.usgs.gov/pubprod).

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Northern Spotted Owl Monitoring on Marin County Open Space District and Marin Municipal Water District Lands in Marin County, CA

2013 Report

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December 16, 2013

Sensitive location information. Please do not distribute without landowner permission.

INTRODUCTION

The Northern Spotted Owl (NSO; *Strix occidentalis caurina*) is a year-round resident found primarily in older, coniferous forests from southern British Columbia to Marin County, California. The NSO was listed by the U.S. Fish and Wildlife Service (USFWS) as a Federally Threatened subspecies in 1990, with declines mostly attributed to habitat loss. After more than two decades on the Endangered Species list, the NSO is still declining in many parts of its range (Forsman et al. 2011, USFWS 2011). While current and past habitat loss remains a major threat, the range expansion of the Barred Owl (*Strix varia*) also poses a very considerable and complex threat to the NSO (Gutiérrez et al. 2007, USFWS 2011, Wiens 2012). NSO in Marin County are not impacted by commercial tree harvesting operations as in other parts of their range, but they face other unique threats including urban development, human disturbance due to construction and/or recreational activities, noise disturbance, pesticide poisoning, risk of wildfires along the urban-wildland interface, and genetic isolation (Stralberg et al. 2009). Additionally, while the invasion of Barred Owls in Marin County has not yet reached the high densities as in other parts of the NSO range (Jennings et al. 2011), a continued increase in Barred Owl numbers could pose a serious threat to the NSO population in Marin (e.g., Forsman et al. 2011, Wiens 2012).

Since 1997, biologists from Point Blue Conservation Science (formerly PRBO; hereafter Point Blue) have been monitoring NSO in Marin County. Marin County Open Space District (MCOSD) and Marin Municipal Water District (MMWD) have contracted Point Blue to survey NSO since 1999. Surveys are primarily on MMWD and MCOSD lands, but also include sites on private, municipal, state, and national park lands that are adjacent to MMWD and MCOSD lands. The purpose of these surveys is to monitor the population over time (trends and reproductive success). In addition, at other sites where proposed management activities may occur, biologists from Point Blue have been conducting NSO surveys to determine occupancy and nesting status so that disturbance to nesting birds is avoided.

In 2013, Point Blue biologists continued to monitor occupancy, nesting, and reproductive status for known historic NSO activity centers on or adjacent to MMWD and MCOSD lands. We also conducted inventory surveys at new locations based on management plans. In this report, we present a summary of results for 30 historic sites and 8 inventory areas.

METHODS

Surveys in 2013 followed the recently-updated USFWS protocol (USFWS 2012). The updated protocol reflects the best available information for detecting NSO in the presence of Barred Owls, and doubles the number of surveys needed before a site can be classified as unoccupied by NSO. We also used the USFWS protocol (2012) for nesting and reproductive surveys, but whenever possible we attempted to gather nesting and reproductive information without the use of mice, per the modified protocol for surveying NSO in Marin County (Press et al. 2010). The modified protocol attempts to minimize “mousing” owls to avoid habituating NSO to being fed by humans since the owls are often in close proximity to humans and heavily-used trails and roads in Marin County. For sites with planned management activities (e.g., noise disturbance), we conducted mousing surveys if nesting status could not be determined without the use of mice by early April. All 2013 surveys were led by Renée Cormier and Suzanne Winquist of Point Blue from March to July.

We surveyed a total of 30 historic sites on or adjacent to MCOSD and MMWD land. Most sites were chosen based on knowledge of NSO occurrence in previous years, and sites were prioritized where management activities were planned. In addition, we surveyed 8 inventory areas based on management needs (Table 1). We assessed occupancy, nesting, and reproductive status at all historic and inventory sites. We completed site search forms and maps for all fieldwork, status forms for each site, and vegetation measurements for nest trees. All data, including GIS, will be submitted to MCOSD, MMWD, and to the California Department of Fish and Wildlife’s California Natural Diversity Database (CNDDB).

A site is considered unoccupied after 2 years of surveys with 6 nighttime visits each year with no owl response (USFWS 2012). For sites surveyed for disturbance projects only (as opposed to planned habitat modification), 6 visits with no response in one year is sufficient to call a site unoccupied until the start of the next breeding season (USFWS 2012). In this report, I classify any site with no response in 2013 as unoccupied, but specify whether it was unoccupied for one or two years.

For sites where owls are detected, determination of residency status followed USFWS protocols and is summarized as follows (for more details see USFWS 2012): Pair = male and female heard within 0.25 miles on the same survey, and/or nesting is confirmed; Resident Single = response by a single owl on three or more occasions, with no response by an owl of the opposite sex; Unknown = male and/or female detected, but did not meet the above criteria. The Marin protocol (Press et al. 2010) has an additional status designation, Single Unknown, used when a single owl is detected but does not meet the above status categories (excluding Unknown status).

Fecundity is defined here as the total number of female young per territorial female. Fecundity was calculated by dividing the total number of young produced by 2 (assuming a 1:1 sex ratio of young), and then dividing by the total number of territorial females (paired females and resident single females). This method is commonly used with NSO data and can be compared across studies (e.g., Anthony et al. 2006, Forsman et al. 2011). We excluded survey results from 1999 in the fecundity estimate, since very few sites were surveyed that year.

RESULTS

Occupancy at inventory sites. NSO were detected at most of inventory areas (Table 1), but owls were usually not detected on more than one or two visits, therefore not meeting “resident” status. The exception was a Lakeview Fire Road, where a single male was detected on 3 surveys, thus meeting “resident single” status. Two inventory sites were designated as unoccupied.

Occupancy at historic sites. Of 30 historic sites, 27 (90%) were occupied by pairs (Table 2). West Peters Dam was the only unoccupied historic site. This is the first time since 1997, when West Peters Dam was first surveyed, that the site was not occupied by a pair of NSO. Whites Hill was occupied by a resident single male this year, and a single male of unknown resident status was detected at Soulajule Reservoir. This is the first time Whites Hill has not been occupied by a pair since initial surveys in 2003. Soulajule was unoccupied in 2010, but otherwise has been occupied by a pair since it was first surveyed in 1999.

Nesting and reproduction. Of the 27 sites with pairs, 10 (37%) pairs nested, 15 (56%) pairs were confirmed as non-nesting, and 2 (7%) sites were of unknown nesting status (Table 2). Of 10 nesting pairs, 8 (80%) were successful (fledged at least 1 young) but fecundity was below the study average for the second year in a row (Figure 1).

Overall. No Barred Owls were detected during 2013 surveys. No color-banded individuals were detected; however, we did not see the legs of the female at Arroyo Corte Madera and from 2004 to 2012, there was a banded female at this site.

Table 1: Inventory surveys conducted in 2013.

Inventory Route	Description	Sites within Inventory Route	SPOW Status
Jewell Trail	GGNRA[1]/NPS[2] land; culvert replacement (MMWD) & road paving project (by the DPW[3])	Jewell Trail	**Single Unknown**: male detected on two surveys
Lagoon Fire Road	MMWD – planned trail decommission	Arturo Trail, Hidden Lake	**Arturo Trail (Single Unknown)**: male detected on 1st of 6 visits - no other detections; **Hidden Lake (Unknown)**: male and NSO of unknown sex on 3rd of 6 visits - no other detections
Lakeview Road	MMWD – planned fire break	Lakeview Road	**Resident Single**: male detected on 3 of 7 night surveys
Loma Alta	MCOSD - inventory, no management planned	Loma Alta	**Unknown**: NSO of unknown sex detected on 6th of 8 night surveys
Lower Summit	MCOSD - annual roadside mowing by Mill Valley Fire Dept	Lower Summit	**Unoccupied (year 1; 2013 only)**: 6 night surveys with no NSO detected
Madera Park Tank	MMWD - tank work	Madera Park Tank	**Single Unknown**: male detected on 2 of 8 night visits
Sir Francis Drake	SPTSP[4] - between Pioneer Tree Trail and West Peters Dam; management site for Dept of Public Works only, but in area of interest to MMWD.	Sir Francis Drake	**Unknown**: male and female detected on one survey, single NSO of unknown sex detected on another - no other detections
Upper Laurel Dell	MMWD - brushing project along Laurel Dell from Ridgecrest to Cataract Trail	Upper Laurel Dell	**Unoccupied (year 1; 2013 only)**: 6 night surveys with no NSO detected

[1] GGNRA = Golden Gate National Recreation Area; [2] NPS = National Park Service; [3] DPW = Department of Public Works; [4] SPTSP = Samuel P. Taylor State Park.

Table 2. Status of historic Northern Spotted Owl sites on or adjacent to MCOSD and MMWD land in 2013.

Site Name	2013 Status	Landowner
Arroyo Corte Madera	Pair	MCOSD/Private
Baltimore Canyon	Fledged 1	MCOSD
Bates Canyon	Non-nesting	MCOSD
Bike Path	Non-nesting	NPS[1]
Blake Canyon	Failed Nest	MMWD
Camino Alto	Fledged 1	MCOSD
Cascade Park	Non-nesting	Municipal
East Peters Dam	Non-nesting	MMWD
Fairfax	Fledged 1	Private
Five Corners	Non-nesting	MMWD
Forest Knolls	Non-nesting	MCOSD
Indian Tree	Non-nesting	MCOSD
Indian Valley	Fledged 2	MCOSD
Iron Spring	Non-nesting	MCOSD
King Mountain	Fledged 1	MCOSD
Lagunitas	Failed Nest	MCOSD
Larkspur	Non-nesting	MCOSD
Phoenix Lake	Fledged 1	MMWD
Pioneer Tree Trail	Non-nesting	SPTSP[2]
Ross	Fledged 1	Municipal
Roy's Redwoods	Non-nesting	MCOSD
San Anselmo Creek	Pair	Private
Shaver Grade	Non-nesting	MMWD
Soulajule Reservoir	Single Unknown	MMWD
Swimming Hole	Non-nesting	SPTSP[2]
Upper Kent Lake	Fledged 2	MMWD
Warner Canyon	Non-nesting	MCOSD
West Peters Dam	Unoccupied (year 1; 2013 only)	SPTSP[2]
White's Hill	Single Male	MCOSD

[1] **NPS** = National Park Service; [2] **SPTSP** = Samuel P. Taylor State Park.

Failed nest = Nesting pair and no young fledged; **Fledged** = Successful nesting pair (fledged ≥1 young); **Non-nesting** = Pair confirmed, but non-nesting based on mousing results and/or watching female roost for 60 min (Apr 1-May 1); **Pair** = Male & female confirmed but nesting status not confirmed; **Single Unknown** = A male or female was detected, but the site did not meet resident single status (to meet resident single status, an owl of the same sex must be detected on 3 occasions); **Unoccupied** = 6 night surveys (1 or 2 years – see methods) with no response.

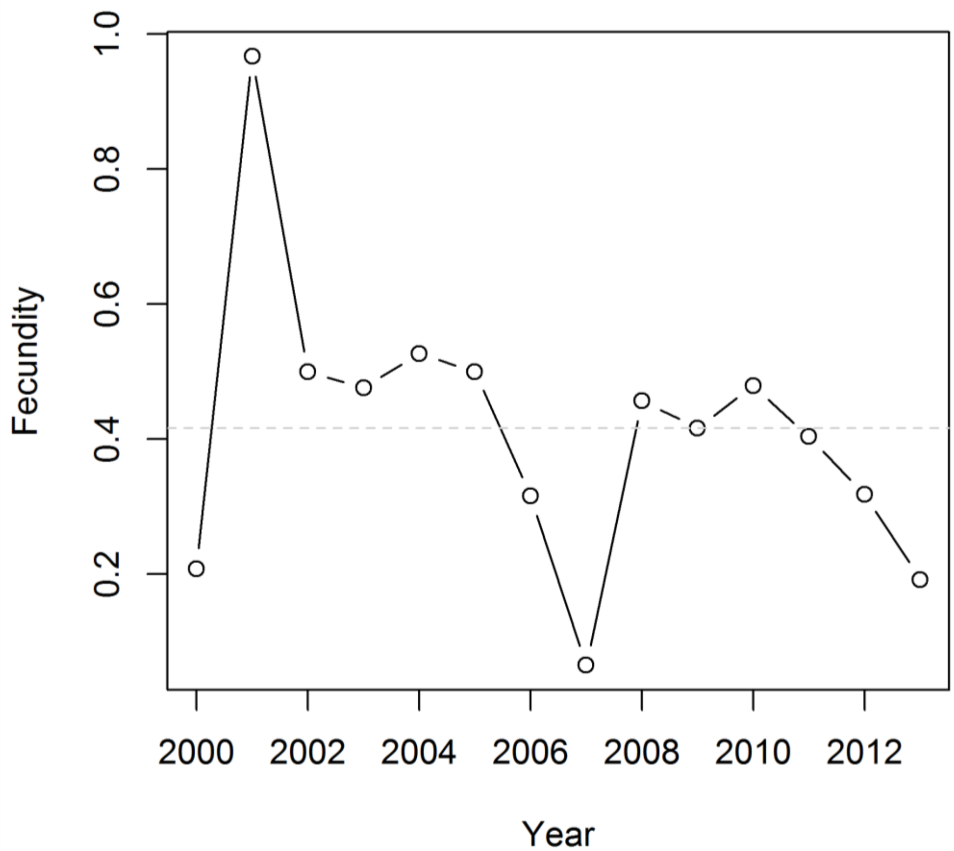

Figure 1. Fecundity (the number of female young produced per territorial female) for Northern Spotted Owls in Marin County on or adjacent to MCOSD and MMWD lands (2000-2013). Sample size varies (from n=9 to n=33) and not all sites were surveyed each year. Study average is shown as a dashed gray line.

DISCUSSION

Occupancy. Ninety percent of historically-occupied sites were confirmed occupied by a pair of NSO in 2013. West Peters Dam was unoccupied for the first time since 1997, when the site was first surveyed. Because NSO are less responsive in the presence of Barred Owls (Olsen et al. 2005, Crozier et al. 2006, Wiens et al. 2011), we also conducted Barred Owl surveys on our last three night surveys, but no Barred Owls were detected. The addition of Barred Owl surveys after the lack of response by NSO is a new optional recommendation in the USFWS (2012) protocol. Surveys should be conducted at West Peters Dam in 2014 to confirm if the site remains unoccupied, or if 2013 was an anomalous year. Whites Hill was occupied by a Resident Single male this year, which is the first time the site has not been occupied by a pair since 2003, when surveys were initiated at the site. Finally, there was a male of unknown resident status at Soulajule; there were no owls detected in the usual NSO drainage at the south end of the reservoir, but instead an owl was detected at the northeast edge of the reservoir near the MMWD ranger house over 1km from the usual drainage.

We surveyed eight inventory sites, and among them, we confirmed two sites as unoccupied (1 year only) and one as occupied by a resident single male. At each of the other five inventory sites, owls were detected on one or two surveys, but may not represent resident owls. However, the detections of NSO in new locations and at sites that are not surveyed each year highlight the importance of NSO surveys in areas with appropriate habitat where proposed management activities are planned. While some of the owls that were only detected on a small proportion of the nights may be transients, they may also prove to be established breeding sites or activity centers if we continue to detect owls at these sites.

Nesting and reproduction. Only 10 of 27 pairs nested in 2013, and of those that nested, most produced only 1 fledgling, resulting in the second lowest fecundity value since 2000. Anthony et al. (2006) determined fecundity to range from 0.306 to 0.560 depending on geographic region; they calculated fecundity on the California coast to be 0.442, similar to our study average in Marin but higher than fecundity at our sites the past two years. Forsman et al. (2011) found that fecundity has declined over time in most parts of the NSO range at long-term study sites, but because fecundity is so variable, models of demographic change were most sensitive to changes (declines) in adult survivorship. While we don’t have a marked population of owls in Marin County to estimate survival, we can estimate trends in occupancy (MacKenzie et al. 2012), and I recommend doing this analysis for the county given the declines in most other parts of the NSO range; plans are in effect for Point Blue and National Park Service staff to collaborate on such an analysis next year.

Barred Owls. No Barred Owls were detecting during NSO surveys on MMWD or MCOSD lands in 2013. The only known pair of Barred Owls in Marin County, at Camp Eastwood, nested successfully and produced two young this year (NPS, unpublished data). This pair has successfully nested in at least five of the last seven years (2007 to 2013), since the pair was first detected. NPS staff also detected one other single Barred Owl in the Olema Valley, but this was not a new Barred Owl location. An increase in Barred Owls may threaten the NSO population in Marin County through competition for space and food (Anthony et al. 2006, Gutiérrez et al. 2007, Wiens 2012). While much still remains unknown about the effects of increasing Barred Owls on NSO, recent studies have found negative associations including on occupancy of nesting territories (Kelly et al. 2003, Olsen et al. 2005 Wiens 2012), fecundity (Olsen et al. 2004, Forsman et al. 2011), and apparent survival (Anthony et al. 2006, Forsman et al. 2011). In Marin County, we are still experiencing relatively low numbers of Barred Owl detections (Jennings et al. 2011, NPS and Point Blue unpublished data), but we predict they will continue to increase based on the pattern of the invasion documented in the northern part of the NSO range. Point Blue will follow the new USFWS-recommended protocol (USFWS 2012) which should increase our ability to detect NSO, if present, and to monitor any changes in the population. Additional surveys specific to Barred Owl may be warranted to increase our detection likelihood of this species (Wiens et al. 2011).

Conclusions. NSO surveys on MMWD and MCOSD lands documented pairs at most historic sites, but with a few notably unoccupied or with single birds. Low nesting and reproductive rates have occurred in the past two years. Monitoring NSO in Marin County during the breeding season is an essential component to evaluating population health and ensuring that management activities do not negatively impact owls. Continued monitoring will help put a low year of reproductive success into context. Frequent communication and cooperation among MMWD, MCOSD and Point Blue staff have been valuable in ensuring that activities that could negatively impact nesting owls are prevented. Project support from MMWD and MCOSD continues to help avoid disturbance to NSO in Marin County.

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LITERATURE CITED

Anthony, R. G., Forsman, E. D., Franklin, A. B., Anderson, D. A., Burnham, K. P., White, G. C., Schwartz, C. J., Nichols, J. D., Hines, J. E., Olson, G. S., Achers, S. H., Andrews, L. S., Biswell, B. L., Carlson, P. C., Diller, L. V., Dugger, K. M., Fehring, K. E., Fleming, T. L., Gerhardt, R. P., Gremel, S. A., Gutiérrez, R. J., Happe, P. J., Herter, D. R., Higley, J. M., Horn, R. B., Irwin, L. L., Loschl, P. J., Reid, J. A., Sovern, S. G. 2006. Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildlife Monographs No.163.

Crozier, M.L, M.E. Seamans, R.J. Gutierrez, P.J. Loschl, R.B.Horn, S.G. Sovern, E.D. Forsman. 2006. Does the presence of Barred Owls suppress the calling behavior of Spotted Owls? Condor 108: 760-769.

Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, J. E. Hines, J. B. Lint, R. J. Davis, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, S. A. Gemel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. Schaberl, T. J. Snetsinger, S. G. Sovern. 2011. Population demography of Northern Spotted Owls: 1985-2008. Studies in Avian Biology No. 40.

Gutiérrez, R. J., M. Cody, S. Courtney, A. B. Franklin. 2007. The invasion of Barred Owls and its potential effect on the Spotted Owl: a conservation conundrum. Biological Invasions 9: 181–196.

Jennings, S., R. L. Cormier, T. Gardali, D. Press, W. W. Merkle. 2011. Status and distribution of the Barred Owl in Marin County, California. Western Birds 42: 103-110.

Kelly, E. G., E. D. Forsman, R. G. Anthony. 2003. Are Barred Owls displacing Spotted Owls? Condor 105: 45-53.

MacKenzie, D.L., M.E. Seamans, R.J. Gutiérrez, J.D. Nichols. 2012. Investigating the population dynamics of California spotted owls without marked individuals. Journal of Ornithology 152: S597-594.

Olsen, G. S., E. M. Glenn, R. G. Anthony, E. D. Forsman, J. A. Reid, P. J. Loschl, W. J. Ripple. 2004. Modeling demographic performance of Northern Spotted Owls relative to forest habitat in Oregon. Journal of Wildlife Management 68: 1039-1053.

Olsen, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, W. J. Ripple. 2005. Modeling of the site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. Journal of Wildlife Management 69: 918-932.

Press, D., D. Adams, H. Jensen, K. Fehring, W. Merkle, M. Koenen, L. A. Starcevich. 2010. San Francisco Bay Area Network Northern Spotted Owl monitoring protocol: version 6.4. Natural Resource Report NPS/SFAN/NRR—2010/245. National Park Service, Fort Collins, Colorado.

Stralberg, D., K. E. Fehring, L. A. Pomara, N. Nur, D. B. Adams, D. Hatch, G. R. Geupel, S. Allen. 2009. Modeling nest-site occurrence for the Northern Spotted Owl at its southern range limit in central California. Landscape and Urban Planning 90: 76-85.

U. S. Fish and Wildlife Service. 2011. Revised Recovery Plan for the Northern Spotted Owl (*Strix occidentalis caurina*). U. S. Fish and Wildlife Service, Portland, Oregon. xvi + 258 pp. http://www.fws.gov/oregonfwo/Species/Data/NorthernSpottedOwl/Recovery/Library/Documents/RevisedNSORecPlan2011.pdf

U. S. Fish and Wildlife Service. 2012. Protocol for surveying proposed management activities that may impact Northern Spotted Owls. 2 February 2011, revised 9 January 2012. Endorsed by the U.S. Fish and Wildlife Service. 42pp.

Wiens, J.D. 2012. Competitive interactions and resource portioning between Northern Spotted Owls and Barred Owls in Western Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, OR.

Wiens, J.D., R.G. Anthony, E.D. Forsman. 2011. Barred Owl occupancy surveys within the range of the Northern Spotted Owl. Journal of Wildlife Management 75: 531-538.

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Modeling nest-site occurrence for the Northern Spotted Owl at its southern range limit in central California

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ABSTRACT

At the southern end of its range, the Northern Spotted Owl (*Strix occidentalis caurina*) occurs in high densities and nests in a wide range of forest types and ages, exhibiting different foraging and nesting habits than in the northern part of its range. The intensive monitoring of this subspecies on public lands in Marin County, California, combined with the availability of fine-scale geographic information system (GIS) data, provided a unique opportunity to apply and evaluate a habitat-based species occurrence modeling approach at the scale most relevant to local land managers and planning agencies. We used 4 years of breeding owl survey data (1998–2001) and GIS layers representing topographic, anthropogenic, and vegetation-based landscape characteristics to build logistic regression models of owl nest-site occurrence. Models were used to develop spatial predictions of occurrence within the study area and in adjacent ecoregions, which were validated with an independent dataset. We also compared the predictive performance of two vegetation layers differing in their floristic detail and spatial accuracy. The model based on a local vegetation layer generally exhibited better model performance than the model based on the more generic regional layer. Model results indicated that forest connectivity and topographic conditions, rather than forest type or age, were the strongest predictors of nesting owl presence. Predicting outside the original study area was somewhat successful for a coastal ecoregion similar in vegetation and climate, but not better than random for a nearby inland ecoregion, suggesting that locally derived models are necessary to adequately predict nest-site occurrence.

1. Introduction

Predictive spatial models of species-habitat relationships and predicted occurrence — also known as species or habitat distribution models (Guisan and Zimmermann, 2000; Austin, 2002) and resource selection function (RSF) models (Boyce and McDonald, 1999) — can serve as useful tools to identify and prioritize habitat areas for conservation acquisition, management activities, and new field studies. At regional and continental scales, species occurrence models based on climate, topography, and landcover parameters, have been widely used for over a decade (Lindenmayer et al., 1991; Pereira and Itami, 1991; Aspinall and Veitch, 1993; Boyce and McDonald, 1999). Such models are well suited for predicting the potential distributions of a species under current environmental conditions, as well as future climate change scenarios (Peterson, 2001; Pearson and Dawson, 2003). However, species occurrence models based on regional or continental datasets may have limited utility for land managers who need more specific and fine-scaled information about a species' local distribution and relative habitat suitability (Ferrier, 2002). At the local landscape scale, models based on local survey data and variables such as vegetation cover type/structure, habitat fragmentation patterns, and topographic variation, may be more relevant. The recent availability of high-resolution aerial photography and satellite imagery, and resulting detailed vegetation geographic information system (GIS) layers, have facilitated the development of such fine-scale models of species occurrence (Ozesmi and Mitsch, 1997; Loyn et al., 2001; Gibson et al., 2004). Yet one potential drawback of locally derived models is that they may be limited by the spatial extents of the datasets upon which they are based. Floristically detailed, spatially

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accurate vegetation GIS layers may only exist for small areas, often coinciding with publicly owned lands, thereby limiting the ability to extrapolate predictions to nearby areas with poor data coverage. Furthermore, even if coarser GIS layers with larger extents are used, habitat relationships may differ from one region to the next, also limiting the potential for extrapolation (Thogmartin and Knutson, 2006; Osborne et al., 2007). This highlights the importance of assessing the reliability and generality of the models selected, as well as independently validating model predictions.

This study evaluates the utility of locally derived occurrence models for a federally listed subspecies, the Northern Spotted Owl (*Strix occidentalis caurina*, hereafter "owl"), at its southern range limit. The Northern Spotted Owl ranges from southern British Columbia to central California, with the San Francisco Bay marking the southern end of the subspecies' range (Gutiérrez, 1996). The Marin County population is small (~75 individuals) and relatively isolated from the adjacent populations to the north in Sonoma and Napa counties. While the Marin population appears stable, with the highest reported density for the species and consistently high fecundity (Anthony et al., 2006), it faces threats that are primarily associated with its proximity to the greater San Francisco Bay area, including urban development along open space boundaries, intense recreational pressure, and genetic isolation (Barrowclough et al., 2005).

Throughout its range in the Pacific Northwest, the Northern Spotted Owl has been shown to select mature and old-growth stands for nesting and roosting (Forsman et al., 1984; Carey et al., 1990; Hershey et al., 1998), generally preferring areas with less overall forest fragmentation (Lehmkuhl and Rafael, 1993; Hunter et al., 1995; Meyer et al., 1998). Farther south in northwestern California, a shift in prey from flying squirrels (*Glaucomys sabrinus*) to woodrats (*Neotoma* spp.) is thought to lead to notable differences in habitat suitability (Noon and Franklin, 2002), with greater owl use of ecotones between old-growth forest and other vegetation types (Franklin et al., 2000). At the far southern end of the range in central California, however, habitat relationships are less well known, and this area has not been included in regional habitat suitability analyses (Franklin et al., 2000) or distribution modeling (Zabel et al., 2003) for northwestern California. This isolated population is thought to be somewhat anomalous, with the highest reported densities throughout the subspecies' range (Chow, 2001), and nests that have been found in a wide range of forest types and ages (Chow, 2001).

The goal of this paper was to develop and assess the utility of locally derived occurrence (nest-site location) models for the southernmost Northern Spotted Owl population. We accomplished this via several specific objectives: (1) to generate spatial predictions of nest-site occurrence useful to land managers, local governments, and wildlife biologists; (2) to test the models' applicability outside the original study area using independent datasets from less well-studied regions; (3) to identify forest characteristics associated with owl nest-site occurrence at its southern range edge and compare our findings with those from core northern parts of its distribution; and (4) to determine whether the improved accuracy and floristic detail of locally produced GIS vegetation layers results in higher model accuracy (based on independent test data) than more generic statewide vegetation layers.

2. Methods

2.1. Study area

We conducted owl surveys in western Marin County, California, the majority of which is contained in National Park Service (hereafter "park") ownership. Much of the area's commercially viable coniferous forests were logged in the late 1800s through the 1950s (Evens, 1993) and are now re-growing on public lands, creating a mosaic of mature second-growth conifers, uncut hardwoods and a few old-growth conifer stands. Although timber harvest no longer occurs, residential development, combined with cattle grazing, has resulted in a relatively patchy forest distribution and an extensive wildland–urban interface (Radeloff et al., 2005). Within protected parklands, relatively unperturbed forest occurs within a matrix of habitat patches that includes scrub, rangeland and other non-forest habitats.

Forest types used for nesting by the owl include Douglas-fir (*Pseudotsuga menziesii*), coast redwood (*Sequoia sempervirens*), bishop pine (*Pinus muricata*), and mixed hardwood forests comprised of tanbark oak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), and California bay laurel (*Umbellularia californica*). The most common forest type, Douglas-fir, has an extensive secondary canopy of California bay laurel and other hardwoods as well as an understory of hazel (*Corylus californica*) and coffeeberry (*Rhamnus californica*).

2.2. Owl occurrence data

We systematically surveyed a nearly contiguous 171 km^2 area covering national parkland (Point Reyes National Seashore and Golden Gate National Recreation Area) and a local water district (Fig. 1) for owl occupancy in 1997 and 1998, using modified standard protocols (Forsman, 1995). Selected nest sites and activity centers (areas where we repeatedly observed consistent occupancy by owl pairs, but no nests were found during the study period) within this core study area were annually monitored from 1998 through 2001. Nest-site locations were recorded with GPS units at 15 m accuracy or greater. Owl pairs typically nested within a few hundred meters of the previous year's nest, or re-used the same nest, and we considered the resulting cluster of nest locations as a single site, randomly selecting 1 year's nest to represent each site.

To construct models for nest-site occurrence, we used 44 occupied sites and generated 88 random point locations, inside the survey area but at least 100 m from all known nest or pair locations (minimum nest distance = 178 m; mean distance to nearest nest = 1023 m). Because owl nests occurred exclusively in forest habitat, random points were also constrained to fall inside forest habitat. Random points were generated in a GIS using ArcView 3.2a (ESRI, 2000) and standard extensions. Because the area had been extensively surveyed, and most pairs were monitored over several years, randomly chosen locations were assumed to represent sites not used for nesting. Although owl pairs often nest at sites more than 100 m apart in subsequent years, we allowed this relatively close proximity for random points to maximize spatial coverage of the study area and to improve our ability to discriminate between sites with similar environmental conditions.

2.3. Nest-site metrics

For each nest and random location, we calculated a suite of point and landscape metrics from GIS layers using ArcView 3.2a (ESRI, 2000) and standard extensions. Point metrics were measured at the specific nest site or random point, while landscape metrics were calculated for circular areas around the points, using overlapping 200-, 400- and 800 m radii. To determine the radii for calculating landscape metrics, we started at 200 m and doubled the radius until we reached a value close to half of the median distance between nest sites (661 m) (see similar methods described in Franklin et al., 2000). Thus, circles of 800 m radius were assumed to be the largest possible without significant overlap between adjacent territories.

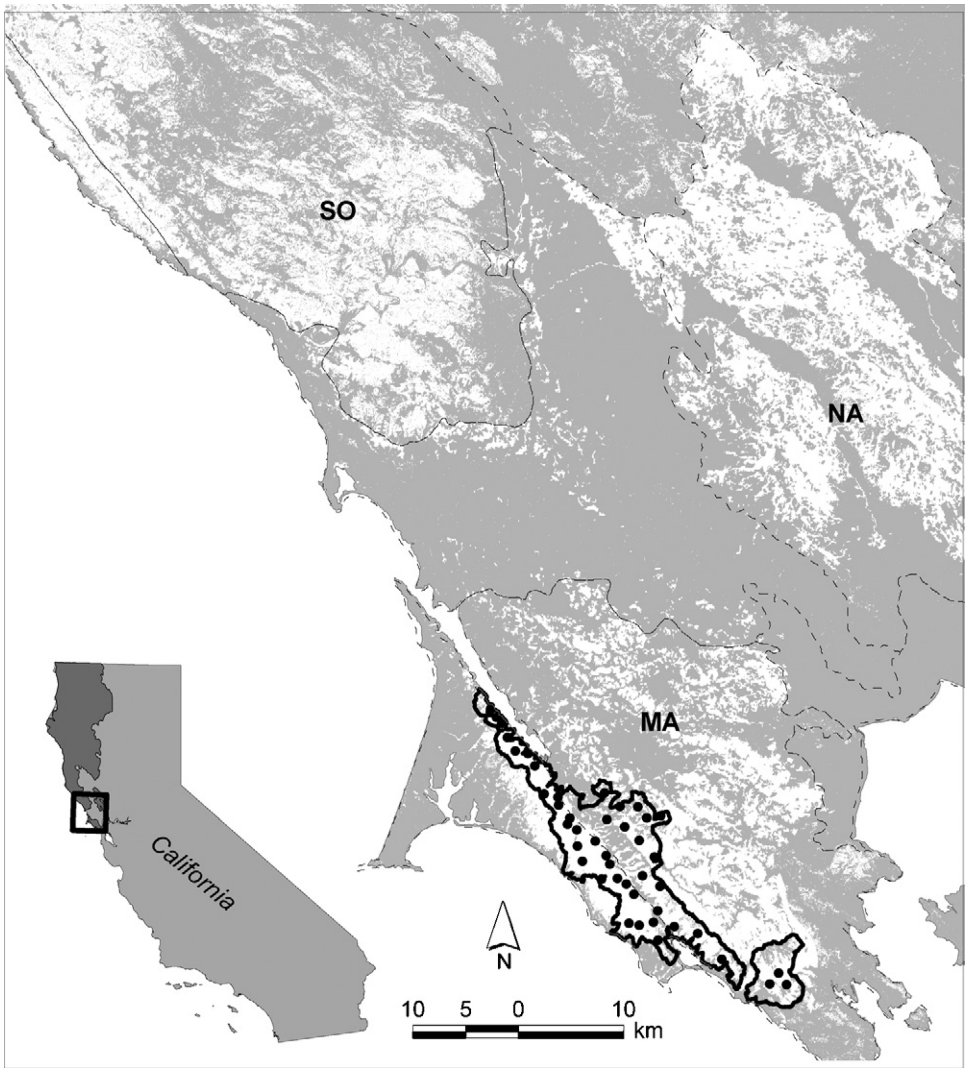

Fig. 1. Marin owl study area exhaustively surveyed in 1997 (bold outline), nest locations (circles), forest cover (white), and subregion boundaries (dashed lines). MA = Marin (263Ak, 263Al); SO = Sonoma (263Ag); NA = Napa (263Am) (Miles and Goudey, 1997). Inset map shows the species' California range.

Nevertheless, there was some overlap between the circles used to calculate landscape metrics for nests and random points: 4639 ha of a 14,543-ha total area for the 800-m radius circles.

Point metrics included south and west aspect (difference between measured aspect, and 180° and 270°, respectively), and distances to the nearest stream and road. Landscape metrics included mean slope, mean elevation, elevational position in watershed ((nest elevation—minimum elevation within a 400-m radius)/total elevation range within a 400-m radius), forest cover proportion, proportion of various vegetation cover types (conifer versus hardwood, and specific dominant tree species), forest stand size class (a proxy for age), and total forest edge (Table 1).

2.4. Vegetation data layers

For model comparison purposes, we calculated all vegetation-related variables from each of two available GIS-based vegetation layers. The first vegetation layer we used was developed by the Point Reyes National Seashore for park-managed areas. It was generated by an intensive mapping process involving the sampling of representative vegetation plots, manual delineation of polygons from 1:24,000 scale true color aerial photos (1994) at a minimum mapping unit of 0.5 ha, and extensive field verification (Schirokauer et al., 2003). Vegetation units were classified at a high botanical resolution following the Manual of California Vegetation (MCV, Sawyer and Keeler-Wolf, 1995). Classification accuracy of general cover types was greater than 80% (Schirokauer et al., 2003). This vegetation layer was combined with a similar vegetation layer for the adjacent water district lands, with vegetation classifications grouped into general cover types. The resulting layer is hereafter referred to as the "local" vegetation layer.

The second vegetation layer used was developed for California forestlands as a joint effort between the U.S. Forest Service and the California Department of Forestry and Fire Protection (1999), and tiled by ecological subregion (Miles and Goudey, 1997). This layer is hereafter referred to as the "regional" vegetation layer. This dataset was developed using an automated classification of 1994 LANDSAT 7 satellite imagery and minimum mapping unit of approximately 1 ha and had no published accuracy assessment. Vegetation types were classified according to the Classification and Assessment with LANDSAT of Visible Ecological Groupings (CALVEG) system (USFS, 1978), which has less floristic detail than MCV.

Both vegetation layers represented conditions in the same year (1994), although they preceded the collection of owl occurrence data (1997–2001). While vegetation was not generally thought to have changed much over that time period, a large area (49 km^2),

Table 1
Names and descriptions of candidate point and landscape variables (200-m, 400-m, and 800-m radius areas around point, denoted with numbers 2, 4, and 8, respectively) used to construct owl nest-site occupancy models, in order of model entry.

Category	Description (units)	Type	Name(s)
Topography	Mean elevation (m)	Landscape	Elevat2-4-8
	Position on slope (proportion)	Point	Shedpos
	Mean slope (degrees)	Landscape	Slope2-4-8
	South aspect (degrees)	Point	Aspectsouth
	West aspect (degrees)	Point	Aspectwest
	Distance to nearest stream (m)	Point	Streamdist
General vegetation	Forested proportion	Landscape	Forest2-4-8
	Conifer proportion	Landscape	Conif2-4-8
	Hardwood proportion	Landscape	Hardwds2-4p-8
Specific vegetation	Douglas-fir (*Pseudotsuga menziesii*) proportion	Landscape	Dougfir2-4-8
	Redwood (*Sequoia sempervirens*) proportion	Landscape	Redwood2-4p-8
	Bishop Pine (*Pinus muricata*) proportion	Landscape	Bishop2p-4p-8
	Coast Live Oak (*Quercus agrifolia*)/Tanbark oak (*Lithocarpus densiflorus*) proportion	Landscape	Oak2p-4p-8
	California Bay Laurel (*Umbellularia californica*) proportion	Landscape	Bay2p-4p-8
	Riparian proportion	Landscape	Riparian2-4-8
	Shrub proportion	Landscape	Shrub2-4-8
	Grass proportion	Landscape	Grass2-4-8
	Urban proportion	Landscape	Urban2-4-8
Forest stand maturity	Mean size class (1-5)	Landscape	Whrsize2-4-8
Forest fragmentation	Total forest edge length (m/ha)	Landscape	Edgelength2-4-8
	Distance to nearest road (m)	Point	Roaddist

containing two random points (but no owl nests through 2007), was burned in a stand-replacing fire in 1995 (Ornduff, 1998; Fellers et al., 2004).

2.5. Model selection

For each variable of specific interest (Table 1), we compared the means and standard deviations of nest locations (occupied sites) and random points (presumed unoccupied) for descriptive purposes. For landscape variables, we compared across the three radii examined (200, 400, and 800 m). We also evaluated the influence of each variable on nest presence/absence using logistic regression analysis (Hosmer and Lemeshow, 2001).

For 44 nests and 88 random points, we then constructed logistic regression models to predict nest-site occurrence using Stata 8.0 (StataCorp, 2003). Logistic regression has been described as inappropriate for modeling habitat selection in use-availability studies where areas of non-use are unknown (Keating and Cherry, 2004). However, the complete coverage of our surveys meant that we were able to use data from nearly an entire population (as opposed to a sample), such that non-use areas were well known. Logistic regression is thought to perform well with presence-only data collected using comprehensive survey strategies such as ours (Wintle et al., 2005).

For each vegetation layer (local and regional), we developed models using a hierarchical approach to variable selection, based on the hypothesized relative importance of each category of variables (Table 1, in order from top to bottom) using the radii for which the univariate relationships in logistic regression models were most significant. For each successive variable added to the model, we used a likelihood ratio statistic (Hosmer and Lemeshow, 2001) to evaluate whether the variable should be retained in the model ($\alpha = 0.05$). We hypothesized that physical topographic characteristics (e.g., slope position, aspect) would have the largest influence on nest-site location, followed by general forest composition (conifer/hardwood proportion), specific forest types (e.g., Douglas-fir, Coast Redwood) and surrounding non-forest vegetation types (e.g., shrub, grassland), forest stand maturity (size class), and forest fragmentation (forest edge length and distance to nearest road).

We compared Akaike's Information Criterion (AIC) (Akaike, 1974) and Receiver Operating Characteristic (ROC) plot area under the curve (AUC) values (Fielding and Bell, 1997) from each of the resulting two models to evaluate model fit and suitability. We also compared the percent of sites correctly classified as occupied or unoccupied by each model, using the probability cut-off that maximized model sensitivity (percent of actual occupied sites identified by the model) plus specificity (percent of model-predicted occupied sites that were actually occupied). A different probability cut-off was determined for each model.

2.6. Model validation

For each vegetation layer, we extrapolated resulting models (hereafter referred to as "local vegetation" and "regional vegetation" models) to the rest of the study area and, where possible, to the ecological subregions (Miles and Goudey, 1997) covering the forested portions of surrounding counties, hereafter referred to as the Marin, Sonoma, and Napa subregions (Fig. 1). We developed 30 m by 30 m model prediction surfaces using ArcGIS 8.1 (ESRI, 2001).

To evaluate our models within the Marin subregion, we used owl nest locations that were identified and monitored using the same protocols as the nest locations used to build our models. To evaluate our models within the Sonoma and Napa subregions, we used a California Department of Fish and Game database of Northern Spotted Owl occurrence records, many of which are not nest locations, but represent approximate activity centers for known pairs.

For the local vegetation models, we were limited to the area covered by the local vegetation layer. Thus, we used a small set of nests from the Marin owl database that were located within this area (Fig. 1). For each owl pair that used more than one nest site, we randomly selected one site for our validation ($N = 10$). For comparison purposes, these nests were also used to evaluate the regional vegetation models. In addition, we were able to use data from a vegetation layer similar to the local layer, but produced for Napa County, to develop predictions for the Napa subregion; the Napa layer was produced with the same mapping protocols as were used in Marin County (Thorne et al., 2004). To evaluate these model pre-

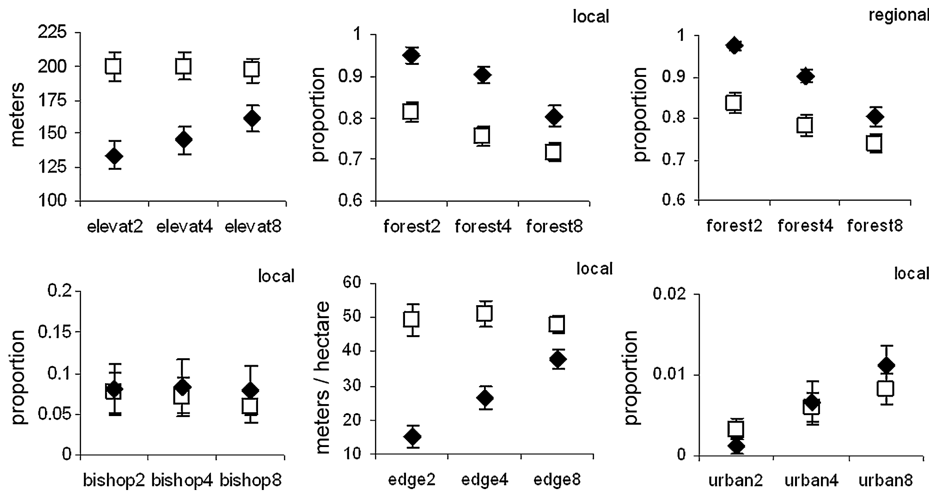

Fig. 2. Means and standard errors of landscape variables retained in final models at one or more scales (200-, 400-, or 800-m radius distances). Filled diamond = nest; open square = random. See Table 1 for variable definitions. Local = derived from local vegetation layer; regional = derived from regional vegetation layer.

dictions, we used records from the California owl database that overlapped this area ($N = 31$).

To evaluate the regional vegetation models, we used all records from the Marin owl database that fell outside the original study area within the Marin ecoregion ($N = 24$), and all records from the California owl database that fell within the Sonoma ($N = 74$) and Napa ($N = 45$) ecoregions. We evaluated the models separately for each of the three subregions in order to assess relative predictive ability.

Logistic regression model predictions consisted of a probability of owl occurrence for each forested pixel within the prediction area (subregion). For comparison of these predicted probabilities with actual owl nest sites, we chose the cut-off probabilities that maximized correct classification (model sensitivity plus specificity) for the original nest locations (Hosmer and Lemeshow, 2001). We then classified our validation points (N actual nest sites) as occupied (X) or unoccupied ($N - X$) based on those cut-off values. The proportion of actual nests classified by the model as occupied (X/N) was compared to the overall proportion of the forested area within a subregion that the model predicted as occupied (P). For each model, we calculated the exact binomial probability of observing X or more occupied sites, given that $Y = P \times N$ were expected. We considered this equivalent to testing whether or not owls used sites with high model values in higher proportions than their regional availability, and thus, whether our models provided more information about potential habitat suitability than did the distribution of forest habitat alone. However, where the model predicted fewer nest sites to be occupied than expected ($X < Y$), we calculated the exact binomial probability of observing X or fewer occupied sites.

3. Results

3.1. Nest-site habitat associations

Of the point- and landscape-level variables examined, the 200-m and 400-m radius variables generally resulted in higher differences than the 800-m radius variables (Fig. 2). Thus, for the local vegetation layer, all but one of the landscape variables (bishop pine) considered for the logistic regression models were based on 200-m or 400-m radius areas around the nest/random sites. For the regional vegetation layer, all but three landscape variables (bishop pine, California bay laurel, and shrub) were based on either 200-m or 400-m radius circles.

Resulting models indicated that owl nest sites were more likely to occur at south-facing sites that were lower in the watershed, as well as lower in mean elevation within 400 m, and with a higher proportion of woodland within 400 m (Table 2). Local vegetation models also indicated that nest sites were more likely to occur at sites with a lower proportion of bishop pine within 800 m, a lower proportion of urban development within 200 m, and less woodland edge within 200 m. Regional vegetation models did not reveal any associations with landscape-level cover of specific tree species or stand maturity/size.

3.2. Model validation

Within the original study area, local vegetation models performed better than regional vegetation models, with respect to AIC, ROC AUC, and proportion of original nest sites correctly classified (Table 3). Of the 18,960 ha of forest contained within this area, 4132 ha were predicted to provide suitable nesting habitat based on the local vegetation models (Fig. 3), while 4942 ha were predicted to be suitable based on the regional vegetation models (Fig. 4). Using independent nest locations as validation points, only the local vegetation model predicted significantly more suitable nest sites than expected by chance (Table 4).

Using the regional vegetation models, suitable nesting habitat across all three subregions was predicted to be 40,049 ha (Fig. 4). Overall, and within the Marin and Sonoma subregions, the model

Table 2
Logistic regression model coefficients and standard errors for nest-site occupancy models based on local and regional vegetation data ($N = 132$). See Table 1 for variable definitions. See Table 3 for model statistics.

Model	Variable	Coefficient	Standard error
Local vegetation	Elevat2	−0.0182	0.00486
	Shedpos	−4.69	1.75
	Aspectsouth	0.0138	0.00543
	Forest4	3.59	2.70
	Bishop8	−2.25	1.56
	Urban2	−46.5	35.1
	Edgelength2	−0.0388	0.0151
	Constant	1.28	2.62
Regional vegetation	Elevat2	−0.0111	0.00361
	Shedpos	−3.44	1.36
	Aspectsouth	0.00773	0.00447
	Forest4	7.40	1.95
	Constant	−4.65	1.68

Table 3
Logistic regression model diagnostics for nest-site occupancy models based on local and regional vegetation data ($N = 132$). The probability cut-offs were based on the values at which model sensitivity + specificity was maximized, and represent the predicted probability above which nest sites were classified as occupied (used to determine the proportion correctly classified).

Model	d.f.	Pseudo R^2	AIC	ROC AUC	Probability cut-off	Proportion correctly classified
Null	1	–	170.0	–	–	–
Local vegetation	8	0.463	98.23	0.916	0.434	0.856
Regional vegetation	5	0.317	124.8	0.865	0.355	0.796

classified the validation points with significantly greater success than would be expected by chance alone (Table 4). Within the Napa subregion, however, the model performed worse than expected by chance alone. The local vegetation model also performed worse than random within the portion of the Napa subregion for which a detailed vegetation layer was available (Table 4).

4. Discussion

4.1. Habitat associations

Other than the proportion of surrounding forest cover, topographic conditions were the strongest predictors of owl nest-site occurrence, with occupied sites lower in the watershed and more southfacing than unoccupied sites. The importance of slope position may be explained by a variety of factors, including susceptibility to heat stress, predator avoidance, prey abundance and availability, and nest structure availability (Barrows, 1981; Carey et al., 1992; Hershey et al., 1998; Folliard et al., 2000). Lower areas are, by definition, closer to surface water and therefore have lower average temperatures than adjacent uplands, possibly providing better growing conditions and larger trees for nesting. South-facing slopes may also contain larger individual trees, and tend to be more sheltered from spring and summer northwesterly winds.

In contrast with other studies, we found that, at the landscape scale, Marin owls were no more likely to be found in conifer-dominated areas than hardwood-dominated areas, and there did not seem to be a major influence of specific tree species composition on owl nest-site occurrence. Although the local vegetation model identified a negative association with the proportion of bishop pine forest within an 800-m radius, this effect may be related to the 1995 Vision fire, in which bishop pine forest was the primary vegetation type burned (Fellers et al., 2004). These results may indicate the generalist characteristics of this subspecies in this part of its range, where it utilizes a variety of forest types and nest tree characteristics. It may also be attributable to the high interspersion of conifer and hardwood types within our study area, which may

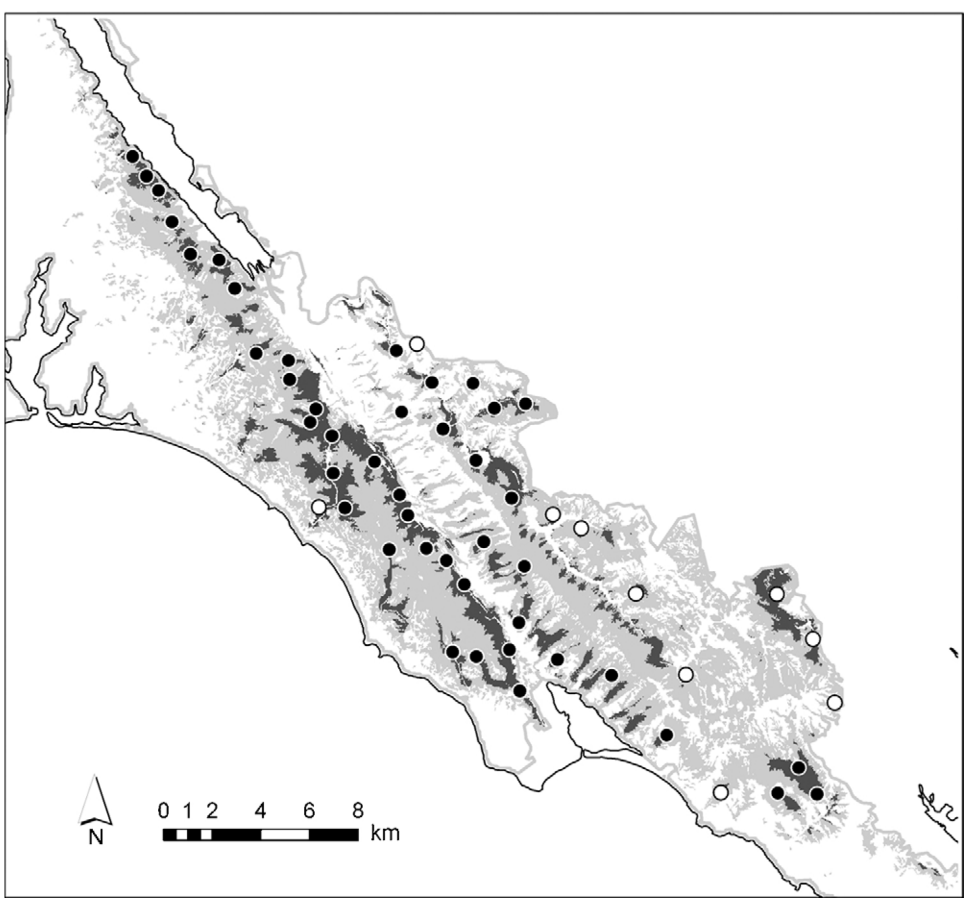

Fig. 3. Predicted probability of Spotted Owl occurrence for the area covered by the local vegetation layer (see Table 2 for model parameters). Dark gray shading represents areas of predicted occurrence based on probability cut-off values that maximized sensitivity vs. specificity in the original datasets (0.43). Light gray shading depicts current forest cover. Black circles are nest sites used for model-building; white circles are validation nest sites.

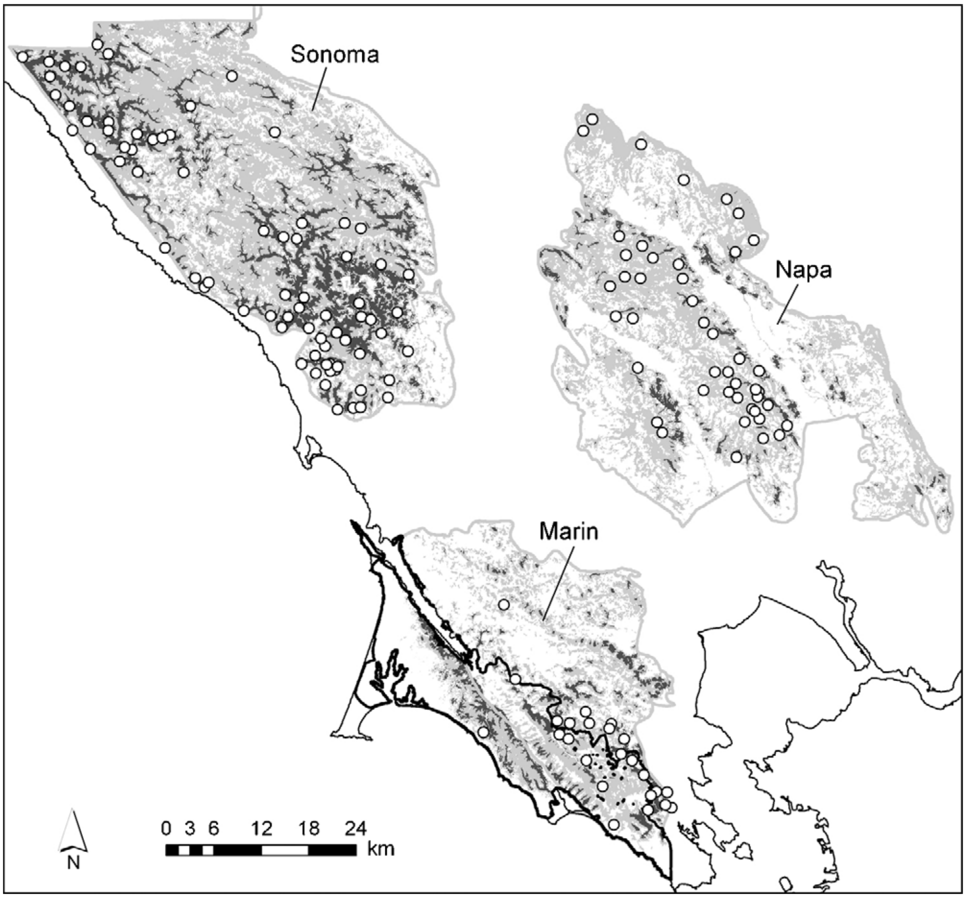

Fig. 4. Predicted probability of Spotted Owl occurrence for the Marin, Napa, and Sonoma subregions based on the regional vegetation layer (see Table 2 for model parameters). Dark gray shading represents areas of predicted occurrence based on probability cut-off values that maximized sensitivity vs. specificity in the original datasets (0.36). Light gray shading depicts current forest cover. White circles are validation nest sites. Black outline indicates the area covered by the local vegetation layer and depicted in Fig. 3.

represent an optimal mix of habitats with respect to prey density and accessibility (Ward et al., 1998). Thus, a conifer versus hardwood classification may be arbitrary in some cases, and may not adequately describe the actual habitat mosaic.

We detected no response to mean stand size, which contrasts with results from many other Northern Spotted Owl studies (Forsman and Griese, 1997; Hershey et al., 1998; Folliard et al., 2000) and may be due to the relatively young age of Marin forests,

Table 4
Classification of validation nest sites in Marin, Napa, and Sonoma subregions, according to local and regional vegetation models (Table 2). For each model, the numbers in the "expected random" column were determined by the overall proportions of the forested area that were predicted to be occupied/unoccupied[a]; the "actual nests" column represents the numbers of actual nests classified by the model as occupied/unoccupied. *P* values represent exact binomial probabilities[b].

	Regional vegetation Subregion (n)	Expected random	Actual nests	Local vegetation Subregion (n)	Expected random	Actual nests
Occupied	Marin (10)	2.97	5.0	Marin (10)	2.18	5.0
Unoccupied		7.03	5.0		7.82	5.0
P			0.146			0.046
Occupied	Marin (24)	4.43	11.0	–	–	–
Unoccupied		19.58	13.0	–	–	–
P			0.0019	–	–	–
Occupied	Napa (45)	3.6	1.0	Napa (31)	2.0	1.0
Unoccupied		41.4	44.0		29.0	30.0
P			0.115			0.388
Occupied	Sonoma (74)	18.9	32.0	–	–	–
Unoccupied		55.1	42.0	–	–	–
P			0.0007	–	–	–
Occupied	Overall (143)	27.2	44.0	–	–	–
Unoccupied		115.8	99.0	–	–	–
P			0.0005	–	–	–

[a] Areas predicted to be occupied were based on cut-off values corresponding to the model probabilities that maximized sensitivity vs. specificity in the original dataset (0.43 for local vegetation model; 0.36 for regional vegetation model).

[b] For the Marin and Sonoma subregions, *P* values represent the exact binomial probabilities of observing at least the number of occupied actual nests, given the proportion of the area that the model predicted as occupied. For the Napa subregion, *P* values represent the exact binomial probability of observing fewer than the occupied actual nests.

as well as the predominance of hardwood tree species. Mature tanbark oak, California bay laurel and coast live oak trees do not attain the same size as Douglas-fir and redwood trees, making it difficult to infer age differences in mixed conifer/hardwood habitat based on size. Apparently, all available stand size classes within the relatively narrow range of available sizes are important to the Marin Northern Spotted Owl population, making it more similar to the Mexican (*S. o. lucida*) and California (*S. o. occidentalis*) subspecies, which also use a wide variety of habitat types and ages (Seamans and Gutiérrez, 1995; Moen and Gutiérrez, 1997; Peery et al., 1999; Folliard et al., 2000).

However, Marin owls did appear to be negatively affected by habitat fragmentation (measured as the amount of woodland edge within 200–800 m) and anthropogenic impact (as represented by the proportion of urban development within the surrounding 200–800 m). The negative edge effect appeared to be due primarily to urban and grassland edges, with the latter consisting primarily of grazed, non-native annual grasslands. For the most part, urban edges within the study area were not hard edges, but represented wooded residential lots. Thus, we suspect that the fragmentation effect may be due to anthropogenic disturbance, rather than habitat non-suitability. However, Great Horned Owls (*Bubo virginianus*) are also known to forage along urban and grassland edges (Bennett and Bloom, 2005), and as an owl predator and competitor (Forsman et al., 1984), they may play a role in edge avoidance.

4.2. Scale of response

Marin owls appeared to respond more strongly to landscape conditions within a 200-m or 400-m radius, compared to an 800-m radius. This corresponds with other studies that found the larger the radius examined, the smaller the differences (Hunter et al., 1995; Meyer et al., 1998; Swindle et al., 1999; Thome et al., 1999), although the ranges of radii examined were larger than ours. Given the relatively high density of this population, as well as high landscape heterogeneity at small spatial scales, we would expect more immediate local conditions to have greater influence on nest-site occurrence. However, the overlap between nest and random point characteristics at the 800-m radius distance may also contribute to the relatively weak relationships at this scale.

4.3. Model performance

Within the study area, the local vegetation layer produced a better model than the coarser regional vegetation layer, in terms of explanatory power, model fit, and classification success (original and independent datasets). Comparing the two models, variables had similar effects, but fewer variables were present in the regional vegetation model, suggesting that this data layer was too coarse to represent habitat edges and discriminate between meaningful vegetation types at a spatial scale relevant for owls. Thus, the higher spatial accuracy and more detailed vegetation classification system of the local layer may better reflect habitat conditions for the owl at a scale meaningful for management. Several researchers have demonstrated the importance of spatial resolution (Li et al., 2006) and botanical detail of vegetation/cover layers (Lawler et al., 2004; Manton et al., 2005), as well as the scale of landscape metrics (Parody and Milne, 2004; Johnson et al., 2005) in the development and interpretation of habitat suitability models.

Nonetheless, some information is always lost in creating a vegetation classification from an aerial image. All vegetation layers rely on human-defined vegetation classifications that may not represent the conditions to which owls respond. Thus, modeling with unclassified raw imagery (spectral signatures, rather than a priori vegetation classes), especially hyperspectral (Ustin and Trabucco, 2000; Tuttle et al., 2006) or high-resolution imagery (Pasher et al., 2007), may be more useful than detailed, accurate vegetation classification for improving model predictive power (Suarez-Seoane et al., 2002). Additional factors not readily captured in remotely sensed imagery or classified vegetation layers, such as nest tree characteristics and prey availability, may also explain additional variability in site suitability.

4.4. Extrapolation to new areas

Although the local vegetation layer resulted in a better model for our study area, it appears that the regional vegetation layer was adequate for prediction purposes within the neighboring Marin and Sonoma subregions. Indeed, distributions of many bird species, especially large-bodied and/or wide-ranging species, have been shown to be well predicted by general land cover data (Seoane et al., 2004) and landscape pattern (Loyn et al., 2001).

While model extrapolation to adjacent subregions generally under-predicted owl sites, this may be due in part to the low spatial resolution of the validation dataset, which represents owl activity centers, and not necessarily specific nest sites. Given the low inter-annual variation in within-pair nest-site locations, however, we would expect these activity centers to be reasonable substitutes for actual nest locations.

The model performed much better in the coastal Sonoma subregion, which is more similar — in elevation, climate and vegetation — to Marin than the inland Napa subregion. This suggests that our model results should only be applied under similar habitat conditions, and that each subregion may require a separate model, preferably with vegetation layers similar to the local layer used here. By extension, our results are certainly not applicable in the Pacific Northwest, or even northern California, where topography, forest types and prey species differ (Forsman et al., 1984). In general, our results support the notion that regional stratification is a prudent approach to modeling species' habitat associations (Cardillo et al., 1999). Geographically weighted regression is another option that allows simultaneous fitting of geographically specific habitat relationships (Osborne et al., 2007).

Although it was not possible to develop a narrow definition of owl nesting areas in this region based on traditional criteria such as forest type or size class, we found that landscape-level characteristics such as forest connectivity and topographic conditions were important predictors of owl occurrence, and that spatial predictions based on locally derived models were useful for understanding the patterns of habitat use. Within our study area, the models fit the data reasonably well and could be used to predict nest-site locations with high certainty. In other similar coastal areas, our models had less certainty, but were well suited to provide a coarse-filter identification of potential habitat, which may then be surveyed on the ground for precise owl locations. Our model predictions have been used by local planning agencies to identify areas where owl surveys should be conducted prior to proposed developments and other projects.

5. Conclusions

The Marin Northern Spotted Owl population is somewhat anomalous, in terms of its high density and generalist vegetation associations. It is possible that the heterogeneous forest conditions along with the dense prey base (Willy, 1992) provide owls with optimal habitat conditions, explaining the localized high density and broad range of habitat types used for nesting. The definition and mapping of locally relevant habitat associations has allowed land managers, local governments, and wildlife biologists to better understand and protect owls and their habitat in Marin. In light of the negative associations that we found between habitat fragmentation, urban development, and nest-site occurrence, it will be important to maintain the continuity of forested habitats and to assess the cumulative impact of development within the home ranges of owls in Marin.

Although logistic regression models can be a useful tool in predicting bird distributions and habitat occupancy, our results also demonstrate the value of using locally derived models to develop predictive maps. Our results also highlight the caution that should be exercised when predicting outside of the range of one's original dataset. However, depending on management goals, simple, hypothesis-driven spatial models may be used successfully as coarse filter detectors of potential owl habitat, saving time and resources for land managers.

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References

Akaike, H., 1974. A new look at statistical model identification. IEEE Trans. Automat. Control 19, 716–722.
Anthony, R.G., Forsman, E.D., Franklin, A.B., Anderson, D.R., Burnham, K.P., White, G.C., Schwarz, C.J., Nichols, J.D., Hines, J.E., Olson, G.S., Ackers, S.H., Andrews, L.S., Biswell, B.L., Carlson, P.C., Diller, L.V., Dugger, K.M., Fehring, K.E., Fleming, T.L., Gerhardt, R.P., Gremel, S.A., Guti, Rrez, R.J., Happe, P.J., Herter, D.R., Higley, J.M., Horn, R.B., Irwin, L.L., Loschl, P.J., Reid, J.A., Sovern, S.G., 2006. Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildl. Monogr. 163, 1–48.
Aspinall, R., Veitch, N., 1993. Habitat mapping from satellite imagery and wildlife survey using a Bayesian modelling procedure in a GIS. Photogramm. Eng. Remote Sens. 59, 537–543.
Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol. Model. 157, 101–118.
Barrowclough, G.F., Groth, J.G., Mertz, L.A., Gutiérrez, R.J., 2005. Genetic structure, introgression, and a narrow hybrid zone between northern and California spotted owls (*Strix occidentalis*). Mol. Ecol. 14, 1109–1120.
Barrows, C.W., 1981. Roost selection by Spotted Owls: an adaptation to heat stress. Condor 83, 302–309.
Bennett, J.R., Bloom, P.H., 2005. *Bubo virginianus*) in southern California. J. Raptor Res. 39, 119–126.
Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. Trends Ecol. Evol. 14, 268–278.
Cardillo, M., Macdonald, D.W., Rushton, S.P., 1999. Predicting mammal species richness and distributions: testing the effectiveness of satellite-derived land cover data. Landscape Ecol. 14, 423–435.
Carey, A.B., Horton, S.P., Biswell, B.L., 1992. Northern Spotted Owls: influence of prey base and landscape character. Ecol. Monogr. 62, 223–250.
Carey, A.B., Reid, J.A., Horton, S.P., 1990. Spotted Owl home range and habitat use in southern Oregon coast ranges. J. Wildl. Manage. 54, 11–17.
Chow, N., 2001. Distribution and habitat associations of Northern Spotted Owls in Marin County, California. M.S. Thesis, Humboldt State University.
ESRI, 2000. ArcView 3. 2a. Environmental Systems Research Institute, Redlands, CA.
ESRI, 2001. ArcInfo 8.1. Environmental Systems Research Institute, Redlands, CA.
Evens, J.G., 1993. The Natural History of the Point Reyes Peninsula. Point Reyes National Seashore Association, Point Reyes, CA.
Fellers, G.M., Pratt, D., Griffin, J.L., 2004. Fire effects on the Point Reyes mountain beaver at Point Reyes National Seashore, California. J. Wildl. Manage. 68, 503.
Ferrier, S., 2002. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Syst. Biol. 51, 331–363.
Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
Folliard, L.B., Reese, K.P., Dillard, L.V., 2000. Landscape characteristics of Northern Spotted Owl nest sites in managed forests of northwestern California. J. Raptor Res. 34, 75–84.
Forsman, E.D., 1995. Spotted Owl monitoring protocols for demographic studies, USDA Forest Service, Corvallis Forestry Sciences Lab.
Forsman, E.D., Meslow, E.C., Wright, H.M., 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87, 1–64.
Forsman, E.D., Griese, A.R., 1997. Nests of Northern Spotted Owls on the Olympic Peninsula. Wash. Wilson Bull. 109, 28–41.
Franklin, A.B., Anderson, D.R., Gutiérrez, R.J., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecol. Monogr. 70, 539–590.
Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. J. Appl. Ecol. 41, 213–223.
Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.
Gutiérrez, R.J., 1996. Biology and distribution of the Northern Spotted Owl. In: Destefano, S., Forsman, E.D., Raphael, M.G., Gutiérrez, R.J. (Eds.), Studies in Avian Biology 17: Demography of Northern Spotted Owls: Workshop Proceedings. Fort Collins, CO, pp. 2–5.
Hershey, K.T., Meslow, E.C., Ramsey, F.L., 1998. Characteristics of forests at Spotted Owl nest sites in the Pacific northwest. J. Wildl. Manage. 62, 1398–1410.
Hosmer, D.W., Lemeshow, S., 2001. Applied logistic regression. In: Textbook and Solutions Manual, 2nd edn. John Wiley & Sons, New York.
Hunter, J.E., Gutiérrez, R.J., Franklin, A.B., 1995. Habitat configuration around Spotted Owl sites in northwestern California. Condor 97, 648–693.
Johnson, C.J., Boyce, M.S., Mulders, R., Gunn, A., Gau, R.J., Cluff, H.D., Case, R.L., 2005. Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. Landscape Ecol. 19, 869–882.
Keating, K.A., Cherry, S., 2004. Use and interpretation of logistic regression in habitat-selection studies. J. Wildl. Manage. 68, 774–789.
Lawler, J.J., O'Connor, R.J., Hunsaker, C.T., Jones, K.B., Loveland, T.R., White, D., 2004. The effects of habitat resolution on models of avian diversity and distributions: a comparison of two land-cover classifications. Landscape Ecol. 19, 517–532.
Lehmkuhl, J.F., Rafael, M.G., 1993. Habitat pattern around Northern Spotted Owl locations in the Olympic Peninsula, Washington. J. Wildl. Manage. 57, 302–315.
Li, X., Li, D., Ma, Z., Schneider, D.C., 2006. Nest site use by crested ibis: dependence of a multifactor model on spatial scale. Landscape Ecol. 21, 1207–1216.
Lindenmayer, D.B., Nix, H.A., McMahon, J.P., Hutchinson, M.F., Tanton, M.T., 1991. The conservation of Leadbeater's possum. Gymnobelideus leadbeateri (McCoy): a case study of the use of bioclimatic modelling. J. Biogeogr. 18, 371–383.
Loyn, R.H., McNabb, E.G., Volodina, L., Willig, R., 2001. Modelling landscape distributions of large forest owls as applied to managing forests in north-east Victoria, Australia. Biol. Conserv. 97, 361–376.
Manton, M.G., Angelstam, P., Mikusinski, G., 2005. Modelling habitat suitability for deciduous forest focal species—a sensitivity analysis using different satellite land cover data. Landscape Ecol. 20, 827–839.
Meyer, J.S., Irwin, L.L., Boyce, M.S., 1998. Influence of habitat abundance and fragmentation on Northern Spotted Owls in western Oregon. Wildl. Monogr. 139, 1–51.
Miles, S.R., Goudey, C.B., 1997. Ecological subregions of California. In: Book Number R5-EM-TP-005. USDA Forest Service. Pacific Southwest Region, San Francisco, CA.
Moen, C.A., Gutiérrez, R.J., 1997. California spotted owl habitat selection in the central Sierra Nevada. J. Wildl. Manage. 61, 1281–1287.
Noon, B.R., Franklin, A.B., 2002. *Strix occidentalis*): opportunities for major contributions to avian population ecology. AUK 119, 311–320.
Ornduff, R., 1998. Three years after the vision fire in Point Reyes. Fremontia 26, 26–27.
Osborne, P.E., Foody, G.M., Suarez-Seoane, S., 2007. Non-stationarity and local approaches to modelling the distributions of wildlife. Divers. Distrib. 13, 313.
Ozesmi, U., Mitsch, W.J., 1997. A spatial habitat model for the marsh-breeding red-winged blackbird (*Agelaius phoeniceus* L) in coastal Lake Erie wetlands. Ecol. Model. 101, 139–152.
Parody, J.M., Milne, B.T., 2004. Implications of rescaling rules for multi-scaled habitat models. Landscape Ecol. 19, 691–701.
Pasher, J., King, D.J., Lindsay, K., 2007. Modelling and mapping potential hooded warbler (*Wilsonia citrina*) habitat using remotely sensed imagery. Remote Sens. Environ. 107, 471–483.
Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371.
Peery, M.Z., Gutiérrez, R.J., Seamens, M.E., 1999. Habitat composition and configuration around Mexican Spotted Owl nest and roost sites in the Tularosa Mountains, New Mexico. J. Wildl. Manage. 63, 36–43.
Pereira, J.M.C., Itami, R.M., 1991. GIS-based habitat modelling using logistic multiple regression: a study of the Mt Graham Red Squirrel. Photogramm. Eng. Remote Sens. 57, 1475–1486.

Peterson, A.T., 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor 103, 599–605.
Radeloff, V.C., Hammer, R.B., Stewart, S.I., Fried, J.S., Holcomb, S.S., McKeefry, J.F., 2005. The wildland–urban interface in the United States. Ecol. Appl. 15, 799–805.
Sawyer, J.O., Keeler-Wolf, T., 1995. A Manual of California Vegetation. California Native Plant Society, Sacramento, CA.
Schirokauer, D., Keeler-Wolf, T., Meinke, T., van der Leeden, P., 2003. Plant Community Classification and Mapping Project Final Report. Point Reyes National Seashore, Point Reyes, CA. http://www.dfg.ca.gov/biogeodata/vegcamp/veg_classification_reports_maps.asp. Accessed 16 June 2008.
Seamans, M.E., Gutiérrez, R.J., 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. Condor 97, 944–952.
Seoane, J., Bustamante, J., Diaz-Delgado, R., 2004. Are existing vegetation maps adequate to predict bird distributions? Ecol. Model. 175, 137–149.
StataCorp, 2003. Intercooled Stata 8. 0 for Windows. Stata Corporation, College Station, TX.
Suarez-Seoane, S., Osborne, P.E., Alonso, J.C., 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. J. Appl. Ecol. 39, 755–771.
Swindle, K.A., Ripple, W.J., Meslow, E.C., Schafer, D., 1999. Old-forest distribution around Spotted Owl nest sites in the central Cascade Mountains, Oregon. J. Wildl. Manage. 63, 1212–1221.
Thogmartin, W.E., Knutson, M.G., 2006. Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. Landscape Ecol. 22, 61–75.
Thome, D.M., Zabel, C.J., Diller, L.V., 1999. Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. J. Wildl. Manage. 63, 44–59.
Thorne, J.H., Kennedy, J.A., Keeler-Wolf, T., Quinn, J.F., McCoy, M., Menke, J., 2004. A new vegetation map of Napa County using the manual of California vegetation classification and its comparison to other digital vegetation maps. Madroño 51, 343–363.
Tuttle, E.M., Jensen, R.R., Formica, V.A., Gonser, R.A., 2006. Using remote sensing image texture to study habitat use patterns: a case study using the polymorphic white-throated sparrow (*Zonotrichia albicollis*). Glob. Ecol. Biogeogr. 15, 349–357.
USFS, 1978. Classification and Assessment with Landsat of Visible Ecological Groupings. USDA Forest Service, Region 5 Ecology Group.
Ustin, S., Trabucco, A., 2000. Using hyperspectral data to assess forest structure. J. Forest. 98, 47–49.
Ward, J.P., Gutierrez, R.J., Noon, B.R., 1998. Habitat selection by northern spotted owls: the consequences of prey selection and distribution. Condor 100, 79–92.
Willy, A.G., 1992. The habitat associations of the Dusky-footed Woodrat in Marin County, CA. M.S. Thesis, University of California, Berkeley.
Wintle, B.A., Elith, J., Potts, J.M., 2005. Fauna habitat modelling and mapping: A review and case study in the Lower Hunter Central Coast region of NSW. Aust. Ecol. 30, 719–738.
Zabel, C.J., Dunk, J.R., Stauffer, H.B., Roberts, L.M., Mulder, B.S., Wright, A., 2003. Northern Spotted Owl habitat models for research and management application in California (USA). Ecol. Appl. 13, 1027–1040.