

Annual Progress Report (Contract#11-CS-11052007-319) to Region 5, USDA Forest Service
Colorado State University

31 March 2014

MONITORING THE POPULATION ECOLOGY OF SPOTTED OWLS
(*Strix occidentalis caurina*)
IN NORTHWESTERN CALIFORNIA: ANNUAL RESULTS, 2013

by

Alan B. Franklin¹, Peter C. Carlson², Jeremy T. Rockweit², Angela Rex², Travis Zaffarano²,
Kelsey L. Navarre², Kerstin Beerwieler², Kristina Kober² and Kenneth R. Wilson³

¹National Wildlife Research Center, Fort Collins, CO 80521

² Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523

³Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523

INTRODUCTION

The northern spotted owl (*Strix occidentalis caurina*) is closely associated with mature and old-growth Douglas-fir (*Pseudotsuga menziesii*) forests on public lands in northwestern California (Gould 1974, Gutiérrez et al. 1984, Solis and Gutiérrez 1990, Sisco 1990, Blakesley et al. 1992, Hunter et al. 1995, Franklin et al. 2000). Logging of these forests was considered to be a major factor in the decline of spotted owl populations which subsequently led to the listing of this species as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1990). Franklin et al. (2000) found that ecotones between older forest and other habitats may be additional important components of northern spotted owl habitat in northwestern California.

Basic demographic data has been useful for assessing the status and management of spotted owl populations (see Burnham et al. 1996). Our study was initiated in 1985 as a long-term monitoring study of the population dynamics of northern spotted owls with the primary objectives of:

1. Estimating life-history parameters such as reproductive output, annual survival, and longevity,
2. Assessing the effects of environmental variation (such as habitat configuration and climate) on life-history parameters,
3. Estimating rates of change in the population over time, and
4. Understanding population behavioral and regulatory mechanisms.

Information has been collected and disseminated for all these objectives. This report provides additional information on estimates and trends in life-history parameters and population rates of change for the northern spotted owl in northwestern California. In this report, we used a different approach to estimate rates of population change than in reports prior to 2002 (e.g., Franklin et al. 2001) because of problems in estimating juvenile survival using mark-recapture estimators. Since 2002, we have used a reverse-time mark-recapture estimator developed by Pradel (1996) and further refined by Nichols and Hines (2002). In addition, we also relied on a random-effects modeling approach to examine trends in both survival and rates of population change (Franklin et al. 2002). In past reports, we had used this approach only in estimating reproductive output. The results of this monitoring study meet the intent and structure of the Effectiveness Monitoring Plan of the Northwest Forest Plan for monitoring northern spotted owl populations (Lint et al. 1999).

As part of the Northern Spotted Owl Effectiveness Monitoring Program, the 2014 Northern Spotted Owl Demography Workshop was held January 5-11, 2014 at Oregon State University, Corvallis, Oregon where data from all northern spotted owl demography studies were collectively analyzed. Most of the analyses normally reported here were conducted during the workshop and, in accordance with the workshop guidelines, we are not reporting those results here; those results will be described in the forthcoming report from the workshop.

STUDY AREA

We studied spotted owls in two areas of northwestern California (Figure 1): a regional study area (RSA) and the Willow Creek Study Area (WCSA). The RSA encompasses approximately 10,000 km² (3,861 mi²) and includes portions of the Six Rivers, Klamath and Shasta-Trinity National Forests and lands administered by the U.S. Bureau of Land Management. The area actually surveyed for northern spotted owls within the RSA is approximately 1,784 km² (688 mi²). Territories in the RSA were selected based on where spotted owls were banded during previous studies (e.g., Gutiérrez et al. 1985) for the purpose of providing a wider geographic sample for estimating demographic parameters.

The Willow Creek Study Area (WCSA) is a “density” study area encompassing 292 km² (113 mi²) where the entire area is surveyed each year. The WCSA is located just south of Willow Creek, Humboldt Co., California in the central portion of the RSA. The WCSA was selected originally in 1985 for intensive study because (1) the study area was easily delineated by geographic boundaries, (2) the history of occupation by spotted owls was well known through previous surveys and research, and (3) the area was accessible by roads. The WCSA is managed primarily by the Lower Trinity Ranger District, Six Rivers National Forest with a small portion managed by the Big Bar Ranger District, Shasta-Trinity National Forest. Elevations range from 200 m (650 ft) to 1700 m (5580 ft).

Climate within the study areas is characterized by cool, wet winters and hot, dry summers. The dominant land use in the WCSA was timber production with clearcutting being the principal method of logging. However, logging declined, and then ceased, on public land within our study areas over the course of the study. The vegetation is Mixed Evergreen, Klamath Montane, Oregon Oak and Tan Oak forest types (Küchler 1977). Additional description of the climate, physiography, and vegetation of the study area was presented by Franklin et al. (1986). Six vegetative cover types occurred on the WCSA; four represented different seral stages of coniferous forest (CF) (Franklin et al. 1990, Hunter 1994). These cover types were described as follows: CF1 - nonvegetated or grass and forbs associated with seedling conifers <2.5 cm diameter at breast height (dbh); CF2 - brush associated with sapling conifers ranging from 2.5-12.6 cm dbh; CF3 - pole and medium conifers ranging from 12.7-53.2 cm dbh; CF4 - mature and old-growth conifers ≥53.3 cm dbh; HDW - hardwood trees comprising >80% of basal area; and Water. Based on analysis of 1992 LANDSAT imagery, 35.3% of the WCSA was covered by CF4, 12.8% by CF3, 14.4% by CF2, 8.9% by CF1, 28.3% by HDW and 0.3% by Water (Hunter 1994).

METHODS

We attempted to locate and identify all individual spotted owls in the WCSA and the RSA. Spotted owls were located using vocal imitations of their calls to elicit responses (Forsman 1983). Individuals were identified by initial capture, marking and subsequent recapture or resighting colored leg bands. Most of our methods were either adapted from Forsman (1983) or developed during previous research projects (Gutiérrez et al. 1984, Gutiérrez et al. 1985, Franklin et al. 1986, Franklin et al. 1990). Methods for recording data collected in the field were described in Franklin et al. (1986, 1996).

Surveys

Northern Spotted Owls. — Both day and night surveys were used to locate spotted owls. Night surveys were conducted between dusk and 0200 hours (Pacific Standard Time) and

consisted primarily of point surveys. A minimum of 10 minutes was devoted to each call station during point surveys. Day surveys were used to locate roosting owls and consisted of walk-in surveys and cruise surveys. Walk-in surveys were initiated during the day at sites where owls had been located previously. Cruise surveys were 1) conducted in habitat considered potentially occupied, or areas presumed occupied based on night surveys and 2) conducted in areas known to contain owls but where no owls were detected during the survey. The two types of surveys differed in that walk-in surveys were successful in detecting owls whereas cruise surveys were unsuccessful in detecting owls.

Once located, owls were checked for reproductive activity by feeding live mice to individuals (Forsman 1983). Breeding spotted owls take prey and fly to the nest or fledged young; non-reproductive owls either eat or cache the mice. Lack of reproductive activity was inferred if (1) an owl took ≥ 2 offered mice, and cached the last mouse taken, (2) a female did not have a well-developed brood patch during the incubation period, or (3) a combination of the above 2 criteria. We attempted to visit owls at least twice during the sampling period to determine the number of fledged young or to confirm lack of reproductive activity. Reproductive activity of each owl visited was characterized as having 0, 1, 2, or (rarely) 3 fledged young. A territory was assumed unoccupied if spotted owls were not detected after five night surveys which completely covered the territory. Occupancy of territories by single birds was assumed if an additional occupant was not found after (1) at least 1 daytime visit where mice were fed to the occupant and (2) at least 4 additional night-time surveys of the territory.

Barred Owls. — To increase our knowledge about the occurrence and potential effect of barred owls, we implemented a pilot study in 2008 to survey a portion of the WCSA using barred owl-specific surveys. These surveys were successful in increasing the detectability of barred owls (Roberts 2009). In 2009 we began barred owl-specific surveys for most of the WCSA, including 53 historic spotted owl territories and 7 matrix areas (forested areas not occupied by spotted owls). Each barred owl survey was conducted between dusk and 2400 hours (Pacific Standard Time) and was similar to spotted owl point surveys except recorded barred owl calls were broadcast and the length of each survey was increased to a minimum of 15 minutes. We attempted to conduct follow up surveys of barred owl detections to confirm occupancy and reproductive status, following similar methods as for spotted owls. This allowed us to confirm resident barred owls in most cases. In the RSA we continued to document barred owl detections in response to spotted owl surveys only.

Capture

Owls were typically captured and marked after their reproductive status had been determined. Several capture techniques were used, including a snare pole, noose pole (Forsman 1983), baited mist net, dip net and, occasionally, by hand. Handling of captured owls was usually less than 20 minutes. Locking aluminum bands provided by the U.S. Geological Survey Bird Banding Laboratory (USGS) were placed on the tarso-metatarsus of each captured spotted owl to verify the identity of individual owls during recaptures. Colored plastic leg bands with colored flexible tabs were placed on the opposing tarso-metatarsus in order to identify individuals without physical recapture (Forsman et al. 1996).

Identifying individual owls marked with only USGS leg bands in previous years required recapturing to check band numbers. Loss of USGS leg bands was assumed to be zero. The identity of owls detected at night was either inferred by the position of the owl relative to known spotted owl territories or by sight identification of color-marked individuals.

Determining Sex and Age

The sexes of adult and subadult spotted owls were distinguished by calls and general behavior. Males produce lower-pitched calls than females (Forsman et al. 1984). However, fledglings could not be accurately sexed until 1992 when we began collecting blood samples from juveniles to determine sex (Dvořák et al. 1992, Fleming et al. 1996). Blood samples taken from juveniles were analyzed by Zoogen, Inc. (Davis, California).

Spotted owls were aged by plumage characteristics (Forsman 1981, Moen et al. 1991). Four age-classes were used: juvenile (J; fledged young of the year); first-year subadults (S1; one year old); second-year subadult (S2; two years old) and adults (A; at least 3 years old). We could not differentiate age beyond the adult age-class.

Data Analysis

Direct inferences from analysis of our data can, at most, be extended to the resident, territorial population of owls on public lands within the scope of the RSA and, at the least, to specific spotted owl sites sampled within the RSA because selection of study areas and spotted owl sites within the RSA were not random. In both cases, inferences are limited to the years when data were collected and temporal trends should not be extrapolated beyond the study period.

Reproduction. — We defined *reproductive output* as the number of young fledged per spotted owl pair, *productivity* as the number of young fledged per pair producing young and *fecundity* as the number of young fledged of a given sex by a parent of the same sex (e.g., female young fledged per female; Franklin 1992). Trends in reproductive activity were examined using mixed-effects (random effects) models where year was considered a random effect. We used PROC GLIMMIX in SAS (mixed logistic regression, Schabenberger 2005) to analyze binomial data to examine annual trends in proportion of pairs that nested, pairs that nested and fledged young, and pairs that fledged young. We used a version of Akaike's Information Criterion corrected for sample size (AICc; Hurvich and Tsai 1995) for model selection where minimum AICc values indicated the best approximating model for the data. Trends in reproductive output were analyzed in the 2014 Northern Spotted Owl Meta-analysis Workshop held in Corvallis, Oregon and methods will be detailed in the report from that workshop.

We tested for a 1:1 sex ratio using Fisher's Exact Test (Sokal and Rohlf 1981) in fledged young of known sex where sex was determined by chromosomal analysis of blood samples.

Survival. — Estimates and trends in annual survival were analyzed in the 2014 Northern Spotted Owl Meta-analysis Workshop held in Corvallis, Oregon and methods will be detailed in the report from that workshop.

Population trends. — Estimates and trends in the northern spotted owl population on our study area were analyzed in the 2014 Northern Spotted Owl Meta-analysis Workshop held in Corvallis, Oregon and methods will be detailed in the report from that workshop.

RESULTS

Surveys

We conducted 1,542 surveys within our study areas in 2013 (Table 1); 14.4% of these were daytime surveys. Ninety-four territories previously occupied by northern spotted owls were surveyed on the RSA and WCSA in 2013 (Table 2, Figure 1). Owls were detected at 33 (35.1%)

and reproduction was assessed at 28 (29.8%) of the 94 territories surveyed (Table 2). We assumed that 60 (63.8%) of the territories were unoccupied. Thus, we were able to assess reproduction to protocol at 84.8% of the territories found occupied. We identified (captured, recaptured or resighted) 63 individual owls in 2013 (Table 3). We found a total of 15 juvenile spotted owls that had fledged, 11 of which were on the WCSA and 4 were on the RSA. We captured and banded 13 of the juveniles located. A total of 3,891 identifications of individuals have been made on the WCSA and RSA from 1985 through 2013 (Table 3), not including multiple recaptures and re-sightings of individuals within the same year.

Sex and Age-Class Distribution

The 2013 age-class distribution for northern spotted owls between sexes was not different (Fisher's Exact $P = 0.74$) (Table 4). If juveniles were included as an age-class in the age-class distribution, only 4.8% of the 63 owls identified and sexed were subadults (Table 4). If juveniles were excluded, subadults were still only 5.9% of the adult/subadult age-classes. Of the 562 juveniles sexed from 1992 through 2013, 274 were females and 288 were males. There was no apparent deviation from a 1:1 sex ratio among the 20 years (Fisher's Exact $P = 0.56$), although males seemed to predominate, especially in 1996 (35 males:20 females), 2007 (8 males:3 females), and 2010 (12 males:6 females), while females seemed to predominate in 2009 (15 females:8 males) and 2012 (5 females, 1 male).

Reproduction

Reproductive activity.— Temporal trends in the proportion of pairs checked annually for reproduction which nested from 1985 through 2013 (Table 5) were best explained by a good vs bad year model (Table A1 in Appendix A) where the years 1993, 1995, 1999, 2003, 2007, 2011, and 2012 had lower proportions nesting and lower proportions fledging young. This model estimated 60.1% (95% CI = 56.7%, 63.6%) of the pairs nesting in good years and 25.1% (95% CI = 19.4%, 30.8%) of pairs nesting in bad years. Overall, an average of 52.2% of the pairs nested annually during the 29 years of study (Table 5).

Temporal trends in the proportion of pairs nesting and fledging young was best explained by a means model (Table A2 in Appendix A), suggesting no evidence for an annual trend in these data (Table 5). This was also supported by considerable uncertainty in model selection (Table A2). Overall, the proportion of nesting pairs which fledged young on both study areas was 77.4% for the 29 years (Table 5), which can be considered a crude measure of nest success.

Temporal trends in the overall proportion of pairs fledging young was also best explained by a good vs bad year model (Table A3 in Appendix A), which estimated 44.1% (95% CI = 41.3%, 47.0%) of the pairs checked for reproduction fledged young in good years and 14.2% (95% CI = 10.4%, 17.9%) of pairs fledged young in bad years. Overall, 37.6% of the pairs successfully checked for reproduction fledged young during the 29 years of the study (Table 5).

Reproductive output.— Details on the analysis of reproductive output will be reported in the final report from the 2014 Northern Spotted Owl Meta-analysis Workshop held in Corvallis, Oregon.

Annual Survival

Details on the analysis of survival will be reported in the final report from the 2014 Northern Spotted Owl Meta-analysis Workshop held in Corvallis, Oregon.

Population Trends

Details on the analysis of population trends will be reported in the final report from the 2014 Northern Spotted Owl Meta-analysis Workshop held in Corvallis, Oregon.

Barred Owls

Barred owls were first detected in the WCSA in 1991 and in the RSA in 1992 (Table 6). In 1994, a male barred × spotted hybrid was detected in Bee Tree Creek in the WCSA, but hybrids have remained rare in the study area. The first nesting pair of barred owls was found in 1999.

Since 1991, we have observed a gradual increase in the number of territories with barred owl detections (Table 6). However, we suspect the large increase in 2008 was due in part to our implementation of barred owl-specific surveys (See *Barred Owl-Specific Surveys* above). The proportion of surveyed spotted owl territories with barred owl detections in 2013 was 0.39, slightly higher but similar to the previous two years. To document long term trends, we also estimated the number of barred owl “sites” in the study area. Prior to 2009, when study area-wide barred owl surveys began, we estimated this number using an estimate of barred owl home range size from Washington (Hamer 1988), and topographic features (e.g., ridges) that may act as natural boundaries between sites. At least 2 barred owl detections (either within a year or between 2 or more consecutive years) were needed to define a barred owl “site”. Beginning in 2009 we were able to confirm the number of sites with occupancy surveys. We estimated 27 barred owl “sites” in 2013, 21 of which occurred in the WCSA (Table 6). We determined that two barred owl pairs had fledged young, but we were unable to confirm the reproductive status for the remaining pairs.

DISCUSSION

Most of the results from 2013 will be reported in the final report from the 2014 Northern Spotted Owl Demography Workshop. Thus, the discussion of results here will be confined to the analyses we conducted here that were not included in the workshop framework.

Despite a relatively constant survey effort each year for the past five years (Table 1), the proportion of territories where owls have been detected has decreased by more than 30%. This has been coincident with an increase in the number of spotted owl territories with barred owl presence, which may be affecting spotted owl survival from interference competition by barred owls (Van Lanen et al. 2011). With an increase in competition, which may have become expressed on our study area, it appears that barred owls may have begun to have a discernible, significant effect on the northern spotted owl population, at least in the WCSA. While anecdotal and correlative evidence (e.g., Van Lanen et al 2011) suggests that barred owls may out-compete spotted owls for resources, it remains unclear what the full impact of barred owls will be on spotted owls (Forsman et al. 2011). The number of barred owl detections in a year is influenced by survey effort and methodology, which have not been consistent across all years. We do not know if the increase in barred owl detections in the WCSA prior to 2009 (Table 6) represents an actual increase in barred owl numbers in the WCSA. However, with consistent barred owl surveys in 2009 through 2013, there appears to be continued recent increase in the numbers of barred owls on our study area and an increase in the number of northern spotted owl territories where barred owls have been detected (Table 6). We recommend that continued monitoring of

both species is necessary to evaluate the extent that barred owls are impacting the spotted owl population on our study area. Covariates on barred owl detections were included in the 2014 meta-analysis workshop and will help elucidate the plausibility of barred owl effects on our population of northern spotted owls. Such effects are important to document for comparison with ongoing barred owl removals on the nearby Hoopa study area for which the WCSA serves as a control area.

ACKNOWLEDGMENTS

We thank Patricia Krueger of the U. S. Forest Service Region 5 for her assistance in financial support. Bill Rice, Rema Sadak and the rest of the staff of the Lower Trinity Ranger District, Six Rivers National Forest were generous with their time and access. Christine Moen, John Hunter and Jennifer Blakesley contributed greatly to the success of this project over the years. We extend our gratitude to Sam Cuenca, Lowell Diller, Desiree Early, Dennis Garrison, Keith Hamm, Tony Hacking, Mark Higley, Amy Krause, Kary Schlick, and Peter Steele for their assistance and willingness to share information.

LITERATURE CITED

- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, second edition. Springer-Verlag, New York, New York
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5, Bethesda, Maryland.
- Burnham, K. P., D. R. Anderson and G. C. White. 1996. Meta-analysis of vital rates of the northern spotted owl. *Studies in Avian Biology* 17:92-101.
- Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ring data. *Journal of Applied Statistics* 29:245-264.
- Blakesley, J. A., A. B. Franklin, and R. J. Gutiérrez. 1992. Spotted owl roost and nest site selection in northwestern California. *Journal of Wildlife Management* 56:388-392.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-438
- Dvořák, J., J. L. Halverson, P. Gulick, K. A. Rauen, U. K. Abbott, B. J. Kelley, and F. T. Shultz. 1992. cDNA cloning of a Z- and W-linked gene in gallinaceous birds. *Journal of Heredity* 83:22-25.
- Fleming, T. L., J. L. Halverson, and J. B. Buchanan. 1996. Use of DNA analysis to identify sex of northern spotted owls (*Strix occidentalis caurina*). *Journal of Raptor Research* 30:118-122.
- Forsman, E. D. 1981. Molt of the Spotted Owl. *Auk* 98: 735-742.
- Forsman, E. D. 1983. Methods and materials for locating and studying Spotted Owls. U.S. Forest Service General Technical Report PNW-12.
- Forsman, E. D., E. C. Meslow and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monograph* 87:1-64.

- Forsman, E.D., A.B. Franklin, F.M. Oliver, and J.P. Ward, Jr. 1996. A color band for spotted owls. *Journal of Field Ornithology* 67:507-510.
- 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. Gremel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. Schaberel, T. J. Snetsinger, and S. G. Sovern. 2011. Population demography of the northern spotted owls. University of California Press, Berkeley, California.
- Franklin, A. B. 1992. Population regulation in northern spotted owls: theoretical implications for management. Pages 815-827 *In* D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: populations*. Elsevier Applied Science, London, England.
- Franklin, A. B., D. R. Anderson, and K. P. Burnham. 2002. Estimation of long-term trends and variation in avian survival probabilities using random effects models. *Journal of Applied Statistics* 29:267-287.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12-20.
- Franklin, A. B., K. P. Burnham, G. C. White, R. G. Anthony, E. D. Forsman, C. Schwarz, J. D. Nichols, and J. Hines. 1999a. Range-wide status and trends in northern spotted owl populations. U. S. Geological Survey - Biological Resources Division, Colorado and Oregon Cooperative Fish and Wildlife Research Units, Fort Collins, CO and Corvallis, OR.
- Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539-590.
- Franklin, A. B., R.J. Gutiérrez, and P. C. Carlson. 1996. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northwestern California: annual results, 1995. Progress report, U. S. Forest Service, Region 5, San Francisco, CA. 18pp.
- Franklin, A. B., R.J. Gutiérrez, and P. C. Carlson. 2001. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northwestern California: annual results, 2000. Progress report, U. S. Forest Service, Region 5, San Francisco, CA. 18pp.
- Franklin, A., J.P. Ward, and R.J. Gutiérrez. 1986. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northwestern California: preliminary results, 1985. Unpubl. Prog. Rep. Project Work No. W_65_R_3 (554). Calif. Dept. Fish & Game. Sacramento, CA. 42pp.
- Franklin, A., J.P. Ward, R.J. Gutiérrez and G.I. Gould. 1990. Density of northern spotted owls in northwest California. *Journal of Wildlife Management* 54:1-10.
- Gould, G.I., Jr. 1974. The status of the Spotted Owl in California. Unpubl. Tech. Rep., Calif. Dept. Fish and Game and USDA Forest Service, Region 5. 34pp.
- Gutiérrez, R.J., D.M. Solis and C. Sisco. 1984. Habitat ecology of the Spotted Owl in northwestern California: implications for management. Pages 368-373 *in* Proc. Soc. Amer. Foresters Natl. Conv., 16_20 Oct., 1983.
- Gutiérrez, R.J., J.P. Ward, A.B. Franklin, W. LaHaye and V. Meretsky. 1985. Dispersal ecology of juvenile northern spotted owls (*Strix occidentalis caurina*) in northwestern California. Unpubl. Tech. Rep., USDA _ Forest Serv., Pacific NW Forest and Range Exper. Sta., Olympia, WA. 48pp.
- Hamer T. E. 1988. Home range size of the northern barred owl and northern spotted owl in western Washington. MS thesis, Western Washington University, Washington, USA.
- Hines, J. E., and J. D. Nichols. 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996)

- model for capture-recapture data. *Journal of Applied Statistics* 29:573-587.
- Hunter, J. E. 1994. Habitat configuration around spotted owl nest and roost sites in northwestern California. M.S. Thesis, Humboldt State University, Arcata, California.
- Hunter, J. E., R. J. Gutiérrez, and A. B. Franklin. 1995. Habitat configuration around spotted owl sites in northwestern California. *Condor* 97:684-693.
- Hurvich, C. M., and C-L. Tsai. 1995. Model selection for extended quasi-likelihood models in small samples. *Biometrics* 51:1077-1084.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247.
- Küchler, A.W. 1977. The map of the natural vegetation of California. Pages 909-938 in M. Barbor and J. Majors, eds. *Terrestrial vegetation of California*. John Wiley and Sons, New York, New York.
- Lebreton, J-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monograph* 62:67-118.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS[®] system for mixed models. SAS Institute, Inc., Cary, North Carolina, USA.
- Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. U. S. Forest Service General Technical Report PNW-GTR-440, Portland, Oregon.
- Moen, C. A., A. B. Franklin, and R. J. Gutiérrez. 1991. Age determination of subadult northern spotted owls in northwest California. *Wildlife Society Bulletin* 19:489-493.
- Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ and demographic contributions to λ , using capture-recapture data. *Journal of Applied Statistics* 29:539-568.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703-709.
- Roberts, A. 2009. Evaluation of northern spotted owl surveys to detect the presence of barred owls. Honors Thesis, Humboldt State University, Arcata, California.
- SAS Institute. 1997. SAS/STAT[®] software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.
- Schabenberger, O. 2005. Introducing the GLIMMIX procedure for generalized linear mixed models. Pages 1-20 In: *Proceedings of the Thirtieth Annual SAS[®] Users Group International Conference*. SAS Institute Inc., Cary, NC: 1-20.
- Seber, G.A.F. 1965. The multi-sample single recapture census. *Biometrika* 49:330-349.
- Sisco, C. L. 1990. Seasonal home range and habitat ecology of spotted owls in northwestern California. M.S. Thesis, Humboldt State University, Arcata, California.
- Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. W.H. Freeman and Co., San Francisco.
- Solis, D. M. and R. J. Gutiérrez. 1990. Summer habitat ecology of northern spotted owls in northwestern California. *Condor* 92:739-748.

- U.S. Fish and Wildlife Service. 1990. 50 CFR Part 17 Endangered and threatened wildlife and plants; determination of threatened status for the northern spotted owl; final rule. *Federal Register* 55:26114-26194.
- U.S. Fish and Wildlife Service. 2012. Experimental removal of barred owls to benefit threatened northern spotted owls. Draft environmental impact statement, Oregon Fish and Wildlife Office, Portland, Oregon.
- Van Lanen, N. J., A. B. Franklin, K. P. Huyvaert, R. F. Reiser II, and P. C. Carlson. 2011. Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls. *Biological Conservation* 144:2194-2201.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (suppl.): S120-S139.
- Zar, J.H. 1984. Biostatistical analysis. Prentice_Hall, Englewood, N.J. 718pp.

Table 1. Annual number of surveys conducted to detect northern spotted owls in northwestern California, from 1985 through 2013.

Year	Survey Type			Total
	Point	Walk-in	Cruise	
1985	521	149	36	706
1986	318	156	20	494
1987	726	219	161	1106
1988	1067	212	107	1386
1989	1387	215	89	1691
1990	1425	199	64	1688
1991	1305	244	84	1633
1992	904	207	55	1166
1993	934	170	104	1208
1994	1020	242	96	1358
1995	1129	202	132	1463
1996	1172	249	123	1544
1997	861	224	107	1192
1998	965	216	113	1294
1999	968	170	120	1258
2000	1129	183	127	1439
2001	1031	228	114	1373
2002	1004	210	126	1340
2003	1035	196	108	1339
2004	905	181	93	1179
2005	1014	206	97	1317
2006	1014	162	110	1286
2007	1121	172	113	1406
2008	982	165	109	1256
2009	1134	167	101	1402
2010	1255	152	147	1554
2011	1219	115	144	1478
2012	1271	98	120	1489
2013	1320	108	114	1542

Table 2. Number of northern spotted owl territories surveyed, occupied and checked for reproduction in 2013 in northwestern California.

No. Territories	Study Area		
	WCSA	RSA	Combined
<i>Surveyed</i>	60	34	94
<i>With Unknown Status</i>	0	1	1
<i>Assumed Unoccupied</i>	39	21	60
<i>Found Occupied By:</i>			
Pairs	15	11	26
Males	6	1	7
Females	0	0	0
Total	21	12	33
<i>Checked For Reproduction Where Occupied By:</i>			
Pairs	14	10	24
Males	4	0	4
Females	0	0	0
Total	18	10	28

Table 3. Number of northern spotted owls identified in northwestern California from 1985 through 2013. New birds were owls that had not been previously banded; old birds were owls that had been previously banded.

Year	No. new birds captured as:			No. old birds which were:			Grand Total
	Adult & Subadult	Juvenile	Total	Recaptured	Resighted	Total	
1985	54	16	70	22	0	22	92
1986	8	17	25	55	0	55	80
1987	48	31	79	42	18	60	139
1988	18	36	54	13	86	99	153
1989	26	39	65	21	87	108	173
1990	25	35	60	14	104	118	178
1991	24	37	61	28	87	115	176
1992	20	49	69	12	114	126	195
1993	12	9	21	13	105	118	139
1994	9	48	57	19	105	124	181
1995	21	15	36	22	83	105	141
1996	11	58	69	17	95	112	181
1997	11	43	54	7	105	112	166
1998	12	32	44	16	93	109	153
1999	17	11	28	10	87	97	125
2000	13	39	52	7	86	93	145
2001	17	51	68	11	85	96	164
2002	21	34	55	13	90	103	158
2003	16	4	20	8	93	101	121
2004	16	41	57	13	87	100	157
2005	16	24	40	11	84	95	135
2006	11	21	32	11	70	81	113
2007	13	11	24	5	83	88	112
2008	9	22	31	5	77	82	113
2009	3	23	26	7	72	79	105
2010	8	21	29	3	68	71	100
2011	6	7	13	7	51	58	71
2012	8	6	14	5	43	48	62
2013	5	13	18	4	41	45	63
Total	478	793	1271	421	2199	2620	3891

Table 4. Age-class distribution, by sex, in 2013 for northern spotted owls in northwestern California. The number observed is represented by *n* and the proportion of each age-class within sex by *p*.

Age-Class	Male		Female		Both Sexes	
	<i>n</i>	<i>p</i>	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>
Adult	27	0.75	21	0.78	48	0.76
2nd-yr Subadult	0	0.00	0	0.00	0	0.00
1 st -yr Subadult	2	0.06	1	0.04	3	0.05
Juvenile	7	0.19	5	0.19	12	0.19

Table 5. Proportion of northern spotted owl pairs checked for reproductive activity (*n*) which nested, which nested and successfully fledged young, and which fledged young in northwestern California from 1985 through 2012. Standard errors are in parentheses.

Year	Proportion of pairs which:					
	Nested		Nested and fledged young		Fledged young	
	n ^a	Proportion	n ^b	Proportion	n ^c	Proportion
1985	32	0.50 (0.088)	16	0.81 (0.098)	42	0.45 (0.077)
1986	25	0.64 (0.096)	16	0.56 (0.124)	37	0.38 (0.080)
1987	31	0.65 (0.086)	20	0.70 (0.102)	57	0.42 (0.065)
1988	36	0.64 (0.080)	23	0.87 (0.070)	62	0.47 (0.063)
1989	52	0.60 (0.068)	31	0.74 (0.078)	65	0.42 (0.061)
1990	53	0.66 (0.065)	35	0.63 (0.082)	67	0.40 (0.060)
1991	58	0.64 (0.063)	37	0.70 (0.075)	67	0.42 (0.060)
1992	49	0.45 (0.071)	22	1.00 (0.000)	74	0.42 (0.057)
1993	25	0.16 (0.073)	4	0.75 (0.217)	59	0.10 (0.039)
1994	50	0.62 (0.069)	31	0.68 (0.084)	62	0.44 (0.063)
1995	49	0.16 (0.053)	8	0.88 (0.117)	59	0.19 (0.051)
1996	40	0.70 (0.072)	28	0.93 (0.049)	57	0.65 (0.063)
1997	49	0.55 (0.071)	27	0.81 (0.075)	61	0.46 (0.064)
1998	47	0.64 (0.070)	30	0.73 (0.080)	56	0.43 (0.066)
1999	42	0.17 (0.058)	7	0.86 (0.132)	54	0.15 (0.048)
2000	40	0.63 (0.077)	25	0.76 (0.085)	52	0.46 (0.069)
2001	35	0.54 (0.084)	19	1.00 (0.000)	53	0.55 (0.068)
2002	45	0.58 (0.074)	26	0.77 (0.083)	58	0.40 (0.064)
2003	40	0.23 (0.066)	9	0.44 (0.166)	53	0.08 (0.036)
2004	39	0.62 (0.078)	24	0.83 (0.076)	56	0.48 (0.067)
2005	36	0.58 (0.082)	20	0.65 (0.107)	53	0.40 (0.067)
2006	29	0.34 (0.088)	10	0.90 (0.095)	44	0.34 (0.071)
2007	35	0.31 (0.078)	11	0.73 (0.134)	49	0.16 (0.053)
2008	35	0.71 (0.076)	25	0.68 (0.093)	45	0.38 (0.072)
2009	33	0.67 (0.082)	22	0.82 (0.082)	40	0.45 (0.079)
2010	29	0.66 (0.088)	19	0.89 (0.070)	38	0.45 (0.081)
2011	17	0.35 (0.116)	6	0.83 (0.153)	28	0.18 (0.072)
2012	19	0.32 (0.107)	5	0.80 (0.179)	23	0.17 (0.079)
2013	20	0.55 (0.110)	11	0.91 (0.087)	24	0.41 (0.100)
Overall ^d	1090	0.52 (0.015)	567	0.77 (0.018)	1495	0.38 (0.013)

^aTotal number of pairs checked each year before 31 May.

^bTotal number of nesting pairs found each year before 31 May.

^cTotal number of pairs checked throughout the entire sampling period in each year.

^dEstimate represents overall outcomes rather than pairs because same pairs often measured across years.

Table 6. Number of sites with barred owl detections in the WCSA and RSA from 1991 through 2013.

Year	Spotted Owl Territories With Detections	Number of Barred Owl Sites ^a		Number of Barred Owl Territories ^b	
		WCSA	RSA	WCSA	RSA
1991	0	1	0	-	-
1992	1	0	1	-	-
1993	0	0	0	-	-
1994	1	1	0	-	-
1995	8	3	2	-	-
1996	4	2	0	-	-
1997	5	4	0	-	-
1998	6	4	0	-	-
1999	7	3	2	-	-
2000	8	5	0	-	-
2001	12	6	1	-	-
2002	10	5	0	-	-
2003	10	5	3	-	-
2004	7	5	1	-	-
2005	8	6	1	-	-
2006	12	7	1	-	-
2007	13	9	1	-	-
2008	20	9	4	8	3
2009	21	9	1	13	1
2010	29	15	2	15	2
2011	36	17	4	17	4
2012	33	21	4	16	4
2013	37	21	6	19	4

^a Estimated using the spatial clustering of detections. This number should be considered an approximate number of barred owl sites.

^b Confirmed territories based on spotted and barred owl survey effort.

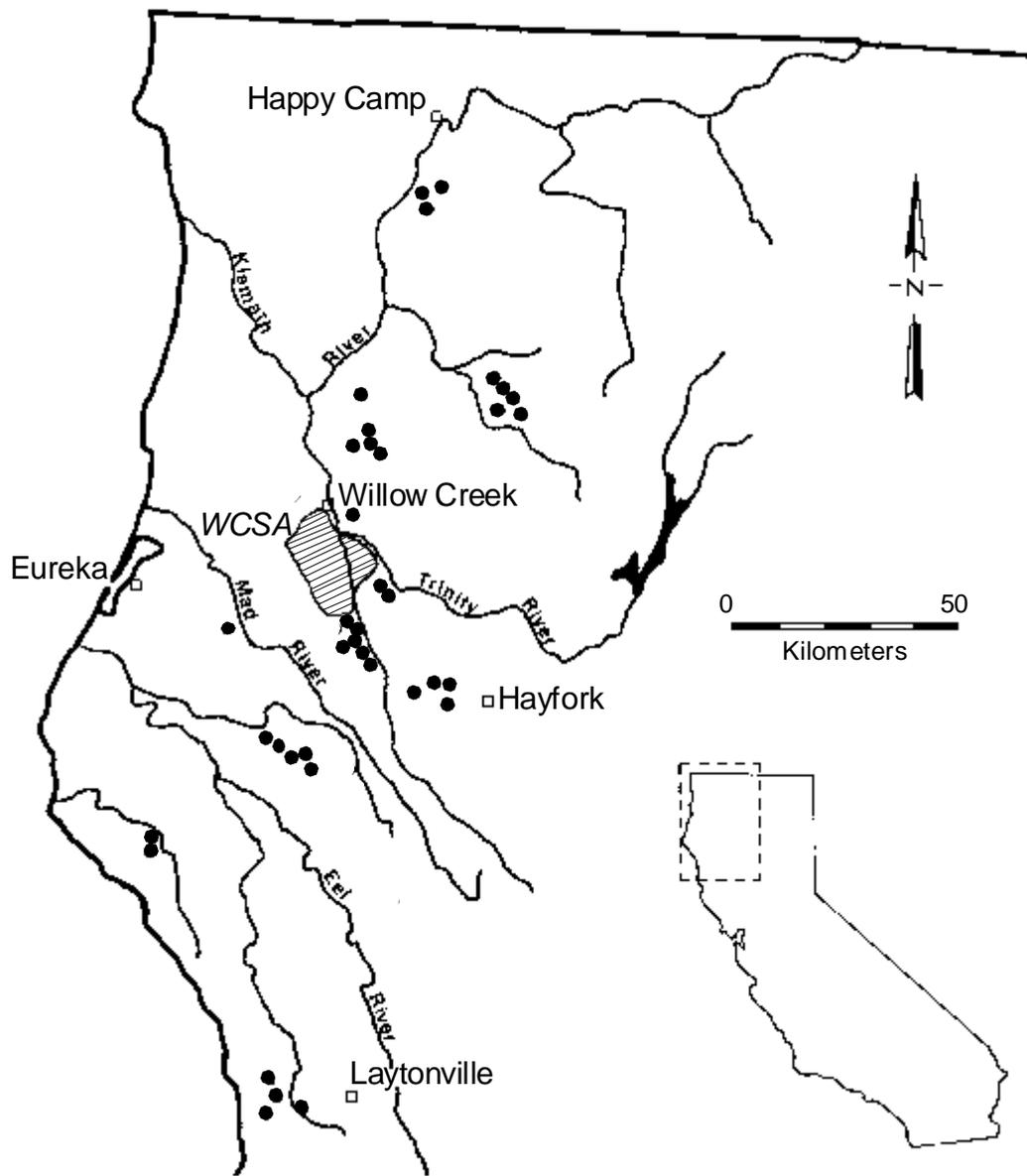


Figure 1. Map of northern spotted owl territories (dots) surveyed in the Regional Study Area, northwestern California. Shaded area represents the Willow Creek Study Area.

APPENDIX A. Tables of model selection results from analyses on reproductive activity for northern spotted owls in northwestern California from 1985 through 2013.

Table A1. Model selection results for random effects models estimating the proportion of pairs nesting.

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
PN.	1508.95	2	1512.95	1512.96	94.88	0.000
PN _t	1375.02	30	1435.02	1436.78	18.69	0.000
PN _T	1506.23	3	1512.23	1512.25	94.17	0.000
PN _{TT}	1502.13	4	1510.13	1510.17	92.09	0.000
PN _{lnT}	1505.00	3	1511.00	1511.02	92.94	0.000
PN_{G vs B}	1412.06	3	1418.06	1418.08	0.000	1.000
PN _{EO}	1485.08	3	1491.08	1491.10	73.02	0.000
PN _{EO+T}	1481.93	4	1489.93	1489.97	71.89	0.000

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, G vs B = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend

Table A2. Model selection results for random effects models estimating the proportion of pairs nesting and fledging young.

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
PNF.	391.64	2	395.64	395.66	0.000	0.360
PNF _t	Not estimable					
PNF _T	391.55	3	397.55	397.59	1.931	0.137
PNF _{TT}	391.54	4	399.54	399.61	3.950	0.050
PNF _{lnT}	391.54	3	397.54	397.58	1.921	0.138
PNF _{G vs B}	391.62	3	397.62	397.66	2.001	0.133
PNF _{EO}	391.63	3	397.63	397.67	2.011	0.132
PNF _{EO+T}	391.54	4	399.54	399.61	3.950	0.050

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, G vs B = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend

Table A3. Model selection results for random effects models estimating the proportion of pairs fledging young.

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
PF _.	1979.47	2	1983.47	1983.48	106.782	0.000
PF _t	1847.74	30	1907.74	1909.01	32.314	0.000
PF _T	1974.77	3	1980.77	1980.79	104.090	0.000
PF _{TT}	1974.77	4	1982.77	1982.80	106.101	0.000
PF _{lnT}	1974.96	3	1980.96	1980.98	104.280	0.000
PF_{G vs B}	1870.68	3	1876.68	1876.70	0.000	1.000
PF _{EO}	1960.07	3	1966.07	1966.09	89.390	0.000
PF _{EO+T}	1955.04	4	1963.04	1963.07	86.371	0.000

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, G vs B = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend