STATUS AND TRENDS IN DEMOGRAPHY OF NORTHERN SPOTTED OWLS, 1985–2003

ROBERT G. ANTHONY

U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

ERIC D. FORSMAN

USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Corvallis, OR 97331, USA

ALAN B. FRANKLIN

Colorado Cooperative Fish and Wildlife Research Unit, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523 USA

DAVID R. ANDERSON

Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523 USA

KENNETH P. BURNHAM

U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523 USA

GARY C. WHITE

Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA

CARL J. SCHWARZ

Department of Statistics and Actuarial Science, 8888 University Drive, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

JIM NICHOLS

U.S. Geological Survey, Patuxent Wildlife Research Center, 11510 American Holly Drive,
Laurel, MD 20708, USA

JIM E. HINES

U.S. Geological Survey, Patuxent Wildlife Research Center, 11510 American Holly Drive,
Laurel, MD 20708, USA

GAIL S. OLSON

Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, Corvallis, OR 97331, USA

STEVEN H. ACKERS

Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, Corvallis, OR 97331, USA

STEVE ANDREWS

Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, Corvallis, OR 97331, USA

BRIAN L. BISWELL

USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory,
Olympia, WA 98502

PETER C. CARLSON

Hoopa Tribal Forestry, P.O. Box 368, Hoopa, CA 95546, USA

LOWELL V. DILLER

Simpson Resource Company, 900 Riverside Road, Korbel, CA, USA

KATIE M. DUGGER

Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

KATHERINE E. FEHRING

Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA

TRACY L. FLEMING

National Council For Air and Stream Improvement, 23308 NE 148th, Brush Prairie, WA 98606, USA

RICHARD P. GERHARDT

Sage Science, 319 SE Woodside Ct., Madras, OR 97741, USA

SCOTT A. GREMEL

USDI National Park Service, Olympic National Park, Port Angeles, WA 98362, USA

R. J. GUTIÉRREZ

Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1880 Folwell Ave., St. Paul, MN 55108, USA

PATTI J. HAPPE

USDI National Park Service, Olympic National Park, Port Angeles, WA 98362, USA

DALE R. HERTER

Raedeke Associates Inc., 5711 NE 63rd Street, Seattle, WA 98115, USA

J. MARK HIGLEY

Hoopa Tribal Forestry, PO Box 368, Hoopa, CA 95546, USA

ROB B. HORN

USDI Bureau of Land Management, Roseburg District Office, 777 Garden Valley Blvd.,
Roseburg, OR 97470, USA

LARRY L. IRWIN

National Council For Air and Stream Improvement, PO Box 68, Stevensville, MT 59870, USA

PETER J. LOSCHL

Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, Corvallis, OR 97331, USA

JANICE A. REID

USDA Forest Service, Pacific Northwest Research Station, Roseburg Field Station, 777 Garden
Valley Blvd., Roseburg, OR 97470, USA

STAN G. SOVERN

Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife,
Oregon State University, Corvallis, OR 97331, USA

Abstract: We analyzed demographic data from northern spotted owls (*Strix occidentalis caurina*) from 14 study areas in Washington, Oregon, and California for the time period of 1985–2003. The purpose of our analyses was to provide an assessment of the status and trends of northern spotted owl populations throughout most of their geographic range. The 14 study areas comprised approximately 12% of the range of the subspecies and included federal, tribal, private, and mixed federal and private lands. The study areas also included all of the major forest types that the subspecies inhabits. The analyses followed rigorous protocols that were

developed *a priori* and were the result of extensive discussions and consensus among the authors. Our primary objective was to estimate fecundity, apparent survival (*N*), and annual rate of population change (*8*) and to determine if there were any temporal trends in these population parameters. In addition to analyses of data from individual study areas, we conducted 2 meta-analyses on each demographic parameter. One meta-analysis was conducted on all 14 areas and the other was restricted to the 8 areas that constituted the Effectiveness Monitoring Plan for northern spotted owls under the Northwest Forest Plan. The average number of years of reproductive data per study areas was 14 (range = 5-19), and the average number of recapture occasions per study area was 13 (range = 4-18). Only 1 study area had <12 years of data. Our results were based on 32,054 captures and resightings of 11,432 banded individuals for estimation of survival, and 10,902 instances in which we documented the number of young produced by territorial females.

The number of young fledged per territorial female (NYF) was analyzed with PROC MIXED in SAS to fit a suite of *a priori* models that included: (1) the effects of age, (2) linear or quadratic time trends, (3) the effects of barred owls (*Strix varia*), and (4) an even-odd year effect. NYF varied among years on most study areas with a biennial cycle of high reproduction in even-numbered years and low reproduction in odd-numbered years. These cyclic fluctuations did not occur on all study areas, and the even-odd year effect waned during the last 5 years of the study. There also were differences in NYF among age classes with highest productivity for adults (>2yrs. old), lower for 2-year olds, and very low for 1-year olds. In addition, we found that fecundity was stable over time for 7 study areas (Wenatchee, Rainier, Olympic, Warm Springs, H.J. Andrews, Klamath, and Marin), likely declining for 5 areas (Cle Elum, Oregon

Coast Range, Southern Oregon Cascades, Northwest California, and Simpson), and slightly increasing for 2 areas (Tyee, Hoopa). We found little association between NYF and the proportion of spotted owl territories where barred owls were detected, although results were suggestive of a negative effect of barred owls for the Wenatchee and Olympic study areas. The meta-analysis on fecundity indicated substantial annual variability with no increasing or decreasing trends, and fecundity was highest in the mixed-conifer region of eastern Washington (Cle Elum, Wenatchee).

We used Cormack-Jolly-Seber open population models in program MARK and information-theoretic statistics to estimate apparent survival rates of owls >1 year old. We did not estimate survival rates of juvenile (<1 year old) owls because of estimation problems and the potential bias due to permanent emigration from the study areas by juveniles. Apparent survival rates for >1 year old owls varied from 0.750 to 0.886 (sexes combined) and were comparable to estimates from previous analyses on the subspecies. Estimates of apparent survival from individual study areas indicated that there were differences among age classes with adults generally having higher survival than 1- and 2- year olds. We found evidence for negative time trends in survival rates on 5 study areas (Wenatchee, Cle Elum, Rainier, Olympic, and Northwest California) and no trends in survival for the remaining areas. There was evidence for negative effects of barred owls on apparent survival on 3 study areas (Wenatchee, Cle Elum, and Olympic). We found no differences in apparent survival rates between sexes except for 1 study area (Marin) which had only a few years of data. Survival rates of owls on the 8 Monitoring Areas generally were high, ranging from 0.85 to 0.89; but were declining on the Cle Elum, Olympic, and Northwestern California study areas. In the meta-analysis of apparent survival, we found differences among regions and changes over time with a downward trend in the mixed-conifer and Douglas-fir (*Pseudotsuga menziesii*) regions of Washington. The meta-analysis also suggested that there was a cost of reproduction on survival the following year, but this effect was limited to the Douglas-fir and mixed conifer regions of Washington and the Douglas-fir region of the Oregon Cascade Mountains.

We estimated annual rate of population change with the reparameterized Jolly-Seber method (λ_{RJS}) which refers to the population of territorial owls on the study areas. It answers the question: *are these territorial owls being replaced in this geographically open population*? Point estimates of λ_{RJS} were <1.0 for 12 of 13 study areas. The analyses provided strong evidence that populations on the Wenatchee, Cle Elum, Rainier, Olympic, Warm Springs, H.J. Andrews, Oregon Coast Ranges and Simpson study areas were declining during the study. The mean $\hat{\lambda}_{\mathrm{RJS}}$ for the 13 study areas was 0.963 (SE=0.009), suggesting that populations over all of the areas were declining about 3.7% per year during the study. The mean $\hat{\lambda}_{\mathrm{RJS}}$ for the 8 monitoring areas on federal lands was 0.976 (SE = 0.007) compared to a mean of 0.942 for the other study areas, a 2.4 vs 5.8% decline per year. This suggested that owl populations on federal lands had better demographic rates that elsewhere. Populations were doing poorest in Washington where apparent survival rates and populations were declining on all 4 study areas. Our estimates of λ_{RJS} were generally lower than those reported in a previous analysis ($\hat{\lambda}_{\mathrm{RJS}}$ = 0.997, SE = 0.003) for many of the same areas at an earlier date (Franklin et al. 1999). Whether this was due to continued habitat loss from timber harvest and fires, competition with barred owls, weather patterns, or other factors is unclear. The Northwest Forest Plan appeared to be having a positive affect on demography of northern spotted owls, but a recent invasion of barred owls (*Strix varia*) may be having an affect most of their geographic range.

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INTRODUCTION

The northern spotted owl is a medium-sized, nocturnal owl that inhabits coniferous forests along the Pacific Coast of North America from southern British Columbia to central California (Gutierrez et al. 1995). Adult spotted owls are territorial, exhibit high site fidelity, and occupy relatively large home ranges (Forsman et al. 1984, Carey et al. 1990, Thomas et al. 1990). In contrast, juvenile spotted owls are highly mobile and typically do not acquire territories until they are 1–3 years old (Franklin 1992, Forsman et al. 2002). Northern spotted owls feed primarily on small mammals, especially northern flying squirrels (*Glaucomys sabrinus*) in Washington and Oregon, and woodrats (*Neotoma* spp.) in southwestern Oregon and California (Barrows 1980, Forsman et al. 1984, 2001, Ward et al. 1998). The subspecies is closely associated with old forests throughout most of its range (Forsman et al. 1984, Thomas et al. 1990), but is also common in young redwood (*Sequoia sempervirens*) forests in northwestern California (Diller and Thome 1999).

Because of the close association between northern spotted owls and old forests, conservation of the owl and its habitat has been extremely contentious among environmentalists, the timber industry, land managers, and scientists since the early 1970's (Forsman and Meslow 1986, Thomas et al. 1990, Durbin 1996, Gutierrez et al. 1996, Marcot and Thomas 1997, Noon and Franklin 2002). This controversy started when it became apparent that federal agencies were harvesting old forests at levels that were not sustainable (Parry et al. 1983). In spite of these concerns, the U.S. Congress continued to increase harvest levels of old forests on federal lands during the 1970's and 1980's, until harvest levels on federal lands in western Oregon and Washington reached a peak of nearly 2.7 billion cubic feet per year in the late 1980's (Parry et al. 1983, Haynes 2003). As the rate of harvest increased, field surveys suggested that loss of old forests was leading to declines in numbers of northern spotted owls (Forsman et al. 1984, Anderson and Burnham 1992). Meanwhile, management options decreased; litigation increased; and a number of committees, task forces, and work groups were organized to develop solutions that were biologically sound and politically acceptable (Meslow 1993, Durbin 1996). This controversy intensified in 1988–1992, when a series of lawsuits by environmental groups halted all harvest of suitable spotted owl habitat on federal lands (Dwyer 1989) and forced the U.S. Fish and Wildlife Service to list the northern spotted owl as a threatened subspecies (Zilley 1988, U.S. Fish and Wildlife Service 1990). The primary reasons given for listing the owl as threatened were that: (1) suitable habitat was declining, (2) there was evidence of declining populations, and (3) there were inadequate regulatory mechanisms to protect the owl or its habitat.

To meet the requirements of the National Forest Management Act and the Endangered Species Act, federal agencies in the Pacific Northwest adopted the Northwest Forest Plan (NWFP) in 1994. The NWFP was designed to protect habitat for spotted owls and other species associated with late-successional forests (Thomas et al. 1993), while allowing a greatly reduced amount of commercial logging on federal lands (USDA and USDI 1994). The NWFP also placed large amounts of the federal land within the range of the northern spotted owl into riparian and late-successional forest reserves, in which the primary objective was to maintain or restore habitat for spotted owls and other fish and wildlife species. Although the NWFP met the legal requirements for protection of spotted owls and other species associated with old forests, it has continued to be controversial. Some environmental groups argued that it was not adequate because it still allowed some harvest of old forests, while some industry groups argued that it was too extreme because it did not produce the estimated levels of timber harvest on federal lands. Regardless of one's viewpoint, the controversy over management of spotted owls and old forests has led to an almost complete reversal of management objectives on federal forest lands in the Pacific Northwest. With the adoption of the Northwest Forest Plan, the primary focus of forest management has shifted from timber production to maintaining biological diversity and ecological processes.

The controversy surrounding the spotted owl has led to considerable research on the species, including numerous studies of its distribution, population trends, habitat use, home range size, diet, prey ecology, genetics, dispersal, and physiology (for reviews see Gutiérrez et al. 1995, Marcot and Thomas 1997, Noon and Franklin 2002). As a result, the spotted owl is one of the most intensively studied birds in the world. Despite this repository of knowledge, the effectiveness of current management plans for protecting the owl is still uncertain. This uncertainty has increased in recent years, as the barred owl has invaded the entire range of the northern spotted owl (Dunbar et al. 1991, Dark et al. 1998, Pearson and Livezey 2003) and appears to be affecting their territory occupancy (Kelly et al. 2003).

Most of the scientific and public debate regarding the northern spotted owl has focused on the degree to which the owl is negatively influenced by harvest of old forests (FEMAT 1993). To address this issue, the U.S. Forest Service, U.S. Bureau of Land Management, U.S. National Park Service, and several non-federal groups initiated several demographic studies on spotted owls from 1985–1990. These long-term studies were designed to provide information on survival and fecundity rates of territorial owls, which could then be used to estimate annual rates of population change (Forsman et al. 1996, Lint et al. 1999). In 2003, there were 14 of these demographic studies still being conducted on the northern spotted owl. Eight of these studies were part of the Monitoring Plan for the northern spotted owl under the NWFP (Lint et al. 1999). The other 6 were conducted by Indian Tribes, timber companies, and private consulting firms.

Data from the demographic studies have been examined in 3 workshops since 1991, and the results have been reported in 4 different documents (Anderson and Burnham 1992; Burnham et al. 1994, 1996; Franklin et al. 1999). Because of the contentious debate over management of spotted owls, participants in these workshops adopted formal protocols for error-checking data sets and selecting an *a priori* group of models for estimation of survival, fecundity and annual rate of population change (Anderson et al. 1999). These protocols ensured that data were collected and prepared in a consistent manner among study areas and avoided the analyses of additional models after *post-hoc* examination of results (i.e., data dredging).

Subsequent to the analysis conducted by Franklin et al. (1999), we collected an additional 5 years of data from most of the demographic study areas. In January 2004, we conducted a workshop at Oregon State University, during which we updated and analyzed all of these data, using a process and protocols that were similar to those used in previous analyses (Anderson et al. 1999). Our primary objectives were to:

(1) estimate age-specific survival and fecundity rates, and their sampling variances, for territorial owls on individual study areas;

(2) determine if there were any trends in apparent survival or fecundity rates among

study areas;

(3) estimate annual rates of population change (λ) and their sampling variances for individual study areas and across study areas; and

(4) compare the demographic performance of spotted owls on the 8 areas that are the basis of the Monitoring Plan for the NWFP (Lint et al. 1999) to that of owls on other areas.

We were particularly interested in examining the hypothesis that owl populations were stationary or increasing ($\lambda > 1$) versus declining ($\lambda < 1$) during the period of study. We also examined temporal trends in survival and fecundity rates, as increases or decreases in these rates could indicate fundamental changes in the dynamics of owl populations. We also included 2 covariates in the analyses of temporal trends. First, the proportion of spotted owl territories with barred owl detections was used to test the hypothesis that barred owls were having a negative effect on survival and fecundity of spotted owls. Second, we hypothesized that successful reproduction in 1 year had a negative effect on survival of adult owls the following year (i.e., a cost of reproduction). In this paper, we describe the results of our analyses, including an assessment of the status and trends of northern spotted owl populations throughout most of the range of the subspecies.

Acknowledgments.--We are particularly indebted to the many dedicated biologists and field technicians who helped us collect the data used in this report. Although we cannot name them all, they are the ones who made this study possible. We also thank J. Blakesley, M. Conner, S. Converse, S. Dinsmore, P. Doherty Jr., V. Dreitz, P. Lukacs, B. McClintock, T. McDonald, E. Rexstad, M. Seamans, and G. Zimmerman for analytical assistance during the workshop. We thank T. Hamer, K. Hamm, S. Turner-Hane, C. McAfferty, J. Schnaberl, T. Snetsinger, J. Thompson, and F. Wagner for technical assistance before and after the workshop. J. Lint, E. Meslow, and 4 anonymous reviewers provided valuable comments on earlier drafts of the paper. F. Oliver made most of the color bands used to identify individual owls in this study. J. Toliver at the Oregon Cooperative Fish & Wildlife Research Unit and D. Beaton at the Oregon Agricultural Research Foundation provided administrative support for the workshop. We particularly thank J. Lint for his support of these studies and encouragement over the last 2 decades. Funding for demographic studies of northern spotted owls on federal lands was provided primarily by the U.S. Forest Service, U.S. Bureau of Land Management, and U.S. National Park Service. Funding for studies on non-federal lands came from a variety of sources, including the Simpson Resource Company, Plum Creek Timber Company, National Council for Air and Stream Improvement, Louisiana Pacific Lumber Company, Confederated Tribes of Warm Springs, and the Hoopa Tribe. Funding for the workshop was provided by the U.S. Forest Service, U.S. Bureau of Land Management, and U.S. Fish and Wildlife Service.

STUDY AREAS

The 14 study areas included 4 study areas in Washington: Wenatchee (WEN), Cle Elum (CLE), Rainier (RAI), and Olympic Peninsula (OLY); 6 study areas in Oregon: Warm Springs Reservation (WSR), H.J. Andrews (HJA), Oregon Coast Ranges (COA), Tyee (TYE), Klamath (KLA), and southern Oregon Cascades (CAS); and 4 study areas in California: Northwest California (NWC), Hoopa Tribal Area (HUP), Simpson Resource area (SIM), and Marin (MAR)(Table 1, Fig. 1, Appendix A).. The combined area of the 14 study areas was 28,430 km^2

(Table 1), which included about 12% of the 230,690 km^2 range of the northern spotted owl (USDA and USDI 1994). One study area (SIM) was entirely on private land, 2 (HUP, WSR) were on Indian Reservations, 5 (OLY, HJA,CAS, NWC, MAR) were primarily on federal lands, and 6 (CLE, WEN, RAI, COA, TYE, KLA) were characterized by a mixture of federal, private, and state lands (Fig. 1, Table 1). Study areas that were partly or entirely on lands administered by the U.S. Bureau of Land Management (BLM) typically included an ownership pattern in which 2.56 km^2 sections of BLM lands alternated with 2.56 km^2 sections of private land (KLA, TYE, COA, CAS).

Our study areas differed slightly from those in a previous analysis by Franklin et al. (1999) by exclusion of 3 study areas that were discontinued after 1998 (Astoria, Elliott State Forest, and East Eugene BLM) and inclusion 1 study (MAR) that was started in 1998. We also modified the Olympic Peninsula Study Area to exclude non-federal lands that were included in the previous analysis; we did this to distinguish population trends of owls on federal lands on the Olympic Peninsula from trends on non-federal lands. Eight study areas (CLE, OLY, HJA, COA, TYE, KLA, CAS, NWC) were established by the U.S. Forest Service and U.S. Bureau of Land Management to monitor population trends of the northern spotted owl (hereafter referred to as the 8 monitoring areas) under the Northwest Forest Plan (Table 1, Appendix A, Lint et al. 1999).

All study areas were characterized by mountainous terrain, but there was great variation in the types of topographic relief among areas. Study areas in coastal regions of western Oregon and northern California were in areas where elevations rarely exceeded 1250 m and where forest vegetation generally extended from the lowest valleys to the highest ridges. In contrast, study areas in the Cascades Ranges and Olympic Peninsula typically included larger mountains, with the highest peaks and ridges extending well above timberline. Climate and precipitation were highly variable among areas, ranging from relatively warm and dry conditions on study areas in southern Oregon (CAS, KLA) and northern California (NWC, HUP) to temperate rain forests on the west side of the Olympic Peninsula (OLY), where precipitation ranged from 280–460 cm/year. Study areas on the east slope of the Cascades (WEN, CLE, WSR) were generally characterized by warm dry summers and cool winters, with most precipitation occurring as snow during winter.

Vegetation generally consisted of forests dominated by conifers or mixtures of conifers and hardwoods (Franklin and Dyrness 1973, Küchler 1977). Forests on study areas in Washington and Oregon were mostly characterized by mixtures of Douglas-fir and western hemlock (*Tsuga heterophylla*), or by mixed-conifer associations of Douglas-fir, grand fir (*Abies grandis*), western white pine (*Pinus monticola*), and ponderosa pine (*P. ponderosa*). Incense cedar (*Libocedrus decurrens*) was a common associate of mixed-conifer forests in Oregon. Forests on study areas in southwest Oregon and northern California were mostly mixed-conifer or mixed-evergreen associations. In mixed-evergreen forests, evergreen hardwoods such as tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), California laurel (*Umbellularia californica*), and canyon live-oak (*Quercus chrysolepis*) formed a major part of the forest canopy, usually in association with Douglas-fir. The Simpson and Marin study areas in California also included large areas dominated by coastal redwoods and evergreen hardwoods.

Forest condition was highly variable among study areas, ranging from mostly young forests (< 60 years old) on 1 study area (SIM) to some study areas on federal lands (OLY, HJA, MAR, CAS) where >40% of the landscape was covered by mature (80-200 years old) or old-growth (>200 years) forests as described by Thomas et al. (1990). Although the types and amounts of disturbance differed among areas, all study areas were characterized by a diverse mixture of forest seral stages that were the result of historic patterns of logging, wildfire, windstorms, disease, and insect infestations. On some study areas (OLY, RAI), forest cover was also naturally fragmented by high elevation ridges covered by snow, ice, and alpine tundra.

Selection of study areas by the groups that participated in the analyses was based on many considerations, including logistics, funding, and land ownership boundaries. As a result, study areas were not randomly selected or systematically spaced. Nevertheless, we believe that the broad distribution of study areas on federal lands was representative of the overall condition of northern spotted owl populations on federal lands (Fig. 1) and some private lands. Because coverage of state and private lands was less extensive and management practices varied widely, our results likely were not applicable to all state and private lands.

METHODS

Data Analysis

The demographic parameters of interest in our analyses were age-specific survival probabilities (*N*), age-specific fecundity (*b*), and annual rate of population change (*8*). Data sets from each study area included a complete capture history of each owl banded during the study. Data were coded with sex and age (juveniles=0-1year old, S1=1-2 year old, S2=2-3year old, A=adult, S1+S2+A=non-juveniles) of owls when they were first banded. In some analyses we combined age classes (S1 + S2 + A) into a single “non-juvenile” class. We estimated productivity as the number of young fledged (NYF) by each female that was located each year.

We estimated annual rate of population change (*8*) from a file that included the sex, age, and capture histories of all territorial owls that met certain criteria (see Annual Rate of Population Change below). Prior to data analysis, we used an error-checking process similar to Franklin et al. (2004) to ensure that all data sets were accurate and formatted correctly.

Prior to analyzing data, we discussed and agreed upon a protocol for the analyses and developed *a priori* lists of models for estimation of survival (*N*), fecundity (*b*), and annual rate of population change (*8*). The *a priori* models were developed from biological hypotheses following the procedures described by Anderson et al. (1999). These *a priori* models differed somewhat by response variable and whether the analyses were on the individual study areas or part of a meta-analysis of all study areas combined. In all analyses, we examined time effects with models that had variable time (t), linear time (T), or quadratic time (TT) effects. We also included a barred owl covariate in the analyses of survival and fecundity, because we predicted that presence of barred owls would have a negative effect on demographic rates of spotted owls (Kelly et al. 2003). The barred owl covariate that we used was the proportion of spotted owl territories in which barred owls were detected each year (Appendix B). Although we recognized that the impacts of barred owls were more likely to occur at the territory level, the only data that were available for all of the study areas was this year-specific covariate. Thus, we included the presence of barred owls as an exploratory variable to determine if the effects were detectable with this coarse-scale covariate. For the meta-analysis of apparent survival, we also included a covariate for the potential effect of reproduction on survival during the following year (i.e. a cost of reproduction variable). We used the mean number of young fledged (NYF) per occupied territory per year to model this effect (Appendix C). In all meta-analyses, we developed models that grouped study areas into larger categories related to ecological regions, ownership, or latitude (Appendix A).

We used estimates of regression coefficients (\$) and their 95% confidence intervals as evidence of an effect on either fecundity or apparent survival by various factors or covariates. The sign of the coefficient represented a positive (+) or negative (-) effect of a factor or covariate, and the 95% confidence intervals were used to evaluate the evidence for \$< 0.0 (negative effect) or \$> 0.0 (positive effect). Because the choice of ″= 0.05 is somewhat arbitrary, the 95% confidence intervals were not used as a strict test of \$= 0.0 but for the strength of evidence for an effect.

Fecundity

We used the methods described by Franklin et al. (1996) to determine the number of young produced by resident female owls on each study area each year. We will not repeat those methods here except to note that field technicians used a standardized protocol to locate owls, determine their nesting status, and document the number of young that fledged (NYF) from the nest (Franklin et al. 1996). We conducted analyses on NYF per female or nest (also referred to as productivity), but to be consistent with previous analyses of spotted owl demography (Forsman et al. 1996, Franklin et al. 2004), results are reported as fecundity (number of females produced/female). We estimated fecundity as NYF/2, assuming a 1:1 sex ratio of young produced at birth. Our assumption of a 1:1 sex ratio was based on a sample of juveniles that were sexed from genetic analysis of blood samples (Fleming et al. 1996, Fleming and Forsman, unpublished data). We assumed that the owls sampled were a representative sample of the owls in each age class and that sampling was not biased towards birds that reproduced. We believe these assumptions were reasonable, because spotted owls stay on the same territories year-around and usually can be located even in years when they do not reproduce.

Fecundity on Individual Study Areas.—We used PROC MIXED in SAS (SAS Institute 1997) to fit a suite of models for each study area that included: (1) the effects of age (a), (2) linear or quadratic time trends, (3) the barred owl (BO) covariate (Appendix D), and (4) an even-odd year effect (EO). We included the even-odd year effect because a previous analysis (Franklin et al. 1999) suggested a cyclic biennial pattern to the number of young fledged, with higher reproductive rates in even-numbered years compared to odd numbered-years. A full set of models was developed for each study area before analyses began. Model ranking and selection of best models within study areas were based on minimum AICc (Burnham and Anderson 2002).

A plot of the variance-to-mean ratio within years for all study areas indicated that the variance of NYF was nearly proportional to the mean of NYF with some evidence of a reduction in variance at higher levels of reproduction. This plot was consistent with a truncated Poisson distribution, with owls seldom raising more than 2 young. Despite the integer nature of the data, the sample sizes were sufficiently large to justify the assumption of a normal distribution (see White and Bennetts 1996), as long as allowance was made for the dependence of the variation on the mean. We considered using Poisson regression for these data, but the normal regression model is less biased when Poisson assumptions are even modestly violated (White and Bennetts 1996). Consequently, we used the normal regression model for analyses of NYF.

We also reduced the effect of the variance-to-mean relationship by fitting models to the yearly mean NYF by age class. These means for each study area were modeled as:

PROC MIXED; MODEL MEAN_NYF = *fixed effects*.

Thus, residual variation was a combination of year-to-year variation in the actual mean and variation estimated around the actual mean and is approximately equal to:

$$\text{var(residual)} = \text{var(year effects)} + \text{var(NYF)}/n$$

where n = the number of territorial females checked in a particular year. We thought this approach was justified for a number of reasons. First, a variance components analysis on the raw data comparing spatial variance among territories to temporal variance among years showed the former to be small relative to the latter and other residual effects (see Results). Therefore, we concluded that ignoring spatial variance within study areas would not bias the results. Secondly, we were able to support the key assumption that the var(residual) was relatively constant because: (1) var(NYF)/n was small relative to var(year effects), (2) the total number of female owls sampled was roughly constant over time for each study area so that var(NYF)/n was roughly constant, and (3) fewer measurements were taken on subadult owls such that var(NYF)/n was also about constant even though var(NYF) may decline with increasing age class. These assumptions were verified by Levine's test for homogeneity of variances. Thirdly, we assumed that residual effects were approximately normally distributed, because, based on the central limit theorem, the average of the measurements will have an approximate normal distribution with large sample sizes even if the individual measurements are quite discrete. Lastly, covariates that operate on the study-area level (such as BO) are easily modeled.

Because there was no consistent pattern to the best fitting model among study areas, we used a non-parametric approach to estimate the mean NYF. First the mean NYF was computed for each year and age class, then these averages were averaged across years within each age class. The estimated standard error was computed by the standard error of the average of the averages across the years. This method gave equal weight to all years regardless of the number of birds actually measured in a year, and it did not force a model for changes over time. Essentially, it treated years as random effects with year effects being large relative to within-year sampling variation. Estimates weighted by sample sizes in each year were not substantially different.

Meta-analysis of Fecundity on All Study Areas.—We performed 2 meta-analyses of NYF data. In 1 analysis we used all 14 study areas and in the other we used the 8 monitoring areas (Lint et al. 1999). In both analyses, we used data from adult females because samples of 1- and 2-year-old owls were small. In addition, we analyzed NYF for the same geographic regions and ownership categories used in conducting the meta-analyses of survival and λ_{RJS} (Appendix A).

We used mixed models to perform meta-analyses on mean NYF per year for the same reasons specified above for the study area analyses. A particular region*year treatment combination was defined for each study area with owls within study areas as units of measure. Thus, the experimental units were study areas within region*year, which we used as a random effect in the mixed models. As ownership and ecological region apply at the study-area level rather than at the bird level, model selection was performed on average NYF by study area and year. We evaluated models that allowed for effects of ownership, geographic region, even-odd years, barred owls, linear and quadratic time trends, and variable time effects. Model rankings and selection of best models were based on minimum AICc (Burnham and Anderson 2002).

Estimation of Apparent Survival

We used Cormack-Jolly-Seber open population models (Cormack 1964, Jolly 1965, Seber 1965, Burnham et al. 1987, Pollock et al. 1990, Franklin et al. 1996) in program MARK (White and Burnham 1999) to estimate apparent survival of owls for each year (roughly from 15 June to 15 June). Owls that were not banded as juveniles were assigned to age classes based on plumage attributes (Forsman 1983, Moen et al. 1991, Franklin et al. 1996). We did not estimate juvenile survival rates because these estimates were confounded by emigration (Burnham et al. 1996, Forsman et al. 2002). In contrast, annual site fidelity of territorial owls was high (Forsman et al. 2002), so emigration was not a serious bias in survival estimates from territorial owls.

We used capture-recapture data to estimate recapture probabilities (*p*, the probability that an animal alive in year *t* +1 is recaptured, given that it is alive at the beginning of year *t*) and annual apparent survival probabilities (*N*, the probability that an owl survives from time *t* to *t*+1, given that it is alive at the beginning of year *t*. Our general approach to estimate survival rates was to: (1) develop *a priori* models for analysis, (2) evaluate goodness-of-fit and estimate an over-dispersion parameter ($\hat{c}$) for each data set, (3) estimate capture probabilities and apparent survival for each capture-recapture data set with the models developed in Step 1 using program MARK (White and Burnham 1999), (4) adjust the covariance matrices and AICc values with $\hat{c}$ to obtain QAICc values, and (5) select the most parsimonious model for inference based on QAICc model selection (Burnham and Anderson 2002). Additional detail on methods of estimation of survival from capture-recapture data from northern spotted owls are provided by Burnham et al. (1994, 1996) and Franklin et al. (1996). The statistical analyses were based on maximum likelihood theory and methods (Brownie et al. 1978, Burnham et al. 1987) and current philosophy of parametric statistical analysis of large, inter-related data sets (Anderson et al. 1999).

The goal of the data analysis and model selection process was to find a model from an *a priori* list of models that best fit the data and was closest to the truth based on Kullback-Leibler information (Burnham and Anderson (2002). Prior to model fitting we used the global model $\{N(\mathrm{s*t}), p(\mathrm{s*t})\}$ for adults to test each data set for goodness-of-fit to the assumptions of the Cormack-Jolly-Seber model. The global model included estimates of sex (s) and time (t) effects, plus the interaction between sex and time for both N and p. We used program RELEASE (Burnham et al. 1987) to test for goodness-of-fit to the Cormack-Jolly-Seber model and estimate overdispersion. Overdispersion in the data was estimated by $\hat{c} = P^2/df$ using the combined P^2 values and degrees of freedom (*df*) from Test 2 and Test 3 from program RELEASE (Lebreton et al. 1992). Estimates of $\hat{c}$ were used to inflate standard errors and adjust for the lack of independence in the data. We estimated capture probabilities and apparent survival with 56 *a priori* models that were developed during the protocol session (Tables 2, 3). Models, which included age, sex, time, time trends (linear and quadratic), and a barred owl covariate (Appendix B), were then fit to each data set to model apparent survival (Table 3).

We used maximum likelihood estimation to fit models and optimize parameter estimation using program MARK (White and Burnham 1999). We used QAICc for model selection (Lebreton et al. 1992, Burnham and Anderson 2002), which is a version of Akaike's Information Criterion (Akaike 1973, 1985; Sakamoto et al. 1986) corrected for small sample bias (Hurvich and Tsai 1989) and overdispersion (Lebreton et al. 1992, Anderson et al. 1994). We computed QAICc according to Burnham and Anderson (2002:66–70):

$$\mathrm{QAICc} = \frac{-2\ \log(\mathrm{Likelihood})}{\hat{c}} + 2K + \frac{2K(K+1)}{n_{ess} - K - 1} \quad ,$$

where the log(Likelihood) is evaluated at the maximum likelihood estimates under a given model, K is the number of estimable parameters in the model, $\hat{c}$ is the estimated quasi-likelihood variance inflation for overdispersion, and n_{ess} is the effective sample size (number of releases for the capture-recapture data). QAICc was computed for each candidate model and the best model for inference was the model with the minimum QAICc value. Two additional tools based on QAICc values were also computed for each model,) QAICc for model *i* (where) QAICc$_{\mathrm{i}}$ = QAICc$_{\mathrm{i}}$ - minQAICc) and Akaike weights (Buckland et al.1997, Burnham and Anderson 2002). Akaike weights were computed over a set of *R* models as:

$$w_i = \frac{e^{-\left(\frac{\Delta_i}{2}\right)}}{\sum_{r=1}^{R} e^{-\left(\frac{\Delta_r}{2}\right)}}$$

where)$_{\mathrm{i}}$ = the information lost in approximating full reality by model *i* (standardized by the best model) and w_i = the probability that model *i* is in fact the Kullback-Leibler best model (Burnham and Anderson 2002). Akaike weights were used to address model selection uncertainty and the degree to which ranked models were considered competitive. We used Akaike weights to compute estimates of time-specific, model-averaged survival rates and their standard errors for each study area (Burnham and Anderson 2002:162). We did this because there were often several competitive ( ) QAICc < 2.0) models for a given data set (Burnham and Anderson 2002).

For each study area, we used the variance components module of program MARK to estimate temporal ($\sigma^2_{\text{temporal}}$) process variation (White et al. 2002, Burnham and White 2002). This approach allowed us to separate sampling variation (variation attributable to estimating a parameter from a sample) in apparent survival estimates from total process variation. Process variation was decomposed into temporal (parameter variation over time) and spatial (parameter variation among different locations) components.

Meta-analysis of Apparent Survival.—The meta-analysis of apparent survival rates was based on capture histories of adult males and females from the 14 study areas. Apparent survival and capture probabilities were estimated with the Cormack-Jolly-Seber model using program MARK (White and Burnham 1999). The global model for these analyses was {ϕ(g*s*t) *p*(g*s*t)}, where g was study area, t was time (year), and s was sex. Goodness-of-fit was assessed with the global model in program RELEASE (Burnham et al. 1987), and the estimate of overdispersion, *c*, was used to adjust model selection to QAIC and to inflate variance estimates. We initially evaluated 6 models of recapture probability {*p*(g+t), *p*(r), *p*(g+s+t), *p*(r+s), *p*([g+t]*s), *p*(r*s)}with a general structure on apparent survival {N(g*t*s)} where r indicates the effect of reproduction in the current year. Using the model for *p* with minimum QAIC from the initial 6 models, we evaluated 13 additional models for apparent survival to test for various combinations of area, sex, time, barred owl effects (BO), and effects of reproductive output (r) (Table 4). The sex effect was then removed from the best model above to check for strength of the sex effect. Then, we ran 4 more models in which study area (group) effect was replaced with the group surrogates "ownership", "geographic region", "ownership*region", and "latitude" for a total of 27 models. Ownership referred to whether the area was privately owned, federally owned, or of mixed private and federal ownership (Appendix A). Each study area was classified into 1 of 5 geographic regions that incorporated geographic location and the major forest type in the study area (Appendix A). Latitude was a continuous variable measured at the center of each study area.

Annual Rate of Population Change (8)

One of the first topics we discussed during the protocol session was whether we should estimate the annual rate of population change (8) from estimates of age-specific survival and fecundity with the Leslie projection matrix (8_{PM}) (Caswell 2000) or the reparameratized Jolly-Seber method (8_{RJS})(Pradel 1996). The 8_{PM} method was used in the 1993 and 1998 demographic analyses of northern spotted owls (Franklin et al. 1996, 1999). The 8_{RJS} method, which uses direct estimation of 8 from capture-recapture data, was used in an exploratory manner in the 1998 analyses (Franklin et al. 1999) and was used in analyses of data from California spotted owls (*S. o. occidentalis*) (Franklin et al. 2004).

Estimates of 8_{PM} are computed from projection matrices using age-specific survival and fecundity for juvenile, subadult, and adult owls, assuming a stable age distribution (i.e., constant rates over time) over the period of study. The estimate of 8_{PM} represents the asymptotic growth rate of a population exposed to constant demographic rates over time, but it is not necessarily the best estimate of annual rate of population change on a study area for several reasons. First, there is asymmetry in the way movement is treated in vital rates representing gains or losses. In demographic studies of spotted owls, apparent survival rates are estimated using capture-recapture models, whereas fecundity rates are estimated from direct observation of productivity of territorial females. Population losses thus include both death and permanent emigration, whereas gains come solely from reproduction, as reflected by fecundity estimates. Second, λ_{PM} is an asymptotic value expected to result from the absence of temporal variation in the vital rates, whereas we know from previous analyses (Burnham et al. 1996, Franklin et al. 1999) that there is considerable temporal variation in both survival and fecundity of spotted owls. Thus, λ_{PM} is a theoretical, asymptotic rate assuming constant fecundity and survival rates over the period of study, whereas λ_{RJS} is an estimate of a rate that reflects annual variability in rates of population change. Third, values of fecundity may be positively biased if non-breeders or unsuccessful breeders are not detected as readily as successful breeders (Raphael et al. 1996). Lastly and most importantly, estimates of juvenile survival are negatively biased because of permanent emigration from study areas, which is of paramount concern for northern spotted owls. The Cormack-Jolly-Seber estimates of apparent survival can not distinguish between undetected emigrants and individuals that have died. To the extent that banded juveniles (or non-juveniles) emigrate from study areas, survive at least 1 year, and are never observed again, the estimates of survival will be negatively biased. As a result, estimates of λ_{PM} will be biased low (Raphael et al. 1996, Franklin et al. 2004). The strength of the λ_{RJS} method is that it takes into account the combination of gains and losses to the population by direct estimation from the capture-recapture data. Also, the interpretation of λ_{RJS} as a rate of change in the number of territorial owls on the study is clear and unambiguous. Because of these reasons, we used only the λ_{RJS} method to estimate annual rates of population change.

Pradel (1996) introduced a reparameterization of the Jolly-Seber model permitting estimation of $\lambda(t)$, the finite rate of population increase [defined by $N(t+1)/N(t)$ where $N(t)$ represents population size at time t] in addition to apparent survival (ϕ) and recapture probability (p). We used this method to estimate λ_{RJS} and determine whether populations were increasing (λ>1.0), decreasing (λ<1.0), or stationary (λ=1.0). Annual rates of population change, λ(t), were estimated directly from capture history data for territorial owls from areas that were consistently surveyed each year (Pradel 1996). For models that had a variable time structure (t) on λ, we used a random-effects model to estimate $\lambda(t)$ and its standard error. In addition to the ability to obtain time-specific estimates of λ_{RJS}, the models implemented in program MARK also allowed for constraints, such as linear (T) or quadratic (TT) time effects on λ_{RJS}.

Estimates of λ_{RJS} reflect changes in population size resulting from reproduction, mortality, and movement. The data used in the analyses included only territorial individuals of mixed age-classes (e.g., no differentiation between adults and 1-, or 2-year old owls). Thus, estimates of λ_{RJS} from any particular capture-recapture data set should correspond to changes in the territorial population within the area sampled. Gains in the territorial population can result from recruitment of owls born on the study area and from immigration of owls from outside the study area. Losses in the population result from mortality or emigration from the study area. To apply this method correctly, it is critical that the area sampled remains constant from year-to-year, coverage of the area is reasonably constant each year, and all areas or territories in the initial sample be visited during each subsequent year of study, regardless of recent occupancy status (e.g., even if no owls were detected on sites for several consecutive years). Observers on all study areas followed a set of survey protocols to assure these conditions (Franklin et al.

1996). In our analyses, there were 2 kinds of data sets for territorial owls, those for which all of the area within a study area was surveyed each year (density study areas or DSAs) and those for which specific owl territories within a large geographic region were surveyed each year (territorial study areas or TSAs). DSAs included TYE, NWC, HUP, and SIM, and TSAs included WEN, CLE, RAI, OLY, WRS, HJA, COA, KLA, CAS, and MAR. For both survey types, the interpretation of λ_{RJS} is the change in the number of territorial owls in the sampled area. We analyzed the data from DSAs and TSAs separately because the capture-recapture data were collected with different sampling protocols. We did not make direct comparisons of the λ_{RJS} from the 2 types of surveys, because DSAs were mostly in the southern part of the owl's range and TSAs in the northern portion; therefore, survey type and geographic area were confounded.

Annual Rate of Population Change for Individual Study Areas.—Although most areas sampled in TSAs were initially selected because they were occupied by owls or had been occupied by owls prior to the study, any bias towards occupied sites in early years of the study was eliminated, because we removed the first 2-5 years of data from each TSA and from 3 of the 4 DSA's for λ_{RJS} estimates (Appendix A). We did this to avoid any potential bias in estimates of λ associated with any artificial population growth attributable to the initial location and banding of owls that occurs in the first few years of a study. To evaluate whether study areas were saturated with territorial owls (i.e., were capable of population growth), we computed the proportion of territories in which owls were detected in the first year used to estimate λ_{RJS}. Mean estimates for the proportion of territories that were occupied the first year of estimation were 0.629 (range = 0.547–0.700) and 0.791 (range = 0.680–0.906) for DSAs and TSAs, respectively. This indicated there was room for population growth or decline for both types of survey areas. Once the data were truncated, boundaries of 8 study areas remained unchanged for the duration of the study, and 6 areas had a one-time increase in the study area to include areas that were added to the sample after the study was initiated (Appendix A). In the latter cases, owl territories located after the initial year of study were brought into the sample in a single expansion year, with any data prior to the expansion year removed from the capture histories of the owls that occupied those territories.

To estimate $\overline{\lambda}$ (average λ_{RJS}) and λ_{t} (year-specific λ) for each study area, we used the random effects module in program MARK (White et al. 2002). We fit 2 general λ_{RJS} models $\{(\phi(\mathrm{t})\ p(\mathrm{t})\ \lambda(\mathrm{t})\}$ and $\{\phi(\mathrm{s{*}t})\ p(\mathrm{s{*}t})\ \lambda(\mathrm{s{*}t})\}$ to the area-specific data. In some cases, study areas were expanded mid-way through the time interval. In these cases, we used group-effect models $[\{\phi(\mathrm{g{*}t})\ p(\mathrm{g{*}t})\ \lambda(\mathrm{g{*}t})\}$ and $\{\phi(\mathrm{g{*}s{*}t})\ p(\mathrm{g{*}s{*}t})\ \lambda(\mathrm{g{*}s{*}t})\}]$ to model parameters associated with pre-expansion areas differently than post-expansion areas. Regardless of the global models used, we used QAICc to choose the best of the initial models to proceed with the estimation of $\overline{\lambda}_t$ using the following random effects models: constant across time ($8.$), a linear time trend (λ_{T}), and a quadratic time trend (8_{TT}). The first 2 and last 8_{t} estimates were removed from the base model before we fit the 3 models to the data. This was done to eliminate potential biases due to: (1) a trap response, (2) a learning curve often exhibited by field crews on a new study area, or (3) capture probabilities differing between marked and unmarked birds early in each study (Hines and Nichols 2002). As with the survival analysis, we estimated overdispersion (c) for the λ_{RJS} data using program RELEASE and the global model $\{\phi(\mathrm{s{*}t})\ p(\mathrm{s{*}t})\ \lambda(\mathrm{s{*}t})\}$ for each study area.

Estimates of $\overline{\lambda}$ were generated from the best random effects model. In cases where a linear trend (T) or quadratic trend (TT) on λ was supported, we used the beta estimates from the random effects model and the midpoint of the time period of the study as the independent variable to estimate average λ_{RJS}. Standard errors for these estimates were developed using the Taylor series (i.e., "delta method"). We used the variance components module in program MARK to compute estimates of temporal process variation ($\sigma^2_{\mathrm{temporal}}$) for λ_{RJS} on each study area (White et al. 2002, Burnham and White 2002).

Meta-Analyses of Annual Rate of Population Change.—In addition to estimates of λ_{RJS} for each study area, we conducted 2 meta-analyses of λ_{RJS} in which we computed average estimates of λ_{RJS} for multiple study areas combined. One meta-analysis included the 10 TSAs and the other included the 4 DSAs. We used similar procedures in both analyses.

We evaluated goodness-of-fit for the global model {ϕ(g*t) p(g*t) λ(g*t)} using program RELEASE and estimated overdispersion as χ^2/degrees of freedom, as in other analyses. The meta-analysis of λ_t involved the fitting of models focusing on 3 different groups of study areas. The first grouping simply treated each of the study areas separately. The second grouping aggregated study areas by ownership and the third aggregated them by geographic region. For each of these groupings, 3 models for λ_t were fit to the data. Model {ϕ(g*t) p(g*t) λ(g*t)} was the most general model which included full study area by time interactions on all 3 parameters. Model {ϕ(g*t) p(g*t) λ(g+t)} represented the hypothesis that temporal variation in λ_t occurred in parallel among the different groups for shared years, suggesting similar responses to environmental factors of population growth. Model {ϕ(g*t) p(g*t) λ(t)} represented the hypothesis of no variation in λ_t among locations. Model {ϕ(g*t) p(g*t) λ(g)} represented area-specific population growth that did not vary from year to year. We also included the model {*N*(g*t) *p*(g*t) *8*(.)} reflecting constant *8* over areas and years. There were a total of 11 models fit to the data for each of the DSAs.

We attempted to fit the same models to the data from TSAs but the maximum likelihood estimates of *8* would not converge under models with many parameters. The most general model {*N*(g*t) *p*(g*t) *8*(g*t)} could not be fit to the data using a single data structure. Instead, we obtained estimates for this model by fitting a model to each group separately. Goodness-of-fit and model selection statistics were obtained using results of these individual analyses. None of the models retaining the general structure (g*t) on survival and capture parameters could be evaluated. Thus, we tried to fit models in which survival and capture parameters, as well as population growth rate, were grouped by ownership or by geographic region. Because of these numerical difficulties, our final results were limited to 5 models.

Estimates of Realized Population Change.—To provide an additional interpretation to the estimates of *8*(t), we converted them into estimates of realized population change using the methods described by Franklin et al. (2004). Annual realized changes in populations were estimated and expressed relative to the initial population size (i.e., in the initial year used for analysis). Thus, we focused on the ratio of the population size in year *t* to that in the initial year (i.e., $)_t = N_t/N_x$ where *x* is the initial year). Consequently, the estimates of realized change corresponded to the proportional change in the population over the time period for which the *8's* were estimated. Realized change ($)_t$) was estimated as:

$$\hat{\Delta}_t = \prod_{i=x}^{t-1} \hat{\lambda}_i$$

where *x* was the year of the first estimated 8_t. For example, if $\hat{\lambda}_t$ was 0.9, 1.2, and 0.7 for 3 time intervals, then $\hat{\Delta}_t$ would be computed as (0.9)(1.2)(0.7) = 0.756 indicating that the ending population was 75.6% of the size of the initial population. To compute 95% confidence intervals for $\hat{\Delta}_t$, we used a parametric bootstrap algorithm with 1000 simulations. Our approach was similar to that of Franklin et al. (2004) except that our 95% confidence intervals were based on the *i*th and *j*th values of $)_t$ arranged in ascending order where i = (0.025)(1,000) and j = (0.975)(1,000).

RESULTS

Fecundity

Individual Study Areas.—Estimates of fecundity were based on 10,902 observations of the number of young produced by territorial females. Most of the fecundity data were from territories that were occupied by adult females, which reflects the low frequency of territory occupancy and breeding attempts by 1- or 2-year old females (Table 5). For all areas, age was a primary factor that affected fecundity (Table 6). Mean fecundity was lowest for 1-year old females (0 = 0.074, SE = 0.029), intermediate for 2-year olds (0 = 0.208, SE = 0.032), and highest for adults (0 = 0.372, SE = 0.029). Fecundity of adult females was highest (>0.40) on the CLE, WEN, WSR, KLA, and MAR study areas, whereas fecundity was lowest (<0.30) on RAI, OLY, COA, and HUP.

Among the individual study areas, the model that was most frequently selected as best (*n* = 7) was female age + an even-odd year effect (a+EO), indicating high fecundity in even-numbered years and low fecundity in odd-numbered years with parallel changes among age groups (Fig. 2). This model also was within 2 AICc units of the best model for 3 other study areas (Table 6). The best models for 2 additional areas contained the similar effects: (a*EO) for RAI, and (a+EO+TT) for HJA. Thus, age and the even-odd year effects were important in explaining variability in fecundity for most areas, despite some weakening of the latter effect in recent years (Figure 2). The even-odd year pattern was most prevalent for adults during the 1990s. In the 3 areas for which EO was not an important factor, (a+T) was the top model for TYE and NWC, indicating linear changes in fecundity over time (see below). There were no factors (constant model) that affected fecundity on the MAR study area. The MAR study was initiated in 1998 about the time the even-odd year effect waned and had few owls in younger age classes, so it was not surprising that the simplest model was selected.

Our results indicate that changes in fecundity over the period of study was variable among study areas. Linear (T) or quadratic (TT) time trends were evident in the model selection results of NYF on 9 of the 14 study areas (Table 7). On 5 study areas (HJA, TYE, CAS, NWC, HUP), time trends were included in the best model, and on 4 areas (WEN, CLE, COA, SIM) time trends were in models <2 AICc units from the best model. All of these time effects on productivity were linear except for HJA, which was quadratic but stable overall. The time trends for 2 areas (TYE and HUP) were positive with $\hat{\beta} > 0.0$ (Table 7). In contrast, there was evidence for negative trends in fecundity on 5 study areas (CLE, COA, CAS, NWC, SIM) with the upper confidence intervals barely > 0.0 (Table 7). Fecundity appeared to be stable over the period of study on WEN, RAI, OLY, WSR, HJA, KLA, and MAR study areas.

The barred owl covariate (BO) was not a part of the best model structure for any of the study areas, but there were 9 study areas for which BO effects were included in competing ( ) AIC<2.0) models (Table 8). Of these, 5 (WEN, OLY, COA, NWC, SIM) had a negative association between fecundity and barred owl presence and 4 (TYE, KLA, HUP, MAR) had a positive relationship. Confidence intervals were generally large and most substantially overlapped 0.0 except for HUP and MAR for which the relation was positive. Results for these 2 areas were suspect, because barred owls were rare on both areas (detections on <5% of spotted owl territories) and because MAR had only 6 years of data. Northern study areas where barred owls were most common were not more likely to have competing models with the BO covariate; in fact, the reverse seemed to be true with 4 of 4 areas in California, 3 of 6 areas in Oregon, and 2 of 4 areas in Washington having BO models within 2 AICc units of the best model (Table 8). The best BO model for CLE, thought to be the area most affected by barred owl encroachment, was >2.5 AICc units from the best model. In summary, we were unable to show any negative effects of barred owls on spotted owl productivity with the time-specific covariate.

Variance Component Analysis.—Estimation of spatial (site to site), temporal (year to year), and residual variance on the territory-specific data indicated that spatial and temporal variance within all study areas was low relative to the other variance components (Table 9). With the exception of MAR, for which spatial variance was 12% of the total variability in NYF, spatial variability within all study areas was <8%. Temporal variation in NYF ranged from 0.054–0.227, but never accounted for >30% of the total variability. The largest proportion of temporal variation occurred in the data from OLY and CLE (28 and 23%, respectively), but the temporal variation for the other study areas in Washington was not greater than that for the 6 study areas in Oregon (Table 9). Three of the 4 study areas with the lowest (<10%) temporal variation were in California (NWC, SIM, and MAR). Residual variance was by far the greatest component of total variance (ranging from 68–92%) and was largely due to individual heterogeneity among owls. There was no discernable pattern of residual variance among study areas. Total variability ranged from 0.495 (HUP) to 0.969 (CLE), but again there was no discernable pattern to the magnitude of variability among study areas.

Meta-analysis of Fecundity.—The ranking of models in the meta-analysis of all 14 study areas and the 8 monitoring areas was nearly identical. There were differences between the 2 analyses only in the ordering of models with essentially no support (Akaike weights < 0.00); therefore we present the results for only the 14 study areas combined. The best model included additive effects of region and a time effect (region + t) and contained 55% of the weight of evidence (Table 10). Time trends (T) in fecundity were not supported by the meta-analysis; the best ranking trend model was (region + T) with an AIC weight of 0.000. Models that included ownership (O) effects also were ranked much lower than the best model (AIC weight = 0.015). Estimates of adult female fecundity by region, averaged over years, indicated that fecundity was highest for the mixed-conifer region in Washington and lowest for the Douglas-fir region of Washington and the Oregon coast (Table 11). Fecundity was intermediate for the Douglas-fir region of the Oregon Cascades, the mixed-conifer region of California and Oregon, and the redwood region of coastal California.

The even-odd year (EO) effect was not as important in the meta-analysis as it was in the analyses of individual study areas, but was apparent between 1990-2000 (Fig. 3). The higher ranking of the year-specific model (region + t) was likely due to the additional power from the combined data to detect individual year effects. This model also detected the waning of the even-odd year effect in more recent years and the variability in amplitude of the difference between even and odd years. There appeared to be a downward trend in the yearly fluctuations of fecundity (Fig. 3), but we were not able to verify this in our analysis.

Although the model that included the BO covariate was the second best in both meta-analyses, this was attributed primarily to the region and even-odd year effects in the model. The regression coefficient estimate for the BO effect for this model (all areas combined) was -0.404 (SE = 0.340). Thus the 95% CI on this effect was large (-1.069 to 0.262) and overlapped 0.0 substantially. In general, models containing the BO covariate were not highly ranked for both meta-analyses of fecundity.

Apparent Survival Rates

Individual Study Areas.—We used 4,963 banded non-juvenile spotted owls to estimate apparent survival rates, including 574 1-year old owls, 684 2-year old owls, and 3,705 adults (Table 1). The number of recaptures of marked owls was approximately 5 times the number of initial markings which resulted in 32,054 initial captures and recaptures. The overall P^2 goodness-of-fit for the global model from program RELEASE was 1600.03 with 925 degrees of freedom $\hat{c} = 1.73$, $p < 0.001$), indicating that there was good fit of the data to Cormack-Jolly-Seber open population models (Table 12). Estimates of $\hat{c}$ in the individual data sets ranged from 0.84–2.74 (Table 12) which indicated no to moderate overdispersion of recaptured owls and good fit of the data to the models. What little lack of fit that occurred was due to temporary emigration of owls from study areas with subsequent return in later years.

Annual estimates of recapture probabilities, p, were between 0.70–0.99 on most study areas (Appendix D). However, there were occasional years when $\hat{p} < 0.70$ on the WEN, RAI and OLY Study Areas in Washington and the KLA Study Area in Oregon (Appendix D). The most unusual case was a year on the OLY Study Area in which $\hat{p} = 0.26$ following a winter with record snowfall and a persistent snow on the ground during spring (Appendix D). The combination of high recapture probabilities along with high estimates of survival likely reduced any bias that may have been associated with heterogeneity of recapture probabilities (Pollock et al. 1990, Hwang and Chao 1995). The best model structure on recapture probabilities varied among study areas with 1 or more areas having effects of sex, reproductive output, presence of barred owls, time, or time trends (Table 13). For many study areas, there was an increasing time trend, *p*(T), in recapture probabilities in 1 or more of the competitive models ( ) QAICc < 2.0), indicating that field biologists got better at locating and re-observing banded owls as the studies progressed. Recapture probabilities of owls were higher in years with higher productivity, and males were generally easier to re-observe than females.

The best model structure for apparent survival, *N*, was not consistent among study areas (Table 13). Age, sex, presence of barred owls, time, or time trends were important effects on apparent survival in 1 or more of the best models. Age of territorial owls was important on 8 of the 14 study areas (Table 13). On average, apparent survival were higher for older owls with rates ranging from 0.42–0.86 for 1-year olds (0 = 0.68, SE = 0.054), 0.63–0.89 for 2-year olds (0 = 0.81, SE = 0.030), and 0.75–0.92 for adults (0 = 0.85, SE = 0.016) (Table 13). Apparent survival rates for adults were >0.85 for most study areas except WEN, WSR, MAR, and RAI. Apparent survival rates were different between males and females for only the MAR study area, and the effect of barred owls was important only for the WEN and OLY study areas (also see below).

The best or competitive ()QAICc < 2.0) models for apparent survival suggested a linear or quadratic time effect for 11 of the 14 study areas (Table 14, Appendix E). There was strong evidence for declines in apparent survival on 5 study areas (WEN, CLE, RAI, OLY, NWC) (Table 14). In addition, there was evidence for a slight decrease in apparent survival on COA during the last 5 years of study (Table 14, Fig. 4b). Declines in apparent survival were most evident in Washington (Fig. 4a) where all $ estimates were negative and 95% confidence intervals for 3 (WEN, RAI, OLY) of the 4 study areas did not overlap zero. In addition, apparent survival for owls on the WEN and RAI areas during the latter years of the study were <0.80 which were the lowest rates recorded for the 14 study areas. In Oregon, there were no time trends in apparent survival rates for 4 (HJA, KLA, WSR, CAS) of the 6 study areas (Table 14, Fig. 4b). Apparent survival rates for COA increased slightly during the early years of the study, then decreased slightly from 1997-2003. In contrast, apparent survival rates on the TYE study area decreased during the initial years of the study, then increased from 1995-2003. In California, there was a significant linear decline in apparent survival on the NWC study area (Fig. 4c) and evidence of a slight decline on the SIM area. There was little evidence of time trends in apparent survival on the HUP and MAR study areas.

Meta-analysis of Adult Apparent Survival.— We used 5,342 and 3,702 encounter histories (initial captures + recaptures) in the meta-analysis of apparent survival for all 14 study areas and the 8 monitoring areas, respectively. Estimates of overdispersion from program RELEASE were <2.0 for the 14 study areas combined and the 8 monitoring areas ($\hat{c}$ = 1.730 and 1.738, respectively, Table 12) indicating good fit of the data to the Cormack Jolly-Seber open population models. Because the results for all 14 study areas and that of the 8 monitoring areas were similar, we only report the results for all the study areas.

The best model for the meta-analysis of the 14 study areas was {*N*(region + t) *p*(g + t + s)} with 55 parameters. This model indicated both regional and variable time effects on apparent survival, and study area, time, and sex effects on recapture probabilities (Table 15). This model accounted for 78% of the weight of evidence (Akaike weight) among all of the models, so it was strongly supported by the data. There was no evidence of a sex effect on survival as noted by the differences in QAICc for models {*N*(g + t) *p*(g + s + t)} and {*N*(g + t + s) *p*(g + s + t)} (Table 15). The highest ranked model with a sex effect on *N* was {*N*(g + t + s) *p*(g + t + s)}with 64 parameters; this model had a) QAICc of 6.45 and an Akaike weight of only 0.031. Similarly, there was little evidence of latitude or ownership effects in the meta-analysis of survival;) QAICc values for models *N*(latitude + t) and *N*(ownership + t) were >12.00, suggesting that latitude and ownership were not good surrogates for the study area effect in the highest ranked model. Because of the high Akaike weight of the top model, it was used to estimate apparent survival of adults (Fig. 5). This figure suggests a downward trend in survival with time; however, the year-to-year variation was so large that time trend models did not rank high in the list of models (Table 15). As a result, we fit 2 *a posteriori* models {*N*(region * T) *p*(g + t + s)} and {*N*(region + T) *p*(g + t + s)} to the data to test for a time trend in apparent survival. Because {*N*(region * T) *p*(g + t + s)} with 44 parameters was the more highly ranked of these 2 models (Table 15), we investigated the interaction between region and time trends (Fig. 6). This relation indicated that the major downward trends in survival were taking place in the mixed-conifer and Douglas-fir regions of Washington. This result was consistent with the results of individual study areas where we found declines in apparent survival rates for all of the study areas in Washington.

Effects of Reproductive Output on Survival.—The) QAICc for the highest ranked model that included the reproductive effect *(r)* was 18.40 suggesting that it had little effect on survival. However, this value applies to differences among models and not necessarily the importance of individual variables in the model. Consequently, we examined the estimates of the individual variable effects, $ estimates, and their confidence intervals in the best model where the *r* effect occurred. Results from this analysis suggested a cost of reproduction on survival based on model {*N*(region + *r*) *p*(g + t + s)} (Table 15). The $ estimate of the *r* coefficient for this model was ! 0.257 (95% confidence interval = ! 0.432 to ! 0.082). Similarly, the estimate of $ for the *r* coefficient for the same model for the 8 monitoring areas was ! 0.292 (95% confidence interval = ! 0.507 to ! 0.078). These results indicated that high reproductive rates in 1 year were followed by lower survival rates during the following year, but this effect was found in just a few regions as shown by model {*N*(region * *r*) *p*(g + t + s)}. The strength of this relationship was greatest in the more northern latitudes and higher elevation study areas, particularly the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir zone of the Oregon Cascades (Table 16). This effect, if any, was small for study areas in California and the mixed-conifer and coastal Douglas-fir regions in Oregon.

Effects of Land Ownership.—Model {*N*(ownership + t) *p*(g + t + s)} with 52 parameters had a) QAICc of 13.43, and the 95% confidence intervals for the estimate for this effect included 0.0 (Table 15). Similarly, the model with land ownership in the meta-analysis on the 8 monitoring areas {*N*(ownership + t) *p*(g + t + s)} had 45 parameters and a) QAICc of 11.55, and the 95% confidence interval for this effect included 0.0. Thus, there was little evidence that land ownership was an important predictor of apparent survival rates in the meta-analyses.

Effects of Barred Owls in Analyses of Individual Study Areas.—In the analysis of the 14 individual study areas, we found a negative effect of barred owls ($\hat{\beta}$ = !6.75, 95% CI = !11.65 to !1.86) on recapture probabilities (*p*) of spotted owls for only the Warm Springs (WSR) study area. The effects of barred owls on recapture probabilities was positive for some areas, opposite to what we hypothesized. In contrast, we found strong evidence for a negative effect of barred owls on apparent survival on the OLY and WEN study areas (Table 17); estimates of $ and 95% confidence intervals for the 2 areas were !4.24 (!7.83 to !0.65) and !4.69 (-7.32 to !2.07), respectively. There also was some evidence for a negative effect of barred owls on apparent survival on the CLE, HJA, and NWC study areas, as models with the barred owl effect were competitive with the top models. Results for the Rainier study areas suggested that barred owls had a positive effect on spotted owl survival, but we believe this result was spurious. The best model of survival for Rainier, N(T), was 10.86) AICs better than N(BO). In addition, the barred owl covariate for this area was a quadratic function (Appendix B), a much different trend than that for the other study areas. The evidence for the effects of barred owls on survival of spotted owls on the remaining study areas was weak (2.0 <) QAICc < 3.0) to negligible () QAIC > 3.0).

Effect of Barred Owls in the Meta-analysis of Survival.—The barred owl covariate was not a good predictor of time variation in apparent survival in the meta-analysis of the 14 study areas. The) QAICc value for the best model containing barred owls {N(g * BO + s) *p*(g + t + s)} for this analysis was 23.37 (Table 15). This analysis suggested that the effects of barred owls differed by study area with 9 negative and 5 positive estimates of $ (Table 18). There was strong evidence of a negative effect of barred owls on apparent survival for WEN and OLY and some evidence of a negative effect for CLE. In contrast, there was evidence of a positive effect of barred owls on apparent survival for CAS, the opposite of our original hypothesis. This may be a spurious result as the occurrence of barred owls at spotted owl territories on the CAS study area was <10% during most of the study period (Appendix B). Confidence intervals for the effect of barred owls ($\$$) broadly overlapped zero for the remainder of the study areas indicating little evidence of an effect. Study areas in California had the lowest occurrence of barred owls at spotted owl territories (<5%), so the potential effect of barred owls on these study areas was minimal compared to study areas farther north, where barred owls were detected on many spotted owl territories (Appendix B).

Annual Rate of Population Change, 8

Individual Study Areas.—We used 4,963 banded territorial owls to estimate annual rates of population change (8_{RJS}). Estimates of overdispersion (c) in the capture-recapture data ranged from 0.690–3.02 (Table 12) indicating reasonable fit of the data to the Cormack-Jolly-Seber models for most data sets. Estimates of 8 could not be computed for the MAR study area because there were too few years of capture-recapture data for that area.

Model selection indicated that the sex- and time-specific model $\{N(\mathrm{g}{*}\mathrm{t})\ p(\mathrm{g}{*}\mathrm{t})\ 8(\mathrm{g}{*}\mathrm{t})\}$ was not important for any of the study areas; therefore we used the time-specific model $\{N(\mathrm{t})\ p(\mathrm{t})\ 8(\mathrm{t})\}$ for estimating temporal process variation (Table 19). Estimates of 8_{RJS} ranged from 0.896–1.005 for the 13 areas, and all but 1 (TYE) of the estimates were <1.0, suggesting population declines for most areas. There was strong evidence that populations on the WEN, CLE, WSR, and SIM study areas declined during the study (Table 19, Fig. 7), and there also was evidence that populations on the RAI, OLY, COA, and HJA study areas were decreasing. Precision of the λ_{RJS} estimates for RAI and OLY were poor and not sufficient to detect a difference from $\lambda = 1.00$. Moreover, the estimate of λ_{RJS} for RAI (0.896) was the lowest of all of the areas. Populations on TYE, KLA, CAS, NWC, and HUP appeared to be stationary during the study, but there was some suggestion that the last 3 were declining ($\hat{\lambda}_{\text{RJS}} < 1.00$) also. The weighted mean $\hat{\lambda}_{\text{RJS}}$ for all of the study areas was 0.963 (SE = 0.009, 95% CI = 0.945–0.981) which suggested a 3.7% decline per year for all the study areas over the period of study.

Of the 8 monitoring areas, there was evidence that populations were declining on CLE, COA and HJA based on 95% confidence intervals that did not overlap 1.0 or barely included 1.0. The remainder of the areas had confidence intervals that substantially overlapped 1.00, so we could not conclude that those populations were declining. The weighted mean $\hat{\lambda}_{\text{RJS}}$ for the 8 monitoring areas was 0.976 (SE = 0.007, 95% CI = 0.962–0.990) which suggested an overall decline of 2.4% per year. The weighted mean $\hat{\lambda}_{\text{RJS}}$ for the other 6 study areas was 0.942 (SE = 0.016, 95% CI = 0.910–0.974), suggesting a decline of 5.8% per year..

Precision and Variance Components.—Precision of the estimates was good for most study areas; coefficients of variation ranged from 1.2–6.1% with a mean of 2.6% (Table 19). Precision of the estimates for RAI, OLY, CAS, and KLA was lower than those for the other areas, which resulted in wider confidence intervals and lower power to detect a difference in λ from 1.0. Precision of the estimates was generally higher for the density study areas than the territory-specific study areas, possibly because 2 of the density study areas (TYE, NWC) were the longest studies in the sample of areas. Results of the variance components analysis provided little evidence of temporal variability for the CLE, OLY, COA, HJA, WSR, NWC, and HUP study areas (Table 19). Estimated temporal variability was highest for the OLY, CAS, and TYE study areas, but all confidence intervals included zero.

Meta-analysis of the Four Density Study Areas.—The estimate of overdispersion (c) for this analysis was 1.54 indicating a good fit to the Cormack-Jolly-Seber model and, hence, to the Pradel (1996) model. The model with the lowest QAIC for this analysis was {N(g*t) p(g*t) 8(.)} with 113 parameters, which indicated that λ(t) did not differ among the 4 study areas or over time (Table 20). This model received 37% of the weight of evidence, but there were 3 other models that received weight. Those models included {N(g*t) p(g*t) 8(region)}; {N(g*t) p(g*t) 8(ownership)}; and {N(g*t) p(g*t) 8(g)} with Akaike weights of 0.283, 0.244, and 0.098, respectively. Neither the more general model {N(g*t) p(g*t) 8(g*t)} with full time by study area interaction, nor the model {N(g*t) p(g*t) 8(g+t)} with parallel changes in λ(t) over time received any support. The estimate of 8_{RJS} from the best model was 0.988 (SE = 0.006) with a 95% confidence interval of 0.977–0.999.

The results from model {N(g*t) p(g*t) 8(g)}indicated that there are slight differences among the 4 study areas and time effects (Fig. 7). The $\hat{\lambda}$(t) associated with the different geographic regions from model {N(g*t) p(g*t) 8(region)} indicated slightly higher $\hat{\lambda}$(t) for the Douglas-fir region on the Oregon Coast (TYE), lower $\hat{\lambda}$(t) for the mixed-conifer region of California (NWC, HUP), and lowest $\hat{\lambda}$(t) for the redwood region of the California coast (SIM). The $\hat{\lambda}$(t) associated with different ownership categories from model {N(g*t) p(g*t) 8(ownership)} indicated slightly higher $\hat{\lambda}$(t) for mixed ownership lands (TYE), followed by federal (NWC), then by private (HUP, SIM) lands. Confidence intervals for these $\hat{\lambda}$(t) overlapped substantially, and the $\hat{\lambda}_{\text{RJS}}$ for NWC and HUP were similar.

Meta-analysis of Territory-specific Study Areas.—The estimate of overdispersion for this analysis was 1.621 indicating relatively good fit to the Cormack-Jolly-Seber model and, hence, the Pradel (1996) model. The model with the lowest QAIC was {*N*(g*t) *p*(g*t) *8*(g*t)} which indicated that the annual rate of population change varied among study areas and years and that the change over time was different for the study areas (i.e. a strong interaction among areas) (Table 20). This model accounted for 100% of the model weight and was a much better fit to the data than the next best model {*N*(g*t) *p*(g*t) *8*(ownership+t)}. As noted in the *Methods*, this analysis was hampered by numerical problems in fitting models to this large and complicated data set that included different starting and ending times and expansion areas in some studies. Among the small set of models that could be fit to the data, the most general model was the only one receiving any support. Grouping the study areas by ownership or region did not produce models that received any support (Table 20). This limited meta-analysis thus provided little reason to combine the area-specific analyses and suggested that inferences about population change should be based on individual study areas. A plot of the annual rates of population changes for these areas from model {*N*(t) *p*(t) *8*(t)} clearly shows that changes in $\hat{\lambda}$(t) over time were quite different among study areas (Fig. 8).

Estimates of Realized Population Change.—Estimates of realized population change represented the trend in numbers over the entire period of study for each of the 13 study areas (Fig. 9). These estimates were based solely on the estimates of *8*(t) and did not require estimation of annual population size, *N*(t). The trends represent the ratio of the population size in each focal year, expressed relative to the population in the first year. For example, if there were 100 owls on the CLE study area in 1994 and 54 in 2002, then the population in 2002 would be only 54% of the 1994 population. Based on this interpretation, there was strong evidence that populations on the CLE, WEN, OLY, RAI, WSR, HJA, COA, and SIM study areas declined during the study (Fig. 9a-c). Estimated population declines on the CLE, WEN, RAI, and WSR study areas were substantial over the last decade where population sizes were only 50-70% (30-50% decline) of the initial populations. Declines on the OLY, HJA, COA, and SIM study areas were not as great but are noteworthy; population sizes in 2002 were approximately 70-80% (20-30% decline) of the initial populations on those areas. The decline in the population on HJA appeared to occur during 1992-93, whereas the decline on COA occurred during the last 4 years of the study (Fig. 9c). There appeared to be a decline in the population on the NWC study area, but precision was insufficient to detect a difference from 8= 1.0 (Fig. 9a). In contrast, populations on the KLA, TYE, CAS, and HUP study areas remained relatively stationary, as confidence intervals around the)s overlapped 1.0 substantially. There were not enough years of data for MAR to assess population trends with estimates of realized population change.

DISCUSSION

This study is the fourth meta-analysis of demographic rates of northern spotted owls in the last 2 decades. The first of these analyses included only 5 study areas common to this study (OLY, TYE, HJA, CAS, NWC) and a limited number of years of data (Anderson and Burnham 1992). The major findings of that analysis were that annual survival rates of adult females had declined significantly, and populations of territorial females had declined an average of 7.5% per year from 1985–91. The second analysis was conducted in 1993 and included 11 study areas, 6 of which were new to the previous study (Burnham et al. 1996, Forsman et al. 1996). The 4 major findings of the second analysis were: (1) fecundity rates varied among years and age classes, with no increasing or decreasing trends over time, (2) survival rates were dependent on age and there was a decreasing trend in adult female survival (i.e., an accelerated rate of female mortality), (3) the annual rate of population change, 8_{PM}, was significantly <1.0 for 10 of 11 areas, and (4) the average rate of population decline was 4.5% (Burnham et al. 1996). The most alarming result of their study was the decline in adult female survival, because the population projection matrices used to estimate 8_{PM} are most sensitive to changes in adult female survival (Lande 1988, Noon and Biles 1990). The third analysis was conducted in 1998 and included 15 study areas (Franklin et al. 1999). Results of this analysis indicated that apparent survival of adult females varied among years, but did not exhibit a negative trend. Thus, the negative trend in apparent survival observed by Burnham et al. (1996) had apparently stabilized during the time between the second and third meta-analyses. Fecundity also varied among years but did not exhibit any consistent linear trend (Franklin et al. 1999). Based on estimates of demographic parameters averaged across study areas, Franklin et al. (1999) estimated an overall 8_{PM} of 0.961 (Leslie matrix models), which indicated a 3.9% decline per year in the population of territorial females. This estimate included an adjustment to juvenile survival rates due to emigration based on a sample of radio-marked juveniles from 3 study areas (see Forsman et al. 2003).

Coincident with the release of the results of the first 2 meta-analyses, the Final Draft Recovery Plan for the Northern Spotted Owl was released (USDI 1992). The final draft recovery plan was soon followed by the Northwest Forest Plan which was developed to conserve habitat for spotted owls and other species of plants and animals associated with late-successional forests

(FEMAT 1993, USDA and USDI 1994). This Plan, and the Record of Decision that followed, established a network of late-successional reserves to protect spotted owl habitat and was based on the reserve design developed for spotted owls by the Interagency Scientific Committee (Thomas et al. 1990). The reserve design in the Northwest Forest Plan excluded large areas of late-successional forests from timber harvest and provided an ad hoc test of the effect of habitat preservation and restoration on population trends of spotted owls. Although no cause-and-effect could be established, results from the third demographic analysis indicated that the declining trends in owl populations and adult female survival in earlier analyses were reduced or stabilized (Franklin et al. 1999).

Before we provide an overview of the results of this study, we must ask: *what is the frame of reference and what kind of inferences can we make from the results of the present study?* From a statistical standpoint, a formal inference can be made only from the sample of marked and recaptured owls to the population of owls on the study areas in which the marked owls were located. Although the 14 study areas covered a large latitudinal as well as elevational gradient, they were not selected randomly. Consequently, the results of our analyses can not be considered representative, by virtue of the study design, of demographic trends of northern spotted owls throughout their entire range. For example, there were no study areas in the northern Coast Range of Oregon, coastal mountains of southwestern Washington, nor the California Cascades province. However, spotted owl populations in those areas were so low that demographic studies of the type we report here would not be possible. Nevertheless, our 14 study areas were large and covered much of the owl's geographic range, including a variety of land ownerships (private, tribal, mixed private and federal, federal lands) and management strategies. Consequently, we believe that our results are representative of most populations of northern spotted owls on federal lands in the United States. In the following sections, we discuss the status and trends in fecundity, apparent survival, and annual rate of population change. This is followed by a discussion of some of the characteristics of spotted owl populations on the individual study areas and the possible causes for the recent population declines.

Fecundity

Our results indicate that there was substantial annual variation in fecundity on most study areas with a biennial cycle of high fecundity in even-numbered years and low fecundity in odd-numbered years. However, this cycle was not apparent on at least 4 study areas, and it waned in the latter years of the study. There also were differences among age classes with highest fecundity for adult (>3 yrs.) owls, lower fecundity rates for 2-year olds, and very low fecundity for 1-year old owls. In addition, we found that time trends in fecundity rates varied among study areas. Fecundity was slightly increasing on TYE and HUP; stable on WEN, RAI, OLY, WSR, HJA, KLA, and MAR; and decreasing on CLE, COA, CAS, NWC, and SIM (Table 21). Our meta-analysis of fecundity indicated differences among regions and substantial annual variability with no apparent time trend. Spotted owls in the mixed-conifer region of Washington (CLE, WEN) had the highest fecundity rates among all study areas.

The high temporal variability in fecundity and the biennial cycle of high and low years was consistent with results of previous meta-analyses on northern spotted owls (Burnham et al. 1996, Franklin et al. 1999). This high temporal variability agrees with general predictions for life history patterns of long-lived species (Gaillard et al. 1998, Pfister 1998) and is typical of reproductive patterns in many species of northern hemisphere owls (Houston and Francis 1995, Rohner et al. 1995, Rohner 1996, Brommer et al. 2002). Temporal variability in productivity was probably related to climatic factors, prey abundance, or both (Franklin et al. 2000, Rosenberg et al. 2003). Climatic models explained all of the temporal variation in fecundity in a population of northern spotted owls in northern California (Franklin et al. 2000), which was due to a negative effect of precipitation on reproductive output during the late nesting period. Other studies of northern spotted owls have shown a negative effect of precipitation on fecundity during the preceding fall and winter (Wagner et al. 1996) or during the nesting season (Zabel et al. 1996, Olson et al. 2004). Mean fledgling production was negatively correlated with precipitation during the nesting season for California spotted owls (*S. o. occidentalis*) in both oak woodlands and conifer forests (North et al. 2000). In contrast, reproductive output of Mexican spotted owls (*S. o. lucida*) in the xeric regions of Arizona and New Mexico was positively related to precipitation during the monsoon season in the previous year (Seamans et al. 2002). They suggested that this response was due to an increase in plant growth that resulted in an increase in small mammals that were used as prey (Seamans et al. 2002). The potential influence of prey abundance on annual variation in reproduction in northern spotted owls has not been well studied. In the Oregon Cascade Mountains, Rosenberg et al. (2003) found a positive correlation between productivity of northern spotted owls and the abundance of deer mice (*Peromyscus maniculatus*) during the nesting season; however, deer mice were not the most important prey in the owl's diet, so this might not have been a cause-and-effect relationship. Similarly, Ward and Block (1995) described a year of high reproduction by Mexican spotted owls in southern New Mexico that was associated with an irruption of white-footed mice (*Peromyscus leucopus*), one of their primary prey species. The relation of spotted owl reproduction to prey abundance needs further study throughout the range of all 3 subspecies.

The effects of female age on fecundity of northern spotted owls has been well documented (Burnham et al. 1996, Franklin et al. 1999) with older females occupying most of the territories and responsible for most of the productivity in any given year. Our estimates of mean fecundity for 1- and 2-year olds and adults (0 = 0.074, 0.208, 0.372, respectively) were similar to those (0 = 0.068, 0.205, 0.339, respectively) reported by Burnham et al. (1996) for many of the same study areas. Similar differences in fecundity among age groups have been reported for California spotted owls (Blakesley et al. 2001) and Mexican spotted owls (Seamans et al. 1999, 2001). Our estimate of mean adult fecundity (0 = 0.372, SE = 0.029) was comparable to estimates for other spotted owl populations. For example, estimates of mean fecundity for the California spotted owl include 0.291 (SE = 0.33) for Lassen National Forest (Blakesley et al. 2001) and 0.400 (SE = 0.005) for the Eldorado National Forest (Seamans et al. 2001). Mean fecundity estimates for adults from 2 populations of Mexican spotted owls were 0.494 (SE = 0.022) and 0.380 (SE = 0.019) (Seamans et al. 1999). The highest adult fecundity rates in our study were 0.574 (SE = 0.069), 0.530 (SE = 0.056) and 0.491 (SE = 0.058) for the CLE, MAR and WEN study areas, respectively. CLE and WEN were in mixed-conifer forests east of the Cascade crest in Washington, and fecundity for these 2 areas were the highest rates recorded for northern spotted owls. The reasons for these high fecundity rates in the mixed-conifer forests of Washington may include a higher diversity or biomass of prey. For example, Lehmkuhl (unpublished data) has found higher abundance of northern flying squirrels on the eastern slope of the Cascade Mountains in Washington in comparison to estimates reported by Carey et al. (1992) for western

Washington. The higher fecundity of spotted owls in eastern Washington also may be a compensatory response to lower survival rates on these areas (see below). The high fecundity rates for MAR are believed to be due to consistent breeding success among years (no even-odd year effects), mild weather, and abundant prey (Willy 1992).

We found that time trends in fecundity rates were variable among study areas, but the reasons for these differences were unknown. We suspect that this variation was due to regional or local variation in weather and prey abundance, but an analysis of these effects was beyond the scope of this study. Contrary to our *a priori* hypothesis, there was no evidence for a negative effect of barred owls on spotted owl fecundity. This result agrees with a previous study in which there was little evidence that fecundity of spotted owls was influenced by the presence of barred owls (Kelly 2001). In contrast, Olson et al. (2004) found a negative effect of barred owls on fecundity of spotted owls with a territory-specific approach on the TYE study area. Kelly (2001) cautioned that surveys of territorial owls may not detect spotted owls that have been displaced by barred owls, which, in turn, would not reflect the real impact of barred owls on fecundity of spotted owls. In addition, the covariate we used for the effect of barred owls was a coarse-scaled, year-specific variable and lacked the specificity to individual territories that may be necessary to fully evaluate the effect of barred owls on spotted owl fecundity. This, along with the small sample of barred owls in some study areas (especially California), may account for some of the counter-intuitive results we observed, particularly the positive relation between barred owls and fecundity on 2 of the California study areas.

Apparent Survival

Our analyses of data from individual study areas indicated that apparent survival differed among age classes for most areas, were declining on 5 (WEN, CLE, RAI, OLY, NWC) of the 14 areas (Table 21), and were negatively associated with the presence of barred owls on 2 (WEN, OLY) areas. Apparent survival of males and females were similar throughout most of the range of the subspecies; only owls on the southernmost study area (MAR) exhibited sex-specific survival rates. We believe that the reason for this result was the small sample size for this area. In the meta-analysis of apparent survival, we found differences among ecological regions and changes over time with a downward trend in apparent survival in the mixed-conifer and Douglas-fir regions of Washington. The meta-analysis also indicated a negative correlation between reproductive output and survival rates the following year (discussed in more detail below), but this effect was limited to the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir region of the Oregon Cascade Mountains.

Estimates of apparent survival of territorial owls in our study ranged from 0.750&0.913 for adults, 0.626&0.890 for 2-year olds, and 0.415&0.817 for 1-year olds. These survival rates were generally comparable to those reported by Burnham et al. (1996) and Franklin et al. (1999) for some of the same study areas at an earlier date. Estimates of apparent survival of adult California spotted owls on 5 areas ranged from 0.813–0877 (SE = 0.015–0.020) and were similar to ours (Franklin et al. 2004). Our estimates of adult survival were comparable to or higher than estimates for adult California spotted owls in Lassen National Forest (0 = 0.827, SE = 0.008) (Blakesley et al. 2001) and Eldorado National Forest (0 = 0.795, SE = 0.006) (Seamans et al. 2001, Franklin et al. 2004), and for adult Mexican spotted owls in Arizona (0 = 0.814, SE = 0.003) and New Mexico (0 = 0.832, SE = 0.015) (Seamans et al. 1999). Our results and those of the authors above, indicate that spotted owls have evolved a life history strategy throughout their range of high adult survival with low annual variability, coupled with high annual variability in fecundity. Because spotted owls inhabit variable environments, high survival rates allow individuals to retain territories and persist through periods of less favorable weather conditions to reproduce in later years. This strategy has been referred to as "bet hedging", where natural selection favors adult survival at the expense of present fecundity if recruitment of offspring is unpredictable from year to year (Stearns 1976, Franklin et al. 2000). High adult survival is also important, because sensitivity analyses on population dynamics of northern spotted owls indicate that annual rates of population change are most sensitive to changes in adult survival (Noon and Biles 1990, Lande 1991, Blakesley et al. 2001).

Our results indicated that apparent survival rates were stable on 9 (COA, HJA, WSR, TYE, KLA, CAS, HUP, SIM, MAR) study areas, but there was strong evidence for declines in apparent survival on 5 study areas (WEN, RAI, OLY, CLE, NWC) (Table 21). Results of the meta-analysis also indicated a significant decline in survival for the mixed-conifer and Douglas-fir regions of Washington which included the WEN, CLE, OLY, and RAI study areas. Declining survival rates were reported in a meta-analysis for some of these same populations in an earlier publication (Burnham et al. 1996), but these declines appeared to have stabilized in a more recent meta-analysis (Franklin et al. 1999). The reasons for these declines in apparent survival are not readily apparent but may include loss of habitat due to timber harvest or wildfire, changing weather patterns, declines in prey abundance, and/or increasing competition with barred owls (see below).

Annual Rate of Population Change, 8

Our decision to use the reparameterized Jolly-Seber method (Pradel 1996) to estimate annual rates of population change (8_{RJS}) was a departure from most demographic analyses on northern spotted owls (Anderson and Burnham 1992, Burnham et al. 1996), California spotted owls (LaHaye et al. 1992, Blakesley et al. 2001) and Mexican spotted owls (Seamans et al. 1999, 2002). Consequently, our results are most comparable to those of Franklin et al. (1999, 2004), who also used the reparameterized Jolly-Seber method. Most of the earlier studies used Leslie matrix models to estimate 8_{PM} (Caswell 2000) but cautioned that the estimates were likely biased low. This bias was due to the fact that estimates of juvenile survival for northern spotted owls from Cormack-Jolly-Seber open population models are negatively biased (Raphael et al. 1996). This assessment was based on the realization that mortality is confounded with emigration in estimates of apparent survival from open population models, and it is well known that juvenile spotted owls often disperse long distances from their natal areas (Forsman et al. 2002). For this reason and others mentioned in the methods section (see also Franklin et al. 2004), we used only 8_{RJS} to estimate the annual rate of population change.

Point estimates of 8_{RJS} for the individual study areas were <1.0 for all areas except TYE. We found strong evidence that spotted owl populations on the WEN, CLE, WSR, and SIM study areas were declining during the period of study. There also was evidence that populations were declining on the RAI, OLY, COA, and HJA areas as well because 95% confidence intervals barely included 1.0. Estimates of realized population change,)8, illustrate that populations on all of the above 8 study areas declined from the initial numbers of territorial owls at the start of the study, and some of the declines were as much as 40-50% over the last decade. Populations appeared to be stationary on the TYE, KLA, CAS, and HUP study areas as a result of high survival and fecundity rates which were stable over the period of study (Table 21). The status of the owl population on the NWC study area was somewhat questionable; we found slight decreases in fecundity and apparent survival on this area, suggesting population declines, but estimates of λ_{RJS} and realized population change lacked the precision to detect any small declines that may have occurred. Our estimate of mean λ_{RJS} for the 13 study areas was 0.963 (SE = 0.009) which suggested that the populations declined 3.7% per year during the period study. These results are consistent with the recent declines in apparent survival on many of the study areas and declines in fecundity on 5 of the areas. This is a higher rate of decline than was reported in a previous analysis (λ_{RJS} = 0.997, SE = 0.043, Franklin et al. 1999), which included many of the same study areas as our analyses.

A demographic analysis of 5 California spotted owl populations (Franklin et al. 2004) indicated that the estimates of λ_{RJS} were not significantly <1.0 and that populations were, therefore, stationary. However, Franklin et al. (2004) stated that estimates of population change in their study were “not sufficiently precise to detect declines” if they occurred. Estimates of λ_{RJS} in our study were reasonably precise for most study areas; coefficients of variation ranged from 1.2–6.1%. Coefficients of variation in this study were >5% for only 1 study area (RAI=6.1%). As a result, the estimate of λ_{RJS} for RAI had a wide confidence interval and lacked the precision to detect a difference from λ_{RJS} = 1.0. Although estimates of temporal process variation were high for the CAS, TYE, and WEN study areas, 95% confidence intervals for all study areas overlapped considerably, and all of the intervals included zero. The rate of population change from the meta-analysis was constant for the 4 density study areas. In contrast, estimates of population change from the meta-analysis for the territory-specific study areas were not constant, and the variation over time was different among areas. This result was expected, as the rate of population change varied considerably among the 10 territorial study areas.

Our estimates of 8_{RJS} apply only to the years during which the studies were conducted, approximately 1990-2003; therefore, any predictions about past or future trajectories of these populations are not recommended. In addition, estimates of 8_{RJS} indicate the average annual rate of population change in the number of owls on each study area. For example, estimates of 8(t) that were <1.0 for any of the areas represented a decrease in the number of owls; however, subsequent values of $\hat{\lambda}$(t) >1.0 for these populations did not indicate that the population had increased to its original numbers. They merely indicated that numbers had increased relative to the number of owls the preceding year. Consequently, a fluctuating pattern in $\hat{\lambda}$(t) can exist that ultimately results in losses or gains in the number of owls, which would be reflected by the mean 8_{RJS} over time for each area. We attempted to understand how changes in $\hat{\lambda}$(t) was related to trends in populations over time by estimating realized changes in populations, $)\,\hat{\lambda}$, for each study area. Based on these estimates, spotted owl populations on the WEN, CLE, RAI, and WRS study areas declined 40-60% during the study, and populations on the OLY, HJA, COA, and SIM study areas declined by 20-30%. The population on the NWC study area appeared to have declined about 15% but the precision of this estimate was too low to detect a significant decline. Populations on the remainder of the areas (TYE, KLA, CAS, and HUP) were approximately stationary during the period of the study. The number of populations that have declined and the rate at which they have declined are noteworthy, particularly the precipitous declines on the 4 Washington study areas and WSR in Oregon.

Effects of Barred Owls

Because barred owls are similar to spotted owls both morphologically and ecologically, and because there is evidence for competitive interactions between these 2 species (Herter and Hicks 2000, Kelly et al. 2003, Pearson and Livezey 2003), we hypothesized that barred owls would have a negative effect on demographic rates of spotted owls. Contrary to our hypothesis, we found little evidence for an effect of barred owls on fecundity of spotted owls, although the results were suggestive of a negative effect for WEN and OLY. In contrast, there was some indication that barred owls may have had an effect on survival rates of spotted owls, but this was specific to 3 study areas in Washington. In the meta-analysis of the 14 study areas, we found evidence of a negative effect of barred owls on spotted owl survival for the WEN and OLY study areas plus this effect was close to being significant for CLE. Similarly, the results for individual study areas indicated a negative effect of barred owls on spotted owl survival for the OLY and WEN study areas with the effect for CLE being suggestive. These results provide some evidence that barred owls may have had a negative effect on spotted owl survival in the northern part of the spotted owl's range. This is the portion of the spotted owl's range where barred owls have been present the longest and are most abundant and where populations of spotted owls are doing the poorest. We found little evidence for an effect of barred owls on survival of spotted owls in Oregon. Kelly (2001) found that barred owls were having a negative effect on occupancy of territories by spotted owls in Oregon but not reproduction. The occurrence of barred owls in spotted owl territories in California was quite low (<5%), so we doubt that they were having much of an effect on the 4 study areas in California. However, barred owls have been increasing their geographic range southward and are becoming more abundant throughout most of the range of the northern spotted owl (Kelly et al. 2003), so their effect on spotted owl populations should be monitored closely in the future.

Many of us were of the opinion that barred owls were having more of an effect on occupancy (a population parameter that we did not analyze) of territories by spotted owls than fecundity or survival. This observation was consistent with previously published reports that have documented a negative influence of barred owls on occupancy of territories by spotted owls (Kelly et al. 2003, Pearson and Livezey 2003). If this is indeed true, this displacement is likely a form of interference competition (Connell 1983). In order to investigate the potential effect of barred owls on spotted owls in the future, any covariate for the occurrence of barred owls should be territory-specific as well as time-specific, and analyses should investigate the effects on occupancy as well as fecundity and survival. The barred owl covariate that we used in this study was not site-specific, so our results can not be considered definitive. The recent methods of MacKenzie et al. (2002, 2003), which incorporate probabilities of detection, could be used to estimate occupancy, colonization, and extinction rates of 1 or both species. This type of analysis is needed to assess the influence of barred owls on spotted owls in future analyses.

Correlation between Fecundity and Apparent Survival Rates

Our meta-analyses of apparent survival of spotted owls indicated a negative correlation between annual survival and productivity in the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir region of Oregon. We found no significant correlations for the Oregon Coast Range, southern Oregon, and California regions. The regions where we found the negative correlations were the more northern or higher elevation areas among our study areas. We also found that productivity was highest during even-number years for most study areas (Figure 2) followed by low survival on all areas the following year (Figure 5). These negative correlations between annual fecundity and apparent survival on some study areas suggest that: 1) there was a cost of reproduction, or 2) there was some other ultimate factor(s) influencing fecundity and survival of owls. The cost of reproduction on body condition of birds has been documented (Maigret and Murphy 1997, Golet and Irons 1999, Hanssen et al. 2003), and there is evidence that reproduction can have a negative effect on survival of western gulls (*Larus occidentialis*; Pyle et al. 1997), greater flamingos (*Phoenicopterus ruber*; Tavecchia et al 2001), great tits (*Parus major*; McCleery et al. 1996), and lesser scaup (*Aythya affinis*; Rotella et al. 2003). Consequently, a cost of reproduction is a plausible explanation for the negative correlations we observed between fecundity and survival. In addition, past research on spotted owls has shown that cold, wet winters or springs can have a negative effect on reproduction of northern spotted owls in southern Oregon (Wagner et al. 1996, Zabel et al. 1996) and on both reproduction and survival in northern California (Franklin et al. 2000) and the Coast Range of Oregon (Olson et al. 2004). Because winter weather is more severe in northern regions and high elevations, where we saw the potential effect of reproduction, this may indicate that the effects of winter weather on fecundity and/or survival may be the ultimate factor. Consequently, the cost of reproduction on survival of spotted owls in the northern regions may be driven ultimately by winter and/or spring weather patterns.

Possible Causes of Population Declines?

Assessment of the possible causes of population declines for the most part was beyond the scope of this study because the potential causes were numerous, and we were unable to develop reliable covariates for the analyses of fecundity, survival, and population change for all study areas. Consequently, we can only speculate about possible causes of population declines.

Based on estimates of 8_{RJS} and realized population change ( ) 8), there was strong evidence for declines in populations on the WEN, CLE, OLY and RAI study areas in Washington and the WSR, HJA, and COA study areas in Oregon. These population declines were due, at least in part, to the declines in apparent survival on some of these study areas, particularly those in Washington. Reasons for these declines in survival and populations were unknown, but may include, but are not limited to, the following possible causes: (1) the high density of barred owls on study areas in Washington and parts of Oregon (Herter and Hicks 2000, Kelly 2001, Pearson and Livezey 2003), (2) loss of habitat due to wildfire, (3) harvest of spotted owl habitat, (4) poor weather conditions, and (5) forest defoliation caused by insect infestations (Hummel and Agee 2003). For example, large areas of spotted owl habitat on private land in the CLE study area were harvested from 1990–2003, and large areas in the WEN study area were impacted by wildfires during the same period (Gaines et al. 1997). Because spotted owls are a long-lived species and large amounts of their habitat was harvested during the 1980s, some of the declines during our study may have been due to “lag effects” from the loss of habitat during that time. In contrast WEN and CLE, RAI is comprised mostly of federal lands, and there was little timber harvest or wildfire on this area during the study, yet populations on this area declined also. The reason for the decline on the WSR study area is probably loss of habitat, as there has been continued logging of old forests on the area over the last 2 decades, and there have been wildfires in some nesting territories. The decline on the HJA area occurred during 1992-93 before barred owls became very abundant, and there also has been very little habitat loss due to timber harvest or wildfire on this area. Consequently, the possible causes of declines on HJA are unknown but may include poor weather conditions and/or declining prey abundance. Population declines on the COA area occurred from 1999 to 2002 and may be the result of continued harvest of owl habitat on private lands within the area and the gradual increase in barred owls. The evidence for declining populations of spotted owls in the northernmost study areas in Washington and Oregon may indicate an effect from barred owls which have invaded much of western North America (Kelly et al. 2003) and are more abundant in Washington and northern Oregon. The cause of this range expansion is unknown, but it is likely a natural event that was triggered by gradual changes in climate and vegetation. If it is a natural event and numbers of barred owls continue to increase, we can only hope that numbers of the two species will reach a stable equilibrium. Although barred owls have invaded the entire range of the northern spotted owl, we suspect that barred owls had little influence on demography of spotted owls in California during our study. This is based on the relatively low frequency of occurrence of barred owls on spotted owl territories in this area during our study. Obviously, no single factor can account for declines in spotted owl populations in Washington and northern Oregon, and this needs further investigation.

The slight declines in fecundity and apparent survival on NWC in California have likely caused a slow but gradual decline in owl populations on that area. The reasons for this decline are not clear, because there has been little loss of habitat and barred owls were not numerous during our study. Populations declined by about 3% per year on SIM during the study. The lands on the SIM study area are privately owned and were subjected to timber harvest during our study, which included incidental take of spotted owls under a federally approved Habitat Conservation Plan. Consequently, this decline was expected and likely reflects the loss of suitable owl habitat on this area. Data from the SIM area were important to our analyses because these are private lands, and this is the only long-term demographic study within the coastal redwood zone of California.

Populations on the TYE, KLA, CAS, and HUP study areas were stationary during the study (Table 21), and these populations had some of the highest demographic rates among the 14 study areas. The stability of populations on these 4 study areas was a result of the high, stable, or increasing rates of survival and fecundity. The TYE and KLA study areas are mixed federal (Bureau of Land Management) and private lands, and there was consistent harvest of young and mature forests on private lands in these areas during our study. The CAS study area is mostly federal land, and there has been minor amounts of harvest in the area. The relative stability of spotted owl populations on HUP was particularly interesting, because harvest of old forests has continued on that area. However, the current Tribal Forest Management Plan does not allow intensive clear-cut logging, and 30% of the forested lands are retained as old-forest reserves in riparian protection zones, tribal reserves, and spotted owl core nesting areas. Selective logging is used throughout most of the Reservation, and some large trees are retained in all harvest units. The reason(s) for the better demographic performance of spotted owls on these 4 areas compared to the other 9 areas is not known.

Status of Owls on the 8 Monitoring Areas

The status of northern spotted owl populations on the 8 monitoring areas (CLE,OLY,TYE, HJA, COA, KLA, CAS, NWC) is of special interest to federal agencies (Lint et al. 1999). These study areas are comprised of federal (U.S. Forest Service, National Park Service) or mixed private and federal lands (Bureau of Land Management), and portions of these study areas are in late-successional reserves for the maintenance and restoration of spotted owl habitat (FEMAT 1993). Consequently, we predicted that demographic rates of spotted owl populations would be higher on these areas than on other areas. Based on the estimates of λ_{RJS} for individual study areas, there was evidence for population declines on CLE, OLY, COA, and HJA. In spite of these declines, demographic rates on the 8 monitoring areas were higher than those on the other study areas. The weighted mean $\hat{\lambda}_{\mathrm{RJS}}$ for the 8 monitoring areas was 0.976 (SE = 0.007) compared to 0.942 (SE = 0.016) for the other areas, a 2.4 vs 5.8% decline per year. Although the overall estimate of λ_{RJS} was higher for the 8 monitoring areas, the negative trends in productivity and survival on some of these areas should be monitored closely in the future.

SUMMARY AND RECOMMENDATIONS

Our objectives were to determine if there were trends in apparent survival and fecundity rates across the range of the northern spotted owl and to determine if populations were increasing, decreasing, or stationary. The federal agencies also wanted to know the status of spotted owl populations on the 8 study areas that comprise the Monitoring Plan for the northern spotted owl (Lint et al. 1999). Our 14 study areas were large in size, encompassed a significant portion of the owl's geographic range, included a variety of land ownerships and management strategies, and spanned a relatively large number of years. Consequently, we believe that our results were representative of most populations of northern spotted owls on federal lands in Washington, Oregon, and California. Because sampling of state and private lands was less extensive and management practices vary widely, we were less certain that the results were generally applicable to non-federal lands.

The 4 major findings of this study were: (1) fecundity rates were variable among the 14 study areas but declining on 5 study areas, (2) survival rates were declining on 5 study areas and stable on the remaining areas, (3) populations were declining on 8 study areas and stationary on the remainder, and (4) the mean 8_{RJS} = 0.963 (SE = 0.009) suggested a 3.7% decline over all study areas (Table 21). Demographic performance of northern spotted owls was poorest in Washington where there were declines in survival rates and populations in all 4 study areas (OLY, WEN, RAI, CLE). Demographic performance was generally better in Oregon where survival was stable, and there was evidence for populations declines on WSR, COA, and HJA but stationary populations on TYE, KLA, and CAS. Spotted owl populations in California were performing slightly better than those in Oregon and much better than those in Washington. Fecundity was variable among the 4 study areas in California; survival was stable on 3 areas but declining on NWC; and populations were declining on SIM.

In general, demographic rates on the 8 monitoring areas were higher than those on other study areas. Overall, populations on 13 study areas that were part of a previous meta-analysis (Franklin et al. 1999) were doing poorer than they were 5 years ago. These results emphasize the need for further monitoring of northern spotted owl populations and research on the potential causes of population declines. Consequently, we recommend the following:

1. Continued monitoring of fecundity, survival, and rates of population change on all of the study areas and particularly the 8 monitoring areas. The apparent

declines in survival and abundance in Washington and parts of Oregon suggest a need for more intensive research to determine the cause(s) of these population declines. Continued monitoring will allow the agencies to determine if the current trends in demographic rates continue and a more detailed analysis of the factors that may be influencing populations. The diversity of ownership, past management strategies, and ecological conditions within the 14 study areas also allows wider interpretations of the results than a more limited set of study areas.

2. Additional covariates should be developed to evaluate the effect of barred owls on fecundity and survival of spotted owls. Any barred owl covariate should be territory-specific and should be used to look at the barred owl effect on territory occupancy as well as fecundity and survival of spotted owls.

3. More intensive studies on the competitive interactions of barred owls and spotted owls are needed, including resource partitioning of prey, habitat, and space as well as behavioral interactions between the species.

4. Research is needed on the effects of weather on demographic performance of spotted owls, both separately and as part of the next meta-analysis. The even-odd year fluctuations in fecundity and survival suggest some underlying cause which could be related to weather patterns or prey abundance. Our results suggested there is a correlation between reproduction and survival rates, and this possibility needs further study also.

5. We anticipate that the reparameterized Jolly-Seber method (Pradel 1996) will be used to estimate annual rates of population change, 8_{RJS}, in the future. Thus, it is

paramount that there are no alterations in study area boundaries and the intensity of monitoring on the study areas be consistent from year to year. Expansion of study area boundaries during the present study created some challenging modeling which was not easily handled (see meta-analysis of 8_{RJS} for the territorial study areas). Contraction of study area boundaries would create similar problems.

6. Sampling within the Density Study Areas versus the Territorial Study Areas was done differently, but it is not clear whether this had an effect on the estimates of 8_{RJS} or not. Additional analyses on these 2 types of data should be completed to more fully understand this question, and these results should be retained and consulted in future demographic analyses.

7. Estimates of demographic rates varied widely among the 14 study areas. This variability in demographic rates could be more fully understood if future analyses included covariates on weather patterns, vegetative characteristics, rates of habitat loss due to logging and wildfire, and territory-specific data on the presence of barred owls. This will require the development of comprehensive and accurate vegetation maps for all of the study areas within the next 5 years.

8. Estimation of survival rates of juvenile spotted owls from capture-recapture data is problematic, because current open population models can not distinguish between mortality and permanent emigration. Another approach would be the use of multi-strata models (Brownie et al. 1993) to estimate the probabilities of juveniles moving from the non-breeding to the breeding population at various ages. These models also may provide less biased estimates of juvenile survival.

Some reviewers of this manuscript urged us to make recommendations regarding management of spotted owl populations and their habitats based on our findings. We do not believe that this would be appropriate for several reasons. First, management of the northern spotted owl has been an incredibly complicated interagency effort that has lead to much federal land being reserved as habitat for owls and other species (USDA and USDI 1994). Because it is not clear if additional protection of owl habitat will reverse the population declines, we think it would not be appropriate for us to propose additional management recommendations. Secondly, the U. S. Department of Interior, U.S. Fish and Wildlife Service, is currently conducting a post-listing Status Review of the northern spotted owl, and they have the mandate and legal authority under the Endangered Species Act to evaluate the status of the species periodically. We anticipate that our results will be considered in their review of all information on spotted owls and their final assessment. Thirdly, the results of our study did not identify the causes of the populations declines, so we can not say with certainty that any management strategies would be successful in halting the declines. Lastly, some of the possible causes of the declines are natural events (e.g., weather, wildfires), so management strategies are not possible nor particularly appropriate.

The northern spotted owl has been studied intensively over the last 3 decades, but there are still questions about the factors that affect its survival and fecundity rates and overall population status. Answers to these questions will be challenging, because the species is long-lived and has high site- and mate-fidelity. These demographic and behavioral characteristics have a tendency to confound any interpretations of the effects of habitat alterations on the species. However, the potential causes of population declines should be the focus of future demographic analyses on the species by using more definitive covariates.

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LIST OF APPENDICES

Appendix A. Study areas included in the January 2004 analysis of demographic trends of northern spotted owls.

Appendix B. Barred owl covariate used to model northern spotted owl fecundity, survival and capture probability on 14 study areas in Washington (WA), Oregon (OR), and California (CA) (study area acronyms specified in Table 1; Appendix A).

Appendix C. Reproductive covariate (number of young fledged per year) used to model northern spotted owl fecundity, survival, and capture probability on 14 study areas in Washington (WA), Oregon (OR), and California (CA) (study area acronyms specified in Table 1; Appendix A).

Appendix D. Estimates of annual recapture probabilities (*p*) for banded northern spotted owls in 14 demographic study areas in Washington, Oregon, and California. Estimates are from the best AICc model for each study area. Study areas that had a sex effect on *p* include separate columns for males and females.

Appendix E. Model averaged apparent survival estimates with 95% confidence intervals for male and female northern spotted owls on the 4 study areas in Washington (WEN, CLE, RAI, OLY), 6 study areas in Oregon (COA, HJA, WSR, TYE, KLA, CAS), and 4 study areas in California (NWC, HUP, SIM, MAR). Study area acronyms specified in Table 1, Appendix A.

Table 1. Descriptions of 14 study areas used to estimate vital rates of northern spotted owls in Washington, Oregon, and California (see also Appendix A). Astrices indicate the 8 study areas that are part of the Federal monitoring program for the owl (Lint et al. 1999).

Study area	Study area acronym	Years	Area in km^2	Number of owls banded by age class [a]				Total owls banded	Total captures plus recaptures [b]
				Juvs.	S1	S2	Adults		
Washington									
Wenatchee	WEN	1990–2003	4,650	752	28	63	357	1,200	2,556
Cle Elum*	CLE	1989–2003	1,784	502	25	30	167	724	1,570
Rainier	RAI	1992–2003	2,133	97	8	7	105	217	530
Olympic*	OLY	1987–2003	3,289	516	35	39	395	985	3,568
Oregon									
Coast Ranges*	COA	1990–2003	3,919	574	27	57	367	1,025	3,386
H. J. Andrews*	HJA	1987–2003	1,526	602	44	54	395	1,095	3,151
Warm Springs	WSR	1992–2003	1,001	233	10	13	125	381	867
Tyee*	TYE	1985–2003	1,741	610	67	63	292	1,032	3,293
Klamath*	KLA	1985– 2003	1,384	698	98	73	278	1,147	2,964
South Cascades*	CAS	1991–2003	3,375	411	22	45	403	881	2,141

California

Table 1. (continued).

				Number of owls banded by age class [a]					
Study area	Study area acronym	Years	Area in km^2	Juv.	S1	S2	Adults	Total owls banded	Total captures plus recaptures [b]
NW California*	NWC	1985–2003	1,790	609	97	73	247	1,026	2,865
Hoopa	HUP	1992–2003	356	116	24	30	109	279	851
Simpson	SIM	1990–2003	1,265	708	80	127	429	1,344	4,087
Marin	MAR	1998–2003	217	41	9	10	36	96	225
Totals			28,430	6,469	574	684	3,705	11,432	32,054

[a] Age class codes indicate owls that were 1 year old (S1), 2 years old (S2) or $ 3 years old (Adults).

[b] All captures and recaptures, regardless of age.

Table 2. *A priori* models used for analysis of recapture probabilities (*p*) of northern spotted owls on 14 demographic study areas in Washington, Oregon, and California. *N* structure for all models was *N*(a*s*t).

Model [a]	Description of *p* structure
1. *p*(a*s*t)	Age, sex, and time effects with all interactions (global model)
2. *p*(.)	Constant model (no effects)
3. *p*(s)	Sex effect
4. *p*(r)	Effect of annual reproduction on *p* in following year
5. *p*(r+s)	Additive reproduction and sex effects
6. *p*(t)	Annual time effect
7. *p*(s+t)	Additive sex and time effects
8. *p*(T)	Linear time trend effect
9. *p*(s+T)	Additive sex and linear time trend effects
10. *p*(BO)	Barred owl effect
11. *p*(s+BO)	Additive sex and barred owl effects
12. *p*(s+BO+r)	Additive sex, barred owl, and reproduction effects
13. *p*(choice)	Biologist's choice [b]

[a] Model notation indicates structure for effects of age (a), sex (s), annual time (t), linear time trend (T), reproduction (r), barred owls (BO), or biologist's choice (choice). Age structure included 3 age classes (1-year-old, 2-year-old, and $ 3 years old).

[b] Up to 3 additional models of choice that incorporated potential area-specific effects on *p* (i.e., survey effort, study area subregions, survey method, etc.)

Table 3. *A priori* models used for analysis of apparent survival (N) of northern spotted owls on 14 demographic study areas in Washington, Oregon, and California. Models for each study area used the best *p*-structure from the initial analysis of *p*-structure on each study area.

Model [a]	Description of N structure
1. N(S1=S2=A)	Constant N, no age, sex or time effects
2. N([S1=S2=A]+s)	Sex effect only
3. N(S1, S2=A)	Age effect (S2=A, S1 different)
4. N([S1, S2=A]+s)	Age effect (S2=A, S1 different), additive sex effect (s)
5. N(S1=S2, A)	Age effect (S1=S2, A different)
6. N([S1=S2, A]+s)	Age effect (S1=S2, A different), additive sex effect (s)
7. N(S1, S2, A)	Age effect (all age classes different)
8. N([S1, S2, A}+s)	Age effect (all age classes different), additive sex effect (s)
9. N(models 1-8+t)	Models 1-8 above with additive time effect (t)
10. N(models 1-8+T)	Models 1-8 above with additive linear time effect (T)
11. N(models 1-8*T)	Models 1-8 above with interactive linear time effect (T)
12. N(models 1-8+TT)	Models 1-8 above with additive quadratic time effect (TT)
13. N(models 1-8*TT)	Models 1-8 above with interactive quadratic time effect (TT)
14. N(models 1-8+BO)	Models 1-8 above with additive barred owl effect (BO)

[a] Model notation indicates structure for effects of age (S1, S2, A), sex (s), annual time (t), linear time trend (T), or quadratic time trend (TT). Age classes (S1, S2, A) indicate owls that were 1, 2, or $ 3 years old, respectively. Symbols separating age classes indicate if they were combined (=) or estimated separately (,).

Table 4. *A priori* models used for meta-analysis of apparent survival (N) and recapture probabilities (*p*) of adult female northern spotted owls on 14 study area in Washington, Oregon, and California.

Model [a]	Description of model structure
1. N(g*t*s) *p*(g*t*s)	N(area, time, and sex effects with all interactions): *p*(area, time, and sex effects with all interactions)
2. N([g*t]+s) *p*(g+t)	N(area and time effects with interactions, plus additive sex effect): *p*(additive area and time effects)
3. N([g*t]+s) *p*(g+s+t)	N(area and time effects with interactions, plus additive sex effect): *p*(additive area, sex, and time effects)
4. N([g*t]+s) *p*([g+t]*s)	N(area and time effects with interactions, plus additive sex effect): *p*(additive area and time effects, interacting with sex)
5. N([g*t]+s) *p*(r)	N(area and time effects with interactions, plus additive sex effect): *p*(reproduction effect)
6. N([g*t]+s) *p*(r+s)	N(area and time effects with interactions, additive sex effect): *p*(additive reproduction and sex effects)
7. N([g*t]+s) *p*(r*s)	N(area and time effects with interactions, plus additive sex effect): *p*(reproduction and sex effects with interactions)
8. N(g+s) *p*(best)	N(additive area and sex effects): *p*(best *p*-structure from models 2-7 above).
9. N(g+s+t) *p(*best)	N(additive area, sex and time effects): *p*(= model 8)

Table 4. (continued).

Model ^{a}	Description of model structure
10. N([g*T]+s) *p*(best)	*N*(area and linear time effects with interactions, plus additive sex effect): *p*(= model 8)
11. *N*(g+T+s) *p*(best)	*N*(additive area, linear time trend, and sex effects): *p*(= model 8)
12. *N*([g*TT]+s) *p*(best)	*N*(area and quadratic time effects with interactions, plus additive sex effect): *p*(= model 8)
13. *N*(g+s+TT) *p*(best)	*N*(additive area, sex, and quadratic time effects): *p*(= model 8)
14. *N*(s+t) *p*(best)	*N*(additive sex and time effects): *p(*= model 8)
15. *N*(s+TT) *p*(best)	*N*(additive sex and quadratic time effects): *p*(= model 8)
16. *N*(s+T) *p*(best)	*N*(additive sex and linear time effects): *p*(= model 8)
17. *N*(s) *p*(best)	*N*(sex effect): *p*(= model 8)
18. *N*(BO+s) *p*(best)	*N*(additive barred owl and sex effects): *p*(= model 8)
19. *N*(g+BO+s) *p*(best)	*N*(additive area, barred owl, and sex effects): *p*(= model 8)
20. *N*([g*BO]+s) *p*(best)	*N*(area and barred owl effects with interactions, plus additive sex effect): *p*(= model 8)
21. *N*(no sex) *p*(best)	*N*(lowest QAICc model from models 8-20 with sex effect removed): *p*(= model 8)
22. *N*(owner) *p*(best)	*N*(replace area effect in lowest QAICc model from models 8-21 with ownership effect): *p*(= model 8)

TABLE 4. (continued).

Model [a]	Description of model structure
23. *N*(region) *p*(best)	*N*(replace area effect in lowest QAICc model from models 8-21 with region effect): *p*(= model 8)
24. *N*(owner*region) *p*(best)	*N*(replace area effect in lowest QAICc model from models 8-21 with ownership and region effects with interactions): *p*(= model 8)
25. *N*(best+latitude) *p*(best)	*N*(additive latitude effect with best area effect model from models 8-24): *p*(= model 8)

[a] Model notation indicates structure for effects of study area (*g*), annual time (t), linear time trend (T), quadratic time trend (TT), geographic region (region), land ownership (owner), latitude (latitude), or barred owls (BO).

Table 5. Estimates of age-specific fecundity (number of female young produced per female) of northern spotted owls on 14 study areas in Washington, Oregon and California.

		1-year-old owls			2-year-old owls			Adults ($ 3 years old)		
Study area	Years	n [a]	$\bar{x}$	SE	n [a]	$\bar{x}$	SE	n [a]	$\bar{x}$	SE
Washington										
WEN	1990–2003	20	0.050	0.050	49	0.290	0.085	758	0.491	0.058
CLE	1989–2003	23	0.136	0.097	34	0.467	0.117	423	0.574	0.069
RAI	1992–2003	4	0.000	0.000	7	0.000	0.000	184	0.253	0.061
OLY	1987–2003	11	0.071	0.050	19	0.267	0.098	883	0.293	0.057
Oregon										
COA	1990–1992	17	0.000	0.000	53	0.111	0.045	1,168	0.260	0.050
HJA	1987–2003	22	0.109	0.091	35	0.113	0.060	1,026	0.321	0.045
WSR	1992–2003	7	0.000	0.000	16	0.311	0.110	303	0.424	0.070
TYE	1985–2003	72	0.054	0.032	90	0.201	0.047	973	0.319	0.040
KLA	1985–2003	69	0.070	0.028	103	0.285	0.052	795	0.445	0.040
CAS	1991–2003	26	0.061	0.046	42	0.223	0.082	780	0.377	0.059
California										
NWC	1985–2003	64	0.101	0.066	78	0.205	0.052	938	0.333	0.032
HUP	1992–2003	10	0.000	0.000	15	0.056	0.056	273	0.216	0.043
SIM	1990–2003	60	0.109	0.040	104	0.118	0.030	1,168	0.326	0.037

MAR	1998–2003	12	0.275	0.195	12	0.271	0.159	156	0.530	0.056

Table 5. (continued).

		1-year-old owls			2-year-old owls			Adults ($ 3 years old)		
Study area	Years	*n* [a]	$\bar{x}$	SE	*n* [a]	$\bar{x}$	SE	*n* [a]	$\bar{x}$	SE
Total/Mean		417	0.074	0.029	657	0.208	0.032	9,828	0.372	0.029

[a] Sample size indicates the number of cases in which we sampled owls in each age class. This is not the sample that was used to calculate means and standard errors. Those estimates were based on the number of years in the survey period. Estimates were determined using a non-parametric approach.

Table 6. Best model and competing models with $)_i < 2.0$, from the analysis of productivity of female northern spotted owls on 14 study areas in Washington, Oregon and California.

Study area and models [a]	-2log‹	*K* [b]	AICc	) AICc [c]	Akaike weight
Washington					
Wenatchee (WEN)					
A+EO	35.30	5	47.37	0.00	0.31
A+EO+BO	33.55	6	48.55	1.18	0.17
A+EO+T	33.70	6	48.70	1.33	0.16
Cle Elum (CLE)					
A+EO	74.94	5	86.70	0.00	0.36
A+EO+T	72.46	6	87.01	0.31	0.31
Rainier (RAI)					
A*EO	-20.18	7	3.16	0.00	0.89
Olympic (OLY)					
A+EO	21.60	5	34.00	0.00	0.55
A+EO+BO	20.25	6	35.75	1.74	0.23
Oregon					
Coast Range (COA)					
A+EO	2.50	5	14.81	0.00	0.43
A+EO+T	0.98	6	16.34	1.53	0.20
A+EO+BO	1.35	6	16.71	1.91	0.16
H.J. Andrews (HJA)					
A+EO+TT	26.92	7	44.42	0.00	0.89
Warm Springs (WSR)					
A	25.08	4	35.58	0.00	0.36

A+EO	22.71	5	36.71	1.13	0.20

Table 6. (continued).

Study area and models [a]	$-2\log \mathcal{L}$	K [b]	AICc	ΔAICc [c]	Akaike weight
Constant	32.57	2	37.23	1.66	0.16
Tyee (TYE)					
A+T	27.31	5	38.62	0.00	0.31
A	30.80	4	39.65	1.03	0.18
A+BO	29.23	5	40.53	1.92	0.12
Klamath (KLA)					
A+EO	30.20	5	41.59	0.00	0.22
A	32.73	4	41.64	0.05	0.22
A*EO	26.69	7	43.42	1.83	0.09
A+BO	32.07	5	43.47	1.88	0.09
S. Cascades (CAS)					
A+EO+T	31.92	6	46.72	0.00	0.36
A+EO	35.84	5	47.78	1.06	0.21
A+EO+TT	30.85	7	48.71	1.99	0.13
California					
NW California (NWC)					
A+T	51.40	5	62.68	0.00	0.27
A+BO	52.66	5	63.93	1.25	0.14
A	55.22	4	64.05	1.37	0.13
A+TT	50.30	6	64.13	1.45	0.13
Hoopa (HUP)					
A+EO+T	-7.99	6	7.83	0.00	0.32
A+EO+BO	-7.47	6	8.35	0.53	0.25
A+EO	-3.73	5	8.88	1.06	0.19

Simpson (SIM)

Table 6. (continued).

Study area and models [a]	-2log ‹	*K* [b]	AICc	) AICc [c]	Akaike weight
A+EO	-0.66	5	11.01	0.00	0.42
A+EO+T	-1.76	6	12.64	1.64	0.19
A+EO+BO	-1.46	6	12.94	1.93	0.16
Marin (MAR)					
Constant	34.34	2	39.20	0.00	0.52

[a] Model notation indicates structure for effects of owl age (A), even-odd years (EO), linear time (T), quadratic time (TT), or barred owls (BO).

[b] *K* = number of parameters in model, including covariance parameters.

[c]) AICc = difference between the model listed and the best AICc model.

Table 7. Regression coefficients ($\hat{\beta}$) from the best productivity model containing a linear (T) or quadratic (TT) time trend for 14 northern spotted owl study areas in Washington, Oregon, and California.

Study area	Best time trend model	) AICc [b]	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington						
WEN	A+EO+T	1.325	-0.022	0.017	-0.055	0.011
CLE	A+EO+T	0.305	-0.038	0.024	-0.085	0.009
RAI	A*EO+T	5.534	0.005	0.011	-0.016	0.026
OLY	A+EO+T	2.935	-0.005	0.013	-0.030	0.020
Oregon						
COA	A+EO+T	1.529	-0.014	0.011	-0.036	0.008
HJA	A+EO+TT [c]	0.000	-0.024	0.011	-0.046	0.002
			0.009	0.003	0.003	0.015
WSR	A+T	3.444	0.007	0.028	-0.048	0.062
TYE	A+T	0.000	0.016	0.008	0.000	0.317
KLA	A+T	2.384	0.004	0.009	-0.014	0.022
CAS	A+EO+T	0.000	-0.034	0.017	-0.067	0.001
California						
NWC	A+T	0.000	-0.019	0.010	-0.039	0.001
HUP	A+EO+T	0.000	0.023	0.011	0.001	0.044
SIM	A+EO+T	1.636	-0.010	0.009	-0.028	0.008
MAR	A+T	7.995	0.029	0.092	-0.151	0.209

[a] Notation indicates model structure for effects of age (A), even-odd year (EO), linear time trend (T), or quadratic time trend (TT).

[b]) AICc = difference between the best time-trend model and the best AICc model for each study area (Appendix F).

[c] The first estimate is the linear term and the second is the quadratic term.

Table 8 . Regression coefficients ($\hat{\beta}$) for the barred owl effect on productivity of northern spotted owls on 14 study areas in Washington, Oregon, and California. Estimates are from the best productivity model containing the barred owl (BO) covariate

					95% CI	
Study area	Model [a]	) AICc [b]	$\hat{\beta}$	SE	Lower	Upper
Washington						
WEN	A+EO+BO	1.173	-0.942	0.701	-2.316	0.433
CLE	A+EO+BO	2.533	-0.550	1.102	-2.710	1.610
RAI	A+EO+BO	10.700	0.202	0.548	-0.871	1.275
OLY	A+EO+BO	1.744	-1.026	0.872	-2.735	0.682
Oregon						
COA	A+EO+BO	1.907	-0.280	0.259	-0.787	0.228
HJA	A+EO+BO	9.604	-0.428	1.011	-2.411	1.554
WSR	A+BO	3.355	-0.503	1.316	-3.081	2.078
TYE	A+BO	1.915	0.733	0.580	-0.404	1.869
KLA	A+BO	1.875	1.316	1.617	-1.853	4.484
CAS	A+EO+BO	2.755	-1.385	1.270	-3.874	1.105
California						
NWC	A+BO	1.253	-2.069	1.278	-4.575	0.436
HUP	A+EO+BO	0.525	2.114	1.058	0.040	4.187
SIM	A+EO+BO	1.929	-1.932	2.144	-6.134	2.270
MAR	BO	1.102	22.533	15.951	8.730	53.797

[a] Notation indicates model structure for effects of age (A), even-odd year (EO), or barred owls (BO).

[b])$_i$ = difference between the best model with the BO covariate and the best AICc model for each study area (Appendix F).

Table 9. Variance components of the number of young fledged per pair of northern spotted owls, from a mixed model analysis of year- and territory-specific estimates. Spatial variability is the random effects estimate of territory variability, and temporal is the random effects estimate of year variability.

	Source of Variation						
	Spatial		Temporal		Residual		Total
Study area	Estimate	% of total	Estimate	% of total	Estimate	% of total	Estimate
Washington							
WEN	0.058	6	0.166	18	0.691	75	0.915
CLE	0.058	5	0.227	23	0.684	70	0.969
RAI	0.000	0	0.109	17	0.505	82	0.613
OLY	0.021	2	0.201	28	0.481	68	0.703
Oregon							
COA	0.015	2	0.127	21	0.450	76	0.592
HJA	0.000	0	0.108	15	0.601	84	0.709
WSR	0.000	0	0.195	22	0.675	77	0.871
TYE	0.030	4	0.079	11	0.569	83	0.678
KLA	0.000	0	0.056	7	0.704	92	0.760
CAS	0.022	2	0.153	19	0.615	77	0.790
California							
NWC	0.028	3	0.059	8	0.623	87	0.710
HUP	0.035	7	0.056	11	0.404	81	0.495

SIM	0.025	3	0.054	8	.0585	88	0.663
MAR	0.108	12	0.058	6	0.701	80	0.867

Table 10. Model selection results from the meta-analysis of productivity of female northern spotted owls on 14 study areas in Washington, Oregon, and California.

Model [a]	-2log ‹	*K* [b]	AICc	) AICc [c]	Akaike weight
region+t	57.215	26	117.238	0.000	0.547
region+t+BO	55.832	27	118.522	1.284	0.288
t	72.838	21	119.972	2.734	0.139
owner+t	72.182	23	124.385	7.147	0.015
region*BO+t	48.627	32	125.124	7.886	0.011
region+EO	141.543	9	160.480	43.242	0.000
region*EO	133.320	14	163.566	46.328	0.000
owner+EO	154.193	6	166.624	49.386	0.000
owner*EO	153.921	8	170.668	53.430	0.000
owner*t	47.154	54	195.562	78.324	0.000
region+T	190.340	9	209.277	92.039	0.000
region+BO	193.846	9	212.784	95.546	0.000
T	205.554	4	213.757	96.519	0.000
region*BO	188.671	13	216.607	99.369	0.000
owner+T	204.825	6	217.255	100.018	0.000
Constant	211.243	3	217.364	100.127	0.000
BO	210.334	4	218.537	101.299	0.000
region*T	188.294	14	218.540	101.302	0.000
owner*T	204.686	8	221.432	104.194	0.000

[a] Notation indicates model structure for effects of geographic region (region), land ownership (owner), even-odd year (EO), annual time (t), linear time (T), or barred owls (BO).

[b] *K* = number of parameters in model, including covariance parameters.

[c]) AICc = difference between the model listed and the best AICc model.

Table 11. Estimates of mean annual fecundity (number of female young produced per female) of adult northern spotted owls, subdivided by geographic regions.

			95% CI	
Geographic region	$\bar{x}$	SE	Lower	Upper
All 14 study areas				
Washington - Douglas-fir	0.313	0.041	0.233	0.393
Washington - Mixed-Conifer	0.560	0.041	0.480	0.640
Oregon Coastal - Douglas-fir	0.306	0.039	0.230	0.382
Oregon Cascades - Douglas-fir	0.404	0.034	0.337	0.471
Oregon/California - Mixed-Conifer	0.350	0.032	0.287	0.413
California Coast	0.442	0.045	0.354	0.530

Table 12. Estimates of overdispersion ($\hat{c}$) in capture-recapture data from 14 northern spotted owl demographic study areas in Washington, Oregon and California.

	CJS [a]			8_{RJS} [a]		
Study area	P^2	df	$\hat{c}$	P^2	df	$\hat{c}$
Washington						
WEN	165.67	71	2.33	147.42	84	1.18
CLE	63.92	68	0.94	35.21	51	0.69
RAI	45.24	46	0.98	33.73	47	0.72
OLY	170.35	86	1.98	156.42	104	1.50
Oregon						
COA	179.51	68	2.64	168.87	56	3.02
HJA	210.40	85	2.47	167.29	78	2.14
WSR	49.31	46	1.07	46.95	41	1.14
TYE	133.41	95	1.40	69.68	64	1.09
KLA	117.93	95	1.24	87.48	74	1.18
CAS	139.67	62	2.25	142.91	65	2.20
California						
NWC	86.84	75	1.16	124.93	81	1.54
HUP	41.07	49	0.84	46.06	52	0.89
SIM	186.39	68	2.74	139.81	50	2.80
MAR	10.33	11	0.94	NA[b]	NA[b]	NA[b]
Totals	1600.04	925	1.73	1366.76	847	1.61

[a] CJS indicates data sets used for Cormack-Jolly-Seber estimates of apparent survival, and λ_{RJS} indicates data sets used to estimate annual rates of population change. Values for P^2, and df are from TEST 2 and TEST 3 in program RELEASE. Estimates of $\hat{c}$ <1.0 were set to 1.00 for analysis.

[b] λ_{RJS} could not be estimated for the MAR Study Area because of small sample size.

Table 13. Estimates of average apparent survival ($\hat{\phi}$) for 3 age-classes of northern spotted owls on 14 study areas in Washington, Oregon, and California.

	Best model [a]		1-year-old [b]		2-year old [b]		$ 3 yrs old [b]	
Study area	ϕ structure	p structure	$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\phi}$	SE($\hat{\phi}$)
Washington								
WEN	(S1=S2,A)+BO	T	0.626	0.073	0.626	0.073	0.750	0.026
CLE	t	s+r	0.860	0.017	0.860	0.017	0.860	0.017
RAI	T	t	0.832	0.020	0.832	0.020	0.832	0.020
OLY	(S1,S2=A)+BO	t	0.570	0.117	0.855	0.011	0.855	0.011
Oregon								
COA	S1,S2=A	(.)	0.721	0.107	0.886	0.010	0.886	0.010
HJA	S1,S2=A	TT	0.415	0.111	0.883	0.010	0.883	0.010
WSR	(.)	r+BO	0.823	0.015	0.823	0.015	0.823	0.015
TYE	(S1,S2=A)+TT	s+T	0.817	0.042	0.878	0.011	0.878	0.011
KLA	(.)	T	0.849	0.009	0.849	0.009	0.849	0.009
CAS	S1=S2,A	TT	0.725	0.079	0.725	0.079	0.854	0.014
California								
NWC	(S1=S2,A)+TT	meth+by	0.810	0.027	0.810	0.027	0.869	0.011

HUP	S1=S2,A	TT*EW		0.781	0.049	0.781	0.049	0.853	0.014

Table 13. (continued).

	Best model [a]			1-year-old [b]		2-year old [b]		$ 3 yrs old [b]	
Study area	ϕ structure	p structure		$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\phi}$	SE($\hat{\phi}$)
SIM	(.)	s		0.850	0.010	0.850	0.010	0.850	0.010
MAR	s	s+r	&	0.824	0.045	0.824	0.045	0.824	0.045
			%	0.913	0.035	0.913	0.035	0.913	0.035

[a] Model notation indicates structure for additive (+) or interactive (*) effects of sex (s), time (t), linear time trend (T), quadratic time trend (TT), reproduction (r), barred owls (BO), age-class (S1, S2, A), east-west binomial subdivision of study area (EW), survey method (meth), or years of poor weather (by). For age-classes, an (=) sign means that age classes were combined, and a (,) indicates that they were modeled separately. Age classes (S1, S2, A) indicate owls that were 1, 2 or $3 years old.

[b] For study areas with time structure in the top model, we estimated average survival as follows: For variable time (t) models we calculated the arithmetic mean and standard error using the delta method. For linear (T) models, we used the median value and its standard error (odd number of survival estimates) or the lower of the 2 median values and its standard error (even number of survival estimates). For quadratic (TT) models we used the annual estimate from the model that was closest to the arithmetic average of the maximum and minimum annual survival estimates.

Table 14. Beta estimates ($\hat{\beta}$) for the best models that included a time-trend on apparent survival of non-juvenile northern spotted owls on 14 study areas in Washington, Oregon, and California..

Study	Model					95% CI	
area	trend ^{a}	Δ QAICc ^{b}	$\hat{\beta}$	SE	CV ^{c}	Lower	Upper
Washington							
WEN	TT^{d}	0.341	-0.078	0.029	0.372	-0.138	-0.021
			-0.020	0.009	0.450	-0.038	-0.002
CLE	T	2.063	-0.030	0.024	0.800	-0.076	0.016
RAI	T	0.000	-0.275	0.069	0.251	-0.409	-0.140
OLY	T	1.253	-0.049	0.025	0.510	-0.097	-0.001
Oregon							
COA	TT ^{d}	0.282	0.016	0.027	1.688	-0.037	0.069
			-0.016	0.009	0.563	-0.033	0.000
HJA	T	1.122	-0.022	0.023	1.045	-0.067	0.023
WSR	(S1, S2=A)*T ^{e}	0.607	-0.012	0.039	3.250	-0.088	0.064
			1.545	0.941	0.609	-0.299	3.389
TYE	TT ^{d}	0.000	-0.003	0.021	7.000	-0.043	0.038
			0.008	0.004	0.500	0.000	0.015
KLA	T	1.973	0.005	0.017	3.400	-0.029	0.038
CAS	T	2.010	0.003	0.032	10.667	-0.059	0.066
California							
NWC	TT ^{d}	0.000	-0.031	0.015	0.484	-0.060	-0.003
			0.003	0.003	1.000	-0.003	0.009
HUP	TT ^{d}	0.441	0.002	0.038	19.000	-0.072	0.077
			0.025	0.014	0.560	-0.002	0.051

SIM	T	1.596	-0.015	0.024	1.600	-0.062	0.032

Table 14. (continued).

Study area	Model trend [a]	)QAICc [b]	$\hat{\beta}$	SE	CV [c]	95% CI Lower	95% CI Upper
MAR	T	2.118	0.048	0.206	4.292	-0.357	0.452

[a] T = linear trend over time, TT = quadratic trend over time.

[b])QAICc = difference between the model listed and the best QAICc model.

[c] Coefficient of sampling variation (CV) computed as $SE(\hat{\beta}_i)|\hat{\beta}_i|$.

[d] The first row estimate is the linear term and the second is the quadratic term.

[e] First row is for linear term, second is for interaction.

Table 15. Model selection criteria for *a priori* models used in the meta-analysis of apparent survival of adult northern spotted owls on 14 demographic study areas in Washington, Oregon, and California, 1985-2003.

Model [a]	QAICc	) QAICc [b]	Akaike weights	*K* [c]	Q Deviance [d]
N(region+t) *p*(g+s+t)	18459.906	0.000	0.780	55	7206.936
N([owner*region]+t) *p*(g+s+t)	18464.024	4.119	0.099	58	7205.020
N(g+t) *p*(g+s+t)	18464.554	4.648	0.076	63	7195.489
N(g+s+t) *p(*g+s+t)	18466.353	6.448	0.031	64	7195.277
N(region*T) *p*(g+s+t)	18468.722	8.816	0.010	44	7237.861
N(latitude+t) *p*(g+s+t)	18472.213	12.307	0.002	51	7227.286
N(s+t) *p*(g+s+t)	18473.263	13.357	0.001	51	7228.335
N(owner+t) *p*(g+s+t)	18473.338	13.433	0.001	52	7226.400
N(region*r) *p*(g+s+t)	18478.302	18.396	0.000	44	7247.441
N(region+r) *p*(g+s+t)	18478.557	18.652	0.000	39	7257.737
N(g+t) *p*(g+t)	18479.624	19.719	0.000	62	7212.572
N(g+s+t) *p*(g+t)	18480.976	21.070	0.000	63	7211.912
N([g*BO]+s) *p*(g+s+t)	18483.279	23.374	0.000	61	7218.240
N([g*T]+s) p(*g*+s+t)	18483.811	23.905	0.000	61	7218.771
N(region+T) *p*(g+s+t)	18484.238	24.332	0.000	39	7263.419
N([g*TT]+s) *p*(g+s+t)	18489.309	29.403	0.000	75	7196.079
N(g+s+T) *p*(g+s+t)	18491.662	31.756	0.000	48	7252.764
N(g+s) *p*(g+s+t)	18492.032	31.126	0.000	47	7255.143
N(g+BO+s) *p*(g+s+t)	18492.843	32.937	0.000	48	7253.945
N(g+s+TT) *p*(g+s+t)	18493.620	33.715	0.000	49	7252.713
N(s) *p*(g+s+t)	18502.671	42.765	0.000	34	7291.888

N(s+T) *p*(g+s+t)	18502.852	42.946	0.000	35	7290.062

Table 15. (continued).

Model [a]	QAICc	) QAICc [b]	Akaike weights	*K* [c]	Q Deviance [d]
N(BO+s) *p*(g+s+t)	18503.635	43.729	0.000	35	7290.845
N(s+TT) *p*(g+s+t)	18504.377	44.471	0.000	36	7289.581
N([g*t]+s) *p*(g+s+t)	18601.916	142.010	0.000	223	7008.269
N([g*t]+s) *p*(g+t)	18616.032	156.126	0.000	222	7024.429
N([g*t]+s) *p*([g+t]*s)	18627.672	167.767	0.000	251	6976.690
N([g*t]+s) *p*(r+s)	18810.165	350.259	0.000	191	7281.848
N([g*t]+s) *p*(r*s)	18812.197	352.291	0.000	192	7281.841
N([g*t]+s) *p*(r)	18822.324	362.418	0.000	190	7296.045
N(g*t) *p*(g*s*t)	18929.102	469.196	0.000	553	6649.370
N(g*s*t) *p*(g*s*t)	19215.200	755.295	0.000	728	6562.237

[a] Codes indicate model structure for additive (+) or interactive (*) effects of region (region), study area (g), sex (s), annual time (t), linear time trend (T), quadratic time trend (TT), land ownership (owner), latitude (latitude), barred owls (BO), or reproduction (r).

[b]) QAICc = difference between the model listed and the best QAICc model.

[c] Number of parameters in model.

[d] Q Deviance is the difference between -2log(‹)/$\hat{c}$ of the current model and -2log(‹)/$\hat{c}$ of the saturated model.

Table 16. Estimates of $\hat{\beta}$ for the effect of reproduction (r) on apparent survival of adult northern spotted owls in different regions. Estimates are from model {N(region*r) *p*(g+t+s)} in the meta-analysis of 14 demographic study areas in Washington, Oregon, and California.

			95% CI	
Region	$\hat{\beta}$	SE	Lower	Upper
Washington Douglas-fir	-0.596	0.234	-1.055	-0.136
Washington Mixed-Conifer	-0.315	0.185	-0.677	0.047
Oregon Coastal Douglas-fir	-0.119	0.209	-0.530	0.291
Oregon Cascades Douglas-fir	-0.507	0.182	-0.863	-0.151
Oregon/California Mixed-Conifer	0.010	0.221	-0.424	0.443
California Coast	0.398	0.318	-0.226	1.023

Table 17. Estimates of)QAIC [a] and $\hat{\beta}$ for the effects of barred owls on apparent annual survival of adult northern spotted owls on 14 demographic study areas in Washington, Oregon, and California. Estimates were based on the best QAIC model that included the barred owl effect.

Study area	)QAICc	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington					
WEN	0.00	-4.69	1.34	-7.32	-2.07
CLE	1.58	-1.40	0.99	-3.33	0.54
RAI	10.86	4.44	2.18	0.16	8.72
OLY	0.00	-4.24	1.83	-7.83	-0.65
Oregon					
COA	2.01	0.03	0.68	-1.31	1.37
HJA	0.89	-1.83	1.69	-5.14	1.48
WSR	2.04	0.08	1.57	-2.98	3.15
TYE	2.37	1.35	1.21	-1.03	3.72
KLA	2.05	0.02	3.34	-6.51	6.56
CAS	1.55	1.80	2.70	-3.49	7.10
California					
NWC	0.95	-2.39	1.68	-5.68	0.90
HUP	1.18	-3.18	3.10	-9.26	2.90
SIM	0.70	-5.80	5.05	-15.68	4.08
MAR	1.99	11.61	27.48	-42.26	65.48

[a])QAICc = difference between the best QAICc model and the best model with the barred owl effect.

Table 18. Estimates of $\hat{\beta}$ for the effect of the barred owl parameter on apparent survival of adult northern spotted owls from the meta-analysis of 14 demographic study areas in Washington, Oregon, and California. Model was $\{N(\mathrm{BO*region})\ p(\mathrm{g+s+t})\}$.

			95% CI	
Model/area	$\hat{\beta}$	SE	Lower	Upper
Washington				
WEN	-4.122	1.218	-6.509	-1.734
CLE	-1.884	1.422	-4.671	0.904
RAI	2.241	2.209	-2.089	6.571
OLY	-4.718	1.649	-7.951	-1.485
Oregon				
COA	0.308	0.584	-0.836	1.452
HJA	-0.777	1.894	-4.889	2.936
WSR	-1.141	2.077	-5.211	2.929
TYE	2.544	1.523	-0.441	5.529
KLA	1.775	3.770	-5.614	9.165
CAS	6.813	2.804	1.317	12.309
California				
NWC	-2.256	2.087	-6.347	1.836
HUP	-3.678	4.398	-12.298	4.943
SIM	-4.919	4.245	-13.238	3.401
MAR	-5.702	47.727	-99.247	87.843

Table 19. Estimates of $\hat{\lambda}_{RJS}$ and temporal process standard deviation ($\hat{\sigma}_{temporal}$) for northern spotted owls on 13 study areas in Washington, Oregon, and California. Estimates are based on means (intercepts only) random effects models using time-specific estimates of N, p and 8, except where noted.

					95% CI			95% CI	
Study	Model [a]	$\hat{\lambda}_{RJS}$	SE	CV	Lower	Upper	$\hat{\sigma}_{temporal}$	Lower	Upper
Density study areas									
TYE	N(t) p(t) λ(t) REλ(mean)	1.005	0.019	0.019	0.967	1.043	0.050	0.000	0.126
NWC	N(t) p(t) λ(t) REλ(mean)	0.985	0.013	0.013	0.959	1.011	0.000	0.000	0.017
HUP	N(t) p(t) λ(t) REλ(mean)	0.980	0.019	0.019	0.943	1.017	0.000	0.000	0.131
SIM	N(t) p(t) λ(t) REλ(mean)	0.970	0.012	0.012	0.947	0.993	0.015	0.000	0.077
Territory study areas [b]									
WEN	N(t) p(t) λ(t) REλ(mean)	0.917	0.018	0.019	0.882	0.952	0.038	0.000	0.147
CLE	N(t) p(t) λ(t) REλ(mean)	0.938	0.019	0.020	0.901	0.976	0.000	0.000	0.090
RAI	N(t) p(t) γ(t) [c]	0.896	0.055	0.061	0.788	1.003	[c]	[c]	[c]
OLY	N(ea*t) p(ea*t) λ(ea*t) REλ(mean)	0.956	0.032	0.034	0.893	1.018	0.091	0.000	0.222
COA	N(t) p(t) λ(t) REλ(mean)	0.968	0.018	0.019	0.932	1.004	0.000	0.000	0.067
HJA	N(ea*t) p(ea*t) λ(ea*t) REλ(mean)	0.978	0.014	0.015	0.950	1.005	0.000	0.000	0.064
WSR	N(t) p(t) λ(t) REλ(mean)	0.908	0.022	0.024	0.866	0.951	0.000	0.000	0.152

Table 19. (continued).

Study	Model [a]	$\hat{\lambda}_{RJS}$	SE	CV	95% CI Lower	95% CI Upper	$\hat{\sigma}_{process}$	95% CI Lower	95% CI Upper
KLA	N(t) *p*(t) λ(t) REλ(T)	0.997	0.034	0.042	0.930	1.063	0.026	0.000	0.135
CAS	N(ea*t) *p*(ea*t) λ(ea*t) REλ(mean)	0.974	0.035	0.035	0.906	1.042	0.082	0.000	0.269
Mean for density study areas		0.985	0.016						
Mean for territory study areas		0.951	0.027						
Mean for all areas		0.959	0.024						

[a] Best capture-recapture model structure from analysis of the *a priori* model set. Model notation indicates structure for effects of time (t), expansion year (ea), linear time trend (T) or constant (mean). RE = random effects.

[b] Marin Study Area not included because sample was too small to estimate 8.

[c] Model fit using a N and (parameterization; 8 was calculated via arithmetic mean.

Table 20. Models selected in the meta-analysis of 8_{RJS} of northern spotted owls in Washington, Oregon, and California. Analyses were conducted separately for the 4 Density Study Areas (1985–2003) and 10 Territory Study Areas (1987-2003).

Model [a]	QAICc	) QAICc [b]	Akaike weight	*K* [c]
Density study areas				
N(g*t) *p*(g*t) λ(.)	9302.567	0.000	0.374	113
N(g*t) *p*(g*t) λ(region)	9303.128	0.561	0.283	115
N(g*t) *p*(g*t) λ(owner)	9303.418	0.851	0.244	115
N(g*t) *p*(g*t) λ(g)	9305.241	2.674	0.098	116
N(g*t) *p*(g*t) λ(region+t)	9316.061	13.494	0.000	129
N(g*t) *p*(g*t) λ(owner+t)	9316.800	14.233	0.000	129
N(g*t) *p*(g*t) λ(g+t)	9318.121	15.554	0.000	130
N(g*t) *p*(g*t) λ(t)	9318.896	16.329	0.000	127
N(g*t) *p*(g*t) λ(region*t)	9340.882	38.315	0.000	144
N(g*t) *p*(g*t) λ(owner*t)	9341.759	39.192	0.000	145
N(g*t) *p*(g*t) λ(g*t)	9354.079	51.512	0.000	152
Territory study areas				
N(g*t) *p*(g*t) λ(g*t)	19790.239	0.000	1.000	324
N(owner*t) *p*(owner*t) λ(owner+t)	19956.233	165.994	0.000	114
N(owner*t) *p*(owner*t) λ((owner*t)	19971.521	181.282	0.000	126
N(t) *p*(t) λ(t)	19981.221	190.982	0.000	69
N(region*t) *p*(region*t) λ(region+t)	20090.581	300.342	0.000	226

[a] Model notation indicates structure for study area (g), time (t), geographic region (region), land ownership (owner), or constant (.).

[b]) QAICc = the difference between the model listed and the best QAICc model.

[c] Number of parameters in model.

Table 21. Summary of trends in demographic parameters for northern spotted owls from 14 study areas in Washington, Oregon, and California, 1985-2003.

Study Area	Land ownership [a]	Fecundity	Apparent survival	λ_{RJS}	$\hat{\lambda}$ [b]
Washington					
WEN	Private	Stable	Declining	0.917	Declining
CLE	USFS	Declining [c]	Declining? [d]	0.938	Declining
RAI	USFS	Stable	Declining	0.896	Declining
OLY	NPS & USFS	Stable	Declining	0.956	Declining
Oregon					
COA	USFS & BLM	Declining? [c]	Stable	0.968	Declining
HJA	USFS	Stable? [e]	Stable	0.978	Declining
WSR	Tribal	Stable	Stable	0.908	Declining
TYE	BLM & private	Increasing	Stable	1.005	Stationary
KLA	BLM & private	Stable	Stable	0.997	Stationary
CAS	USFS & BLM	Declining	Stable	0.974	Stationary
California					
NWC	USFS	Declining	Declining	0.985	Declining? [f]
HUP	Tribal	Increasing	Stable	0.980	Stationary
SIM	Private	Declining [c]	Stable	0.970	Declining
MAR	NPS	Stable	Stable	NA [g]	NA [g]

[a] Acronyms indicate U.S. Forest Service (USFS), Bureau of Land Management (BLM), and U.S. National Park Service (NPS).

[b] Trend based on estimates of realized population change ( ) 8).

[c] Best model included age and even-odd year effects, but a competing model had a negative time effect on productivity.

[d] Variable among years, but with a declining trend.

[e] Decreasing in early years, increasing in last 5 years, but stable overall.

[f] Gradual declines in fecundity and apparent survival, plus estimates of realized population change suggest a decline in last 8 years.

[g] Sample too small to estimate 8.

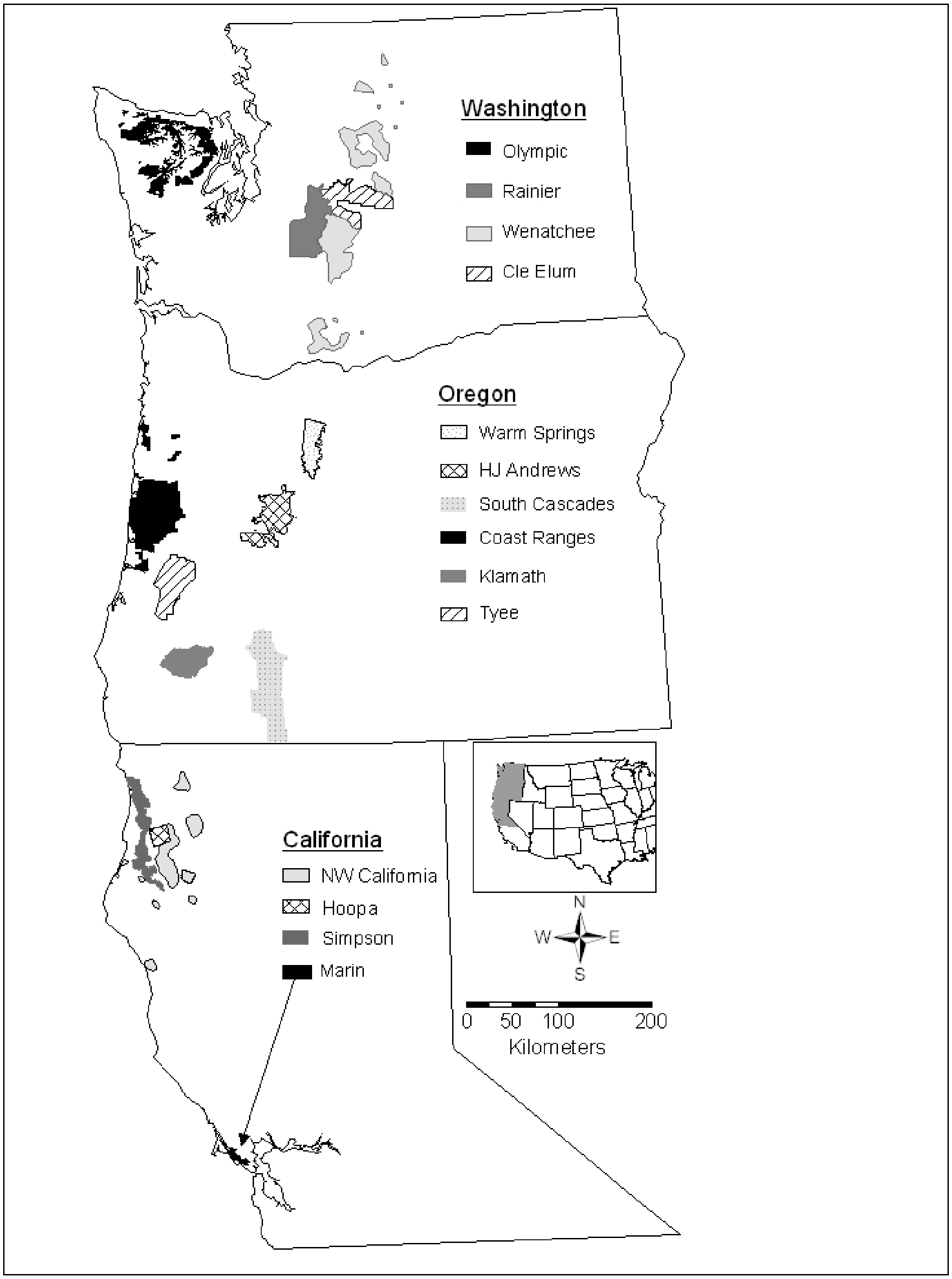

Washington
Olympic
Rainier
Wenatchee
Cle Elum
Oregon
Warm Springs
HJ Andrews
South Cascades
Coast Ranges
Klamath
Tyee
California
NW California
Hoopa
Simpson
Marin
N
W
E
S
0
50
100
200
Kilometers

Fig. 1. The location and distribution of 14 northern spotted owl demographic study areas for which data were analyzed.

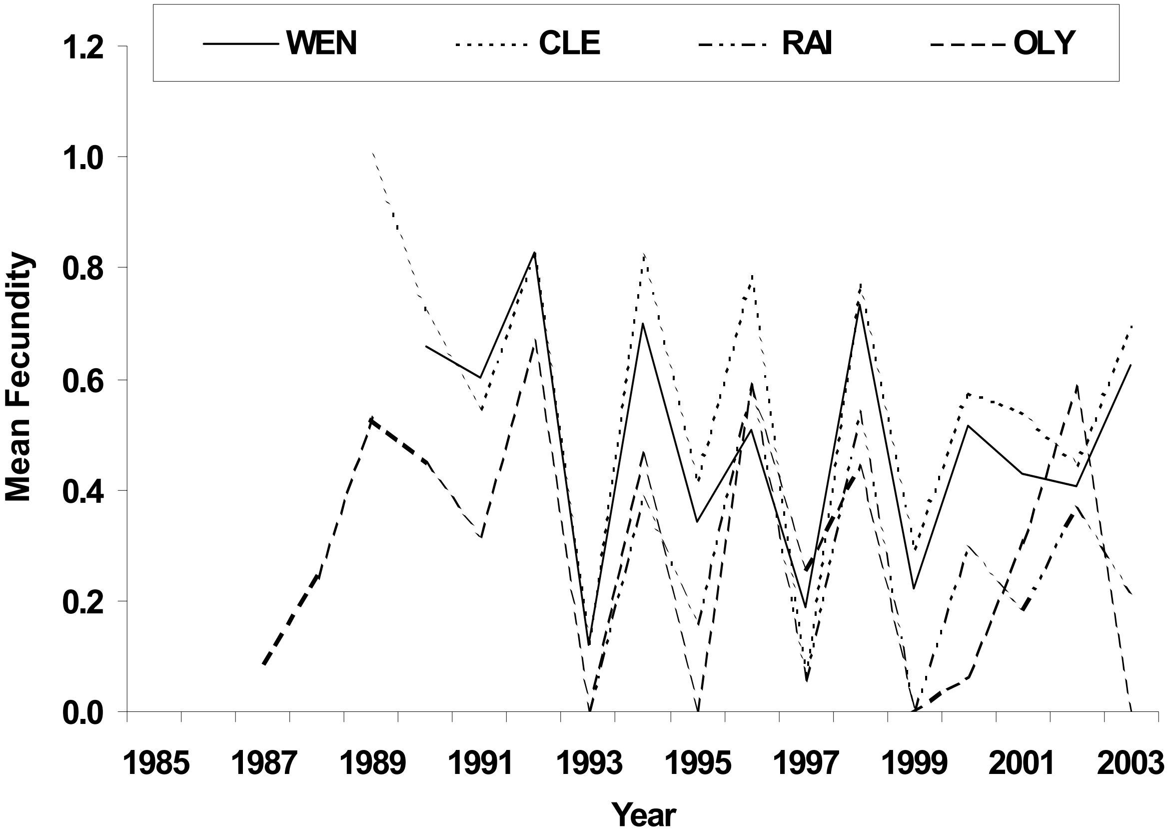


Fig. 2a. Raw estimates of mean annual fecundity (number of young fledged per female) for adult northern spotted owls on 4 study areas in Washington (study area acronyms specified in Table 1; Appendix A).

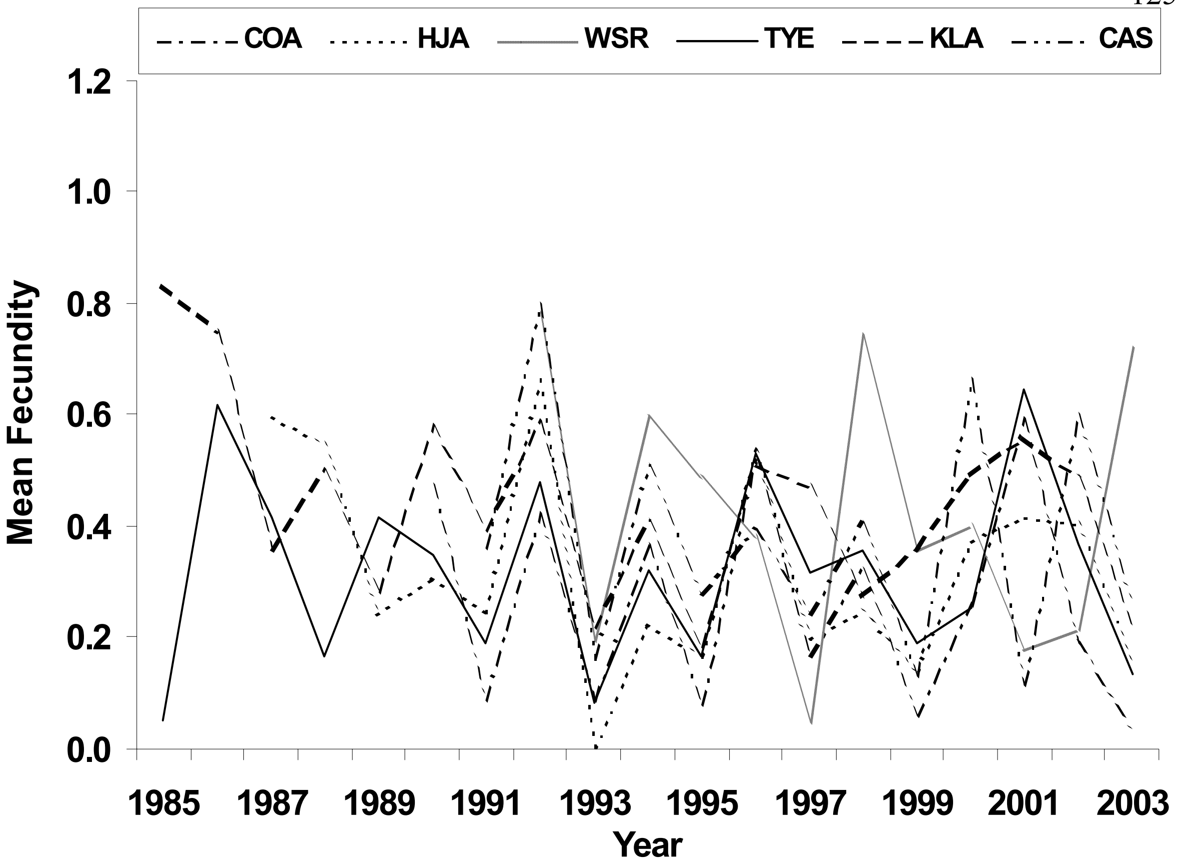


Fig. 2b. Raw estimates of mean annual fecundity (number of young fledged per female) for adult northern spotted owls on 6 study areas in Oregon (study area acronyms specified in Table 1; Appendix A).

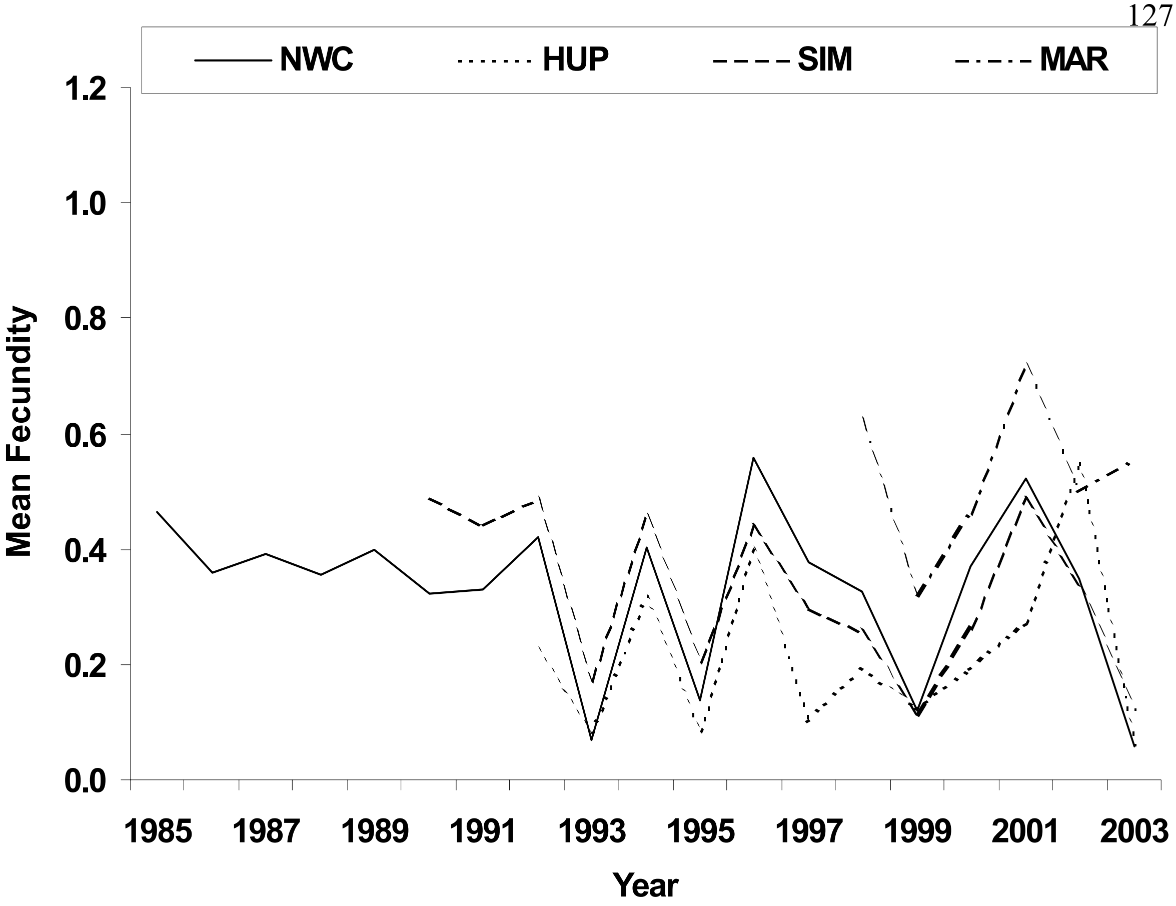


Fig. 2c. Raw estimates of mean annual fecundity (number of young fledged per female) for adult northern spotted owls on 4 study areas in California (study area acronyms specified in Table 1; Appendix A).

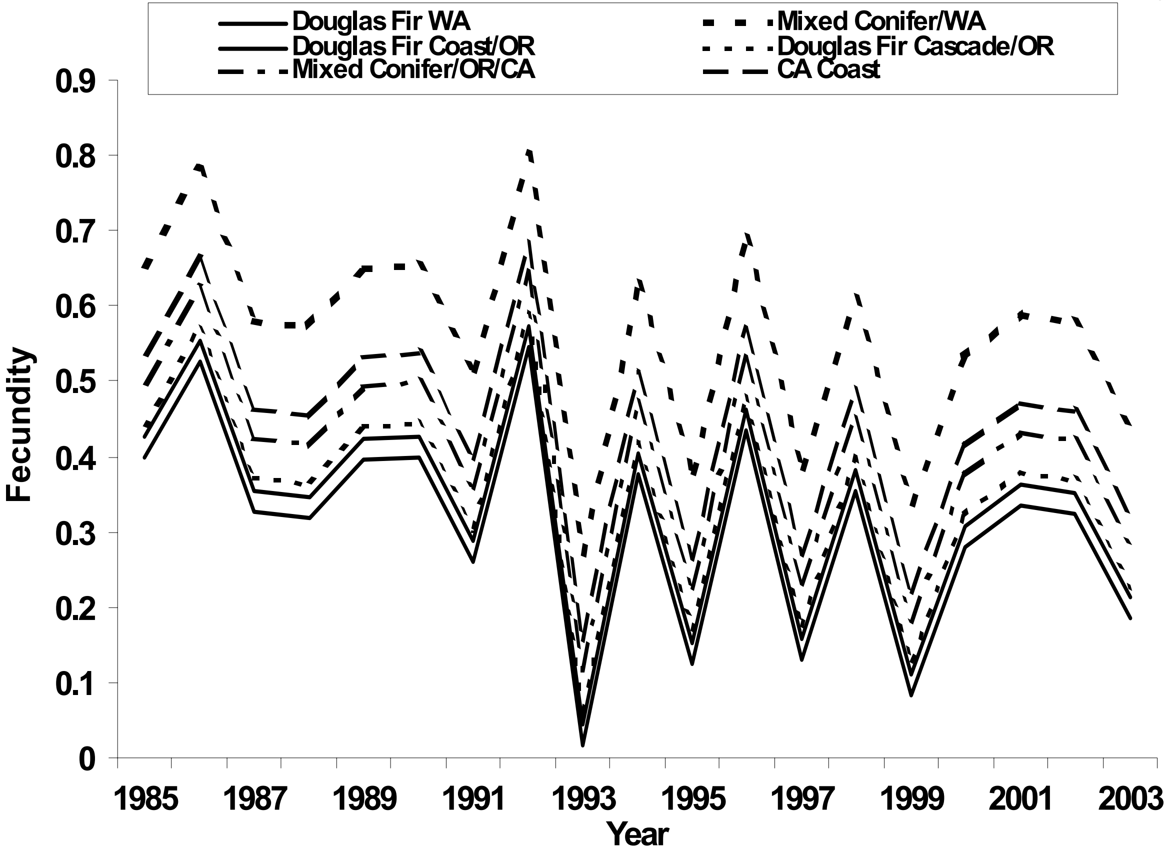


Fig. 3. Estimated annual fecundity (females fledged per adult female) for northern spotted owls in 6 ecological regions, based on the best selected model (region + t) from a meta-analysis of all 14 study areas.

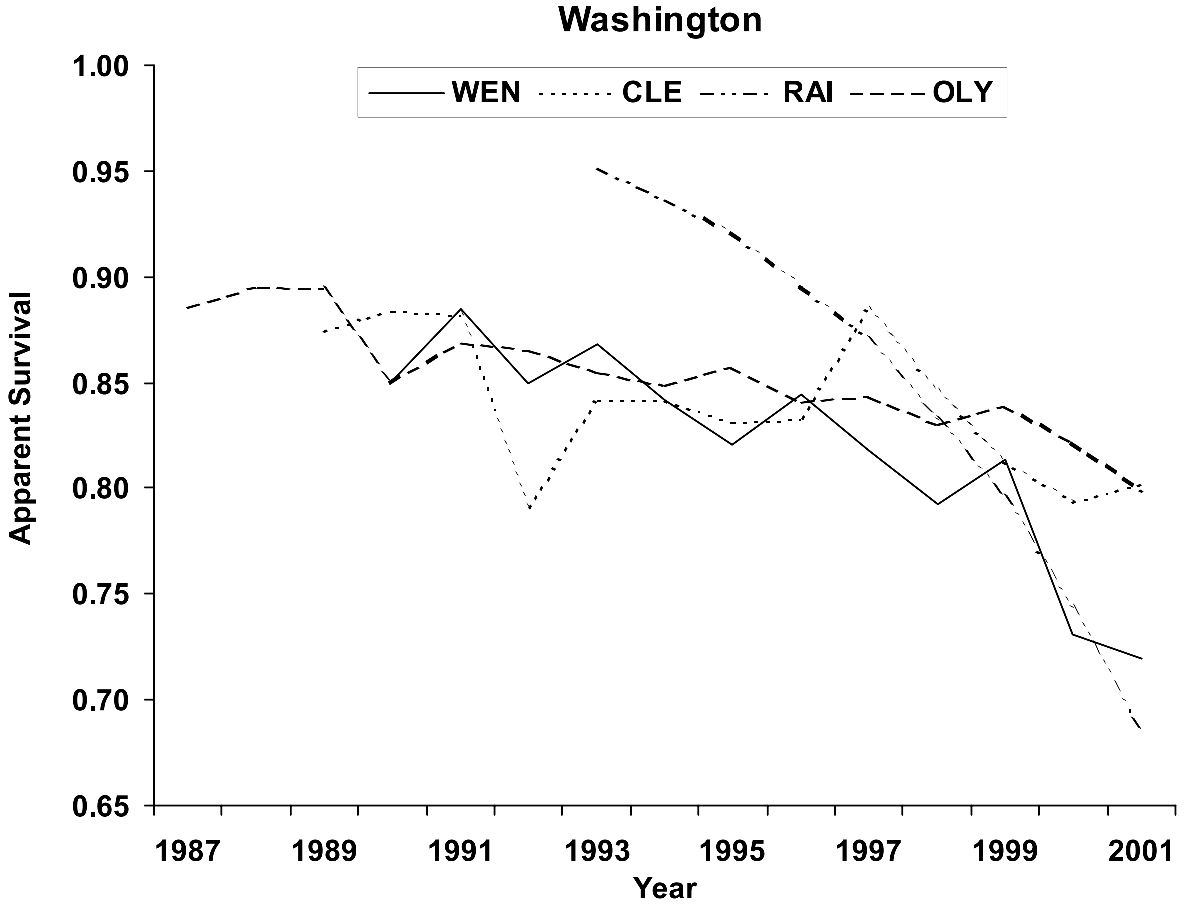

Washington
WEN
CLE
RAI
OLY
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
1987
1989
1991
1993
1995
1997
1999
2001
Year

Fig. 4a. Model averaged estimates of female, non-juvenile apparent survival for northern spotted owls on 4 study areas in Washington (study area acronyms specified in Table 1; Appendix A).

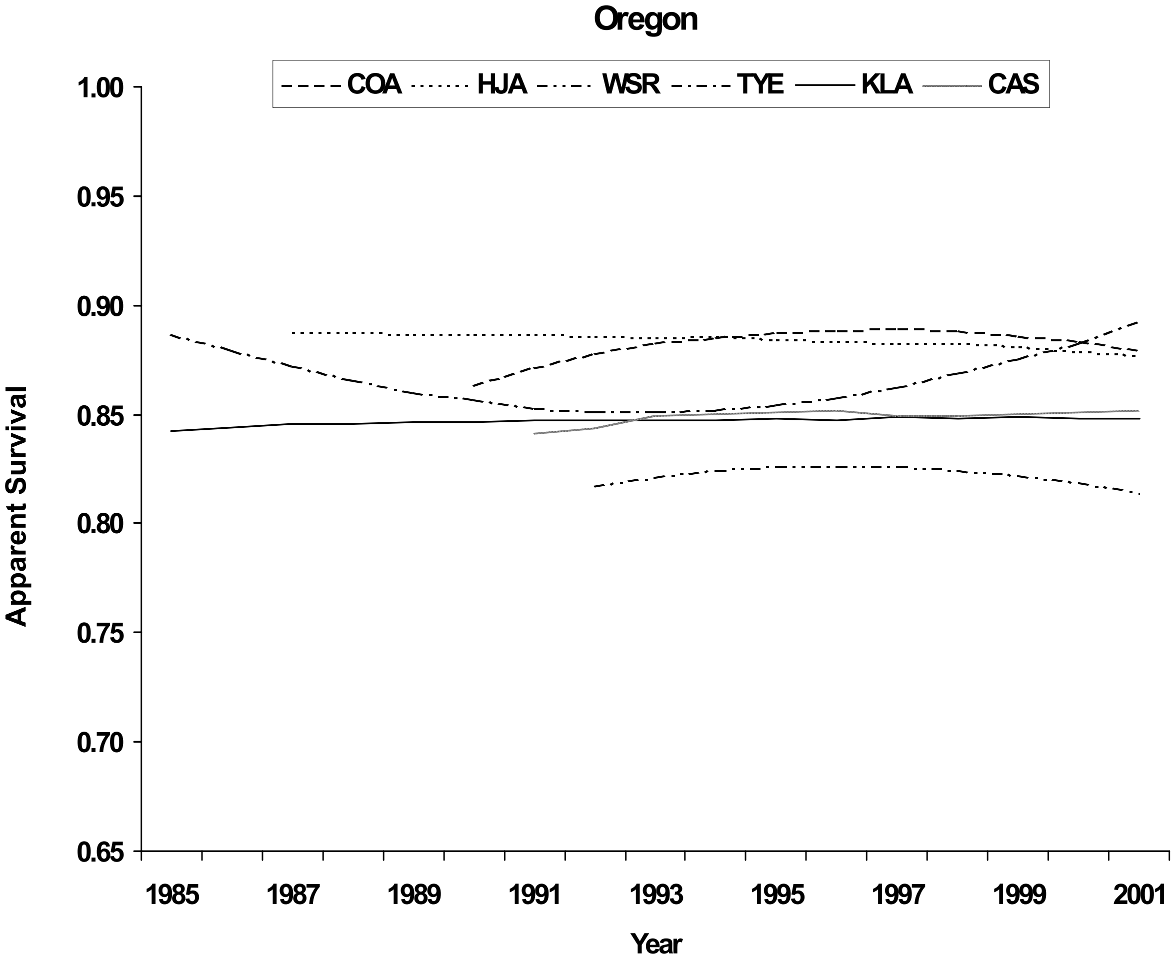


Fig. 4b. Model averaged estimates of female, non-juvenile apparent survival for northern spotted owls on 6 study areas in Oregon (study area acronyms specified in Table 1; Appendix A).

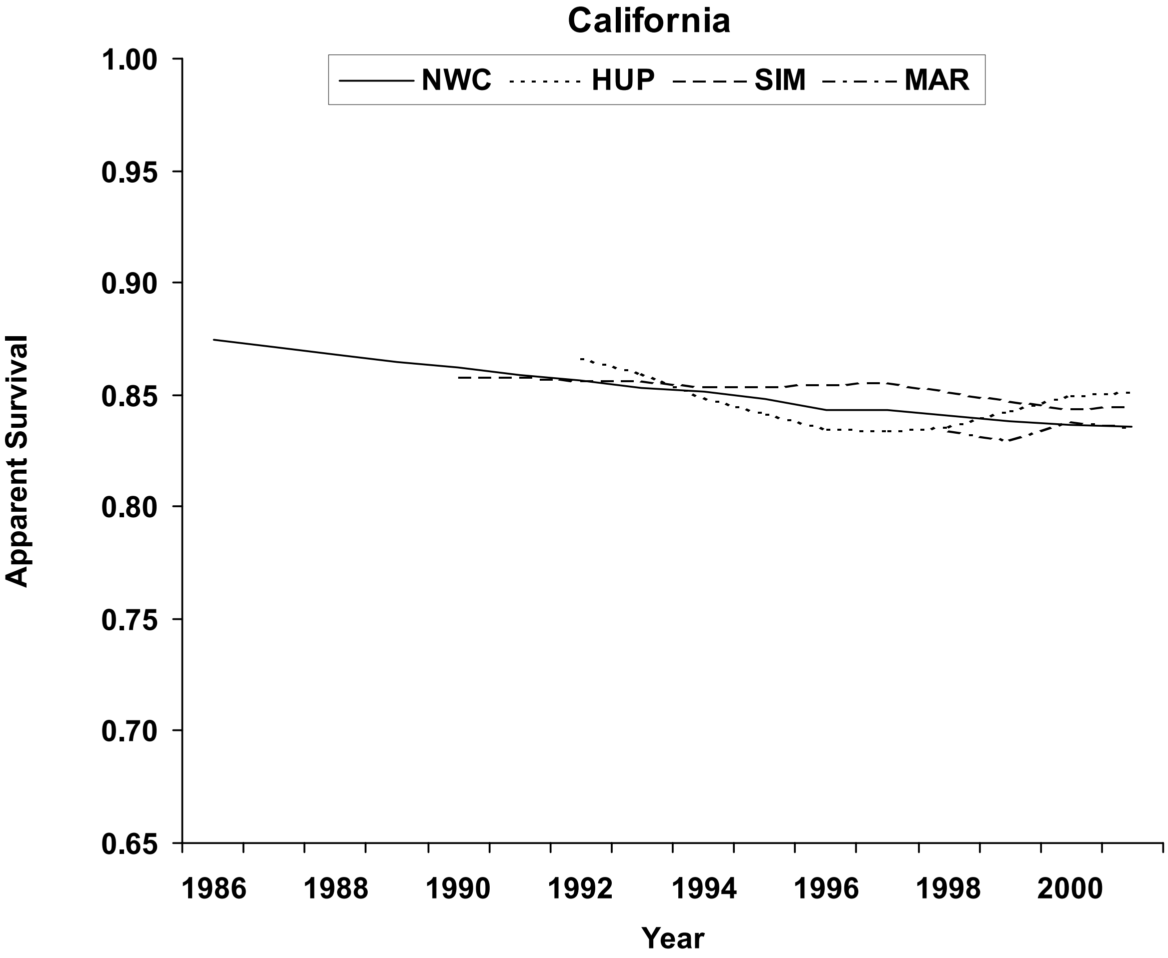


Fig. 4c. Model averaged estimates of female, non-juvenile apparent survival for northern spotted owls on 4 study areas in California (study area acronyms specified in Table 1; Appendix A).

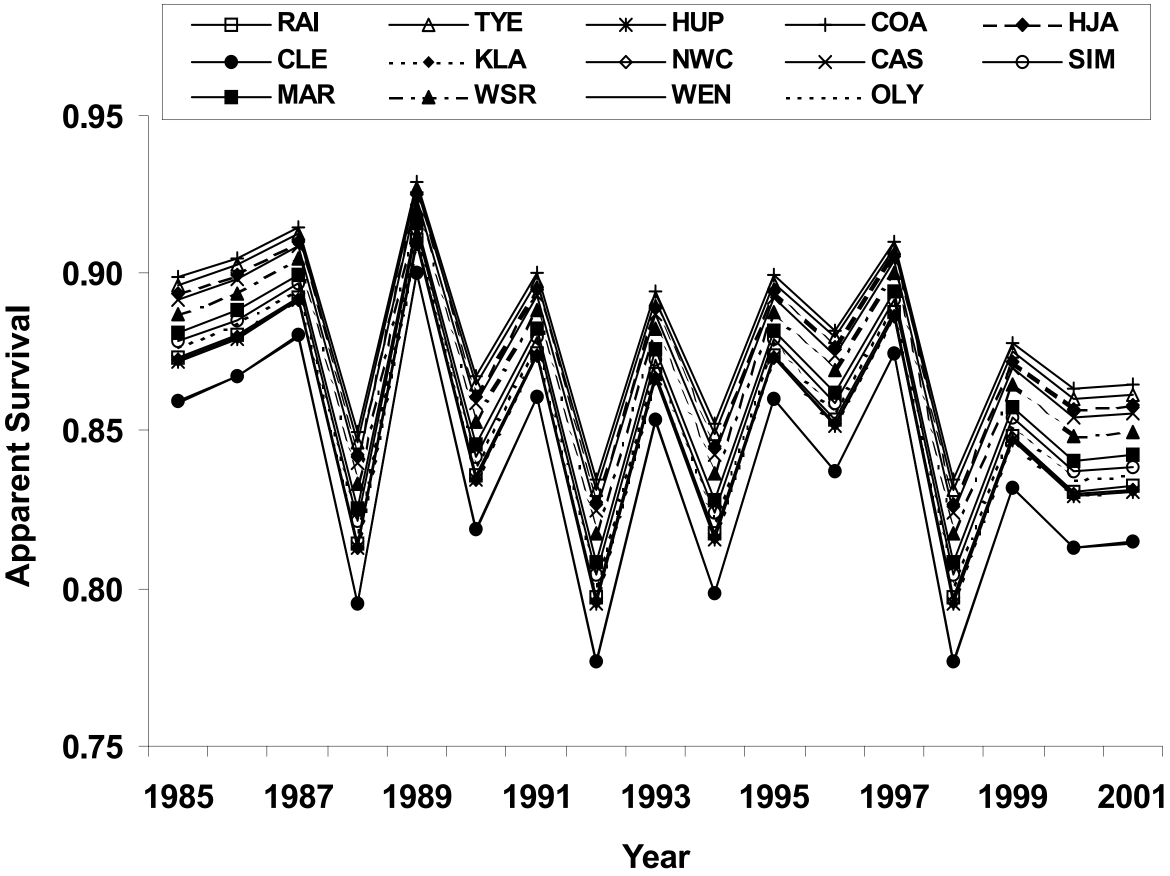


Fig. 5. Model averaged estimates of apparent survival for adult, female northern spotted owls from the meta-analysis of 14 study areas (study area acronyms specified in Table 1; Appendix A).

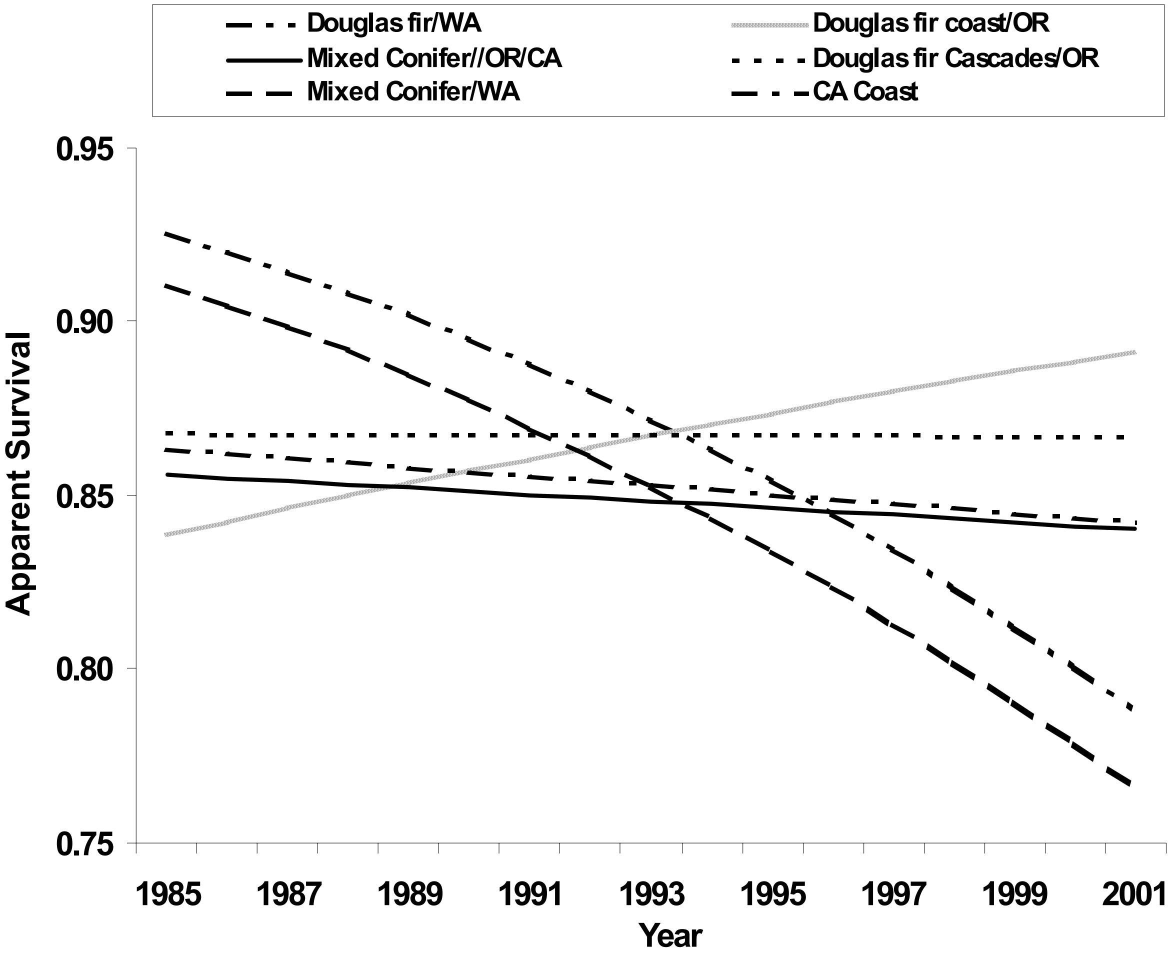


Fig. 6. Estimates of apparent survival from model {ϕ (region*T), p(g+t+s)} for adult northern spotted owls from the meta-analysis of 14 study areas.

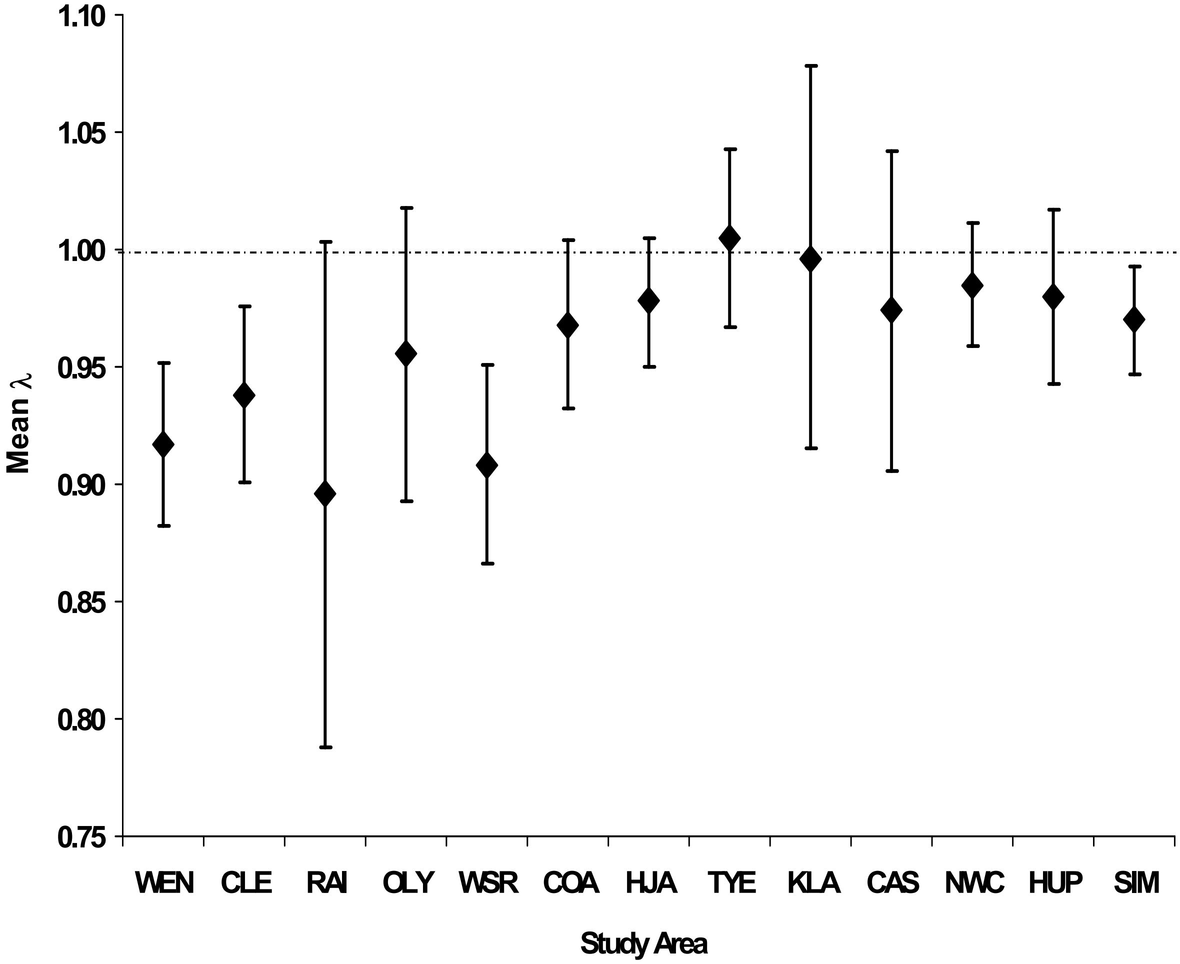
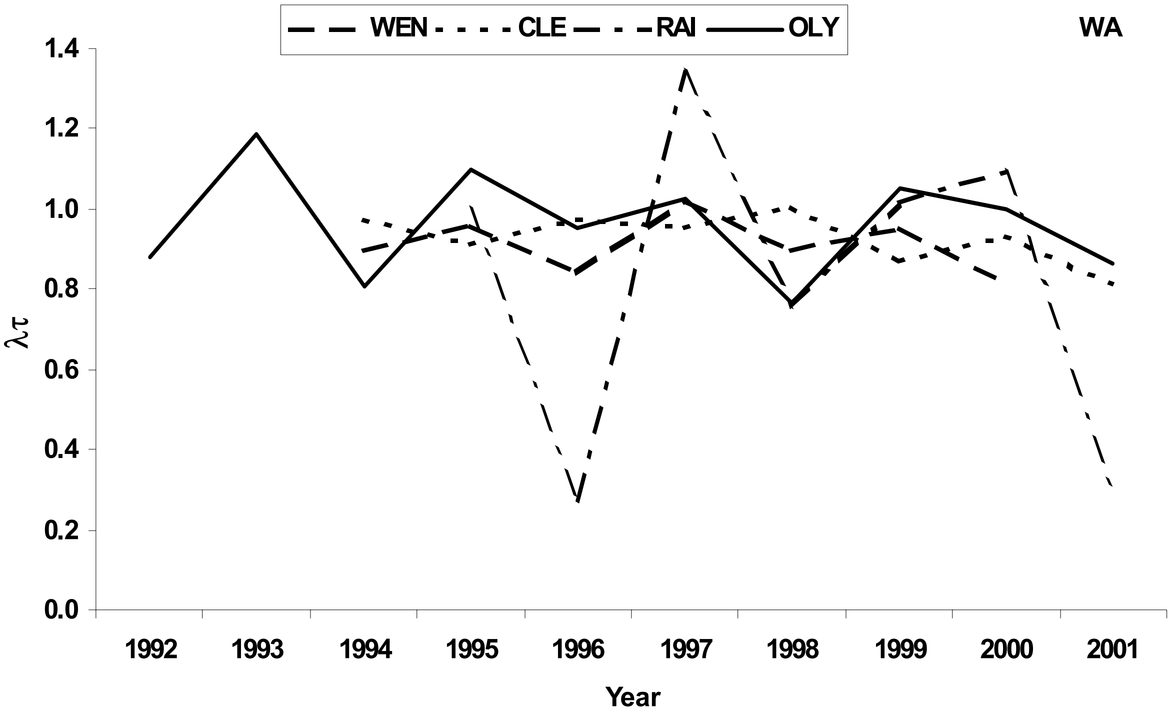


Fig. 7. Estimates of mean λ_{RJS} from random effects models based on ϕ (t) p(t) λ(t), with 95% confidence intervals for northern spotted owls on 13 study areas in Washington

(WEN, CLE, RAI, OLY), Oregon (WSR, COA, HJA, TYE, KLA, CAS), and California (NWC, HUP, SIM) (study area acronyms specified in Table 1; Appendix A).


WEN
CLE
RAI
OLY
WA
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
λτ
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
Year

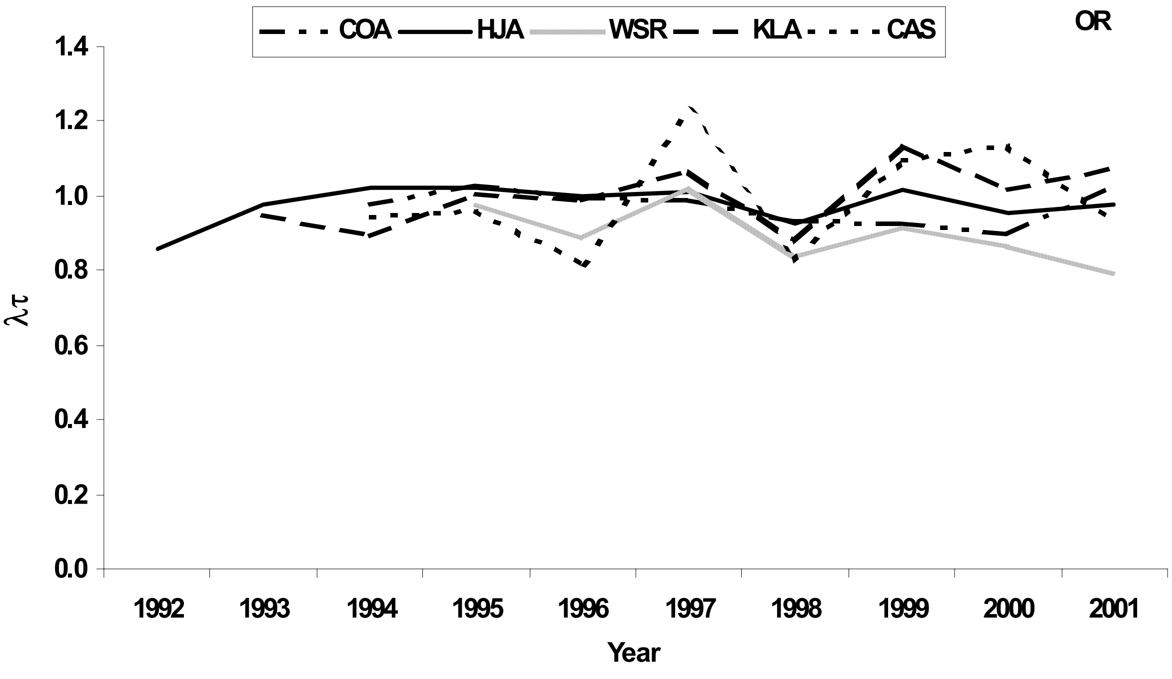

COA
HJA
WSR
KLA
CAS
OR
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
λτ
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
Year

Fig. 8. Annual estimates of λ_{RJS} for adult northern spotted owls on 9 Territory Study Areas (TSA) in Washington (WEN, CLE, RAI, OLY) and Oregon (COA, HJA, WSR, KLA, CAS), generated from model $\{\phi(t), p(t), \lambda(t)\}$ for each study area where t represents time (study area acronyms specified in Table 1; Appendix A).

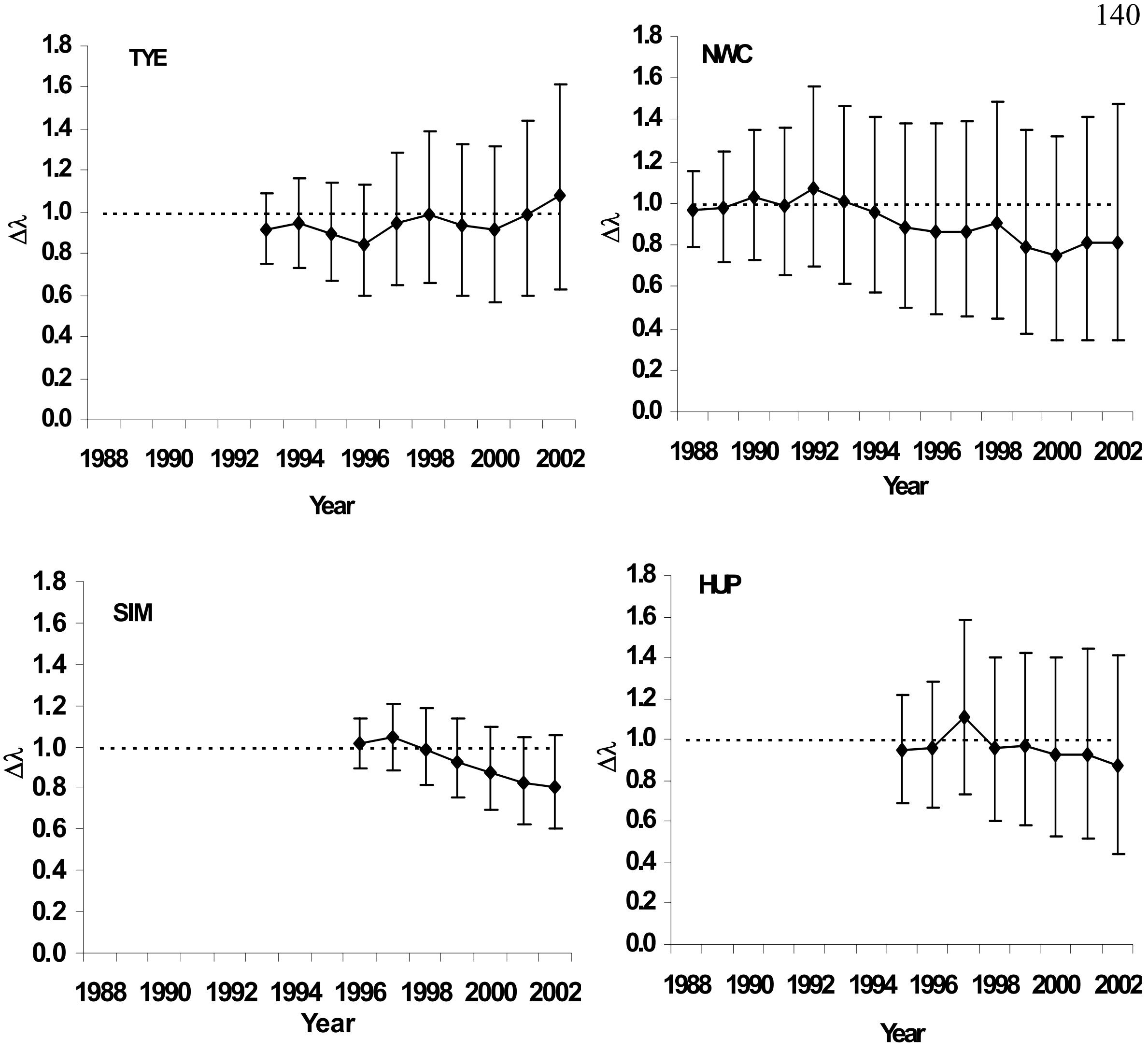
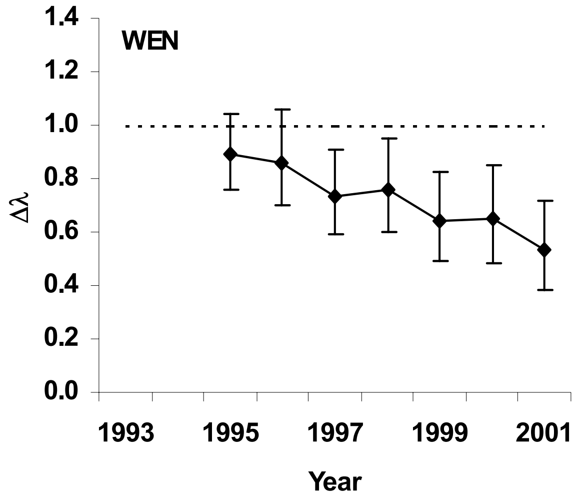
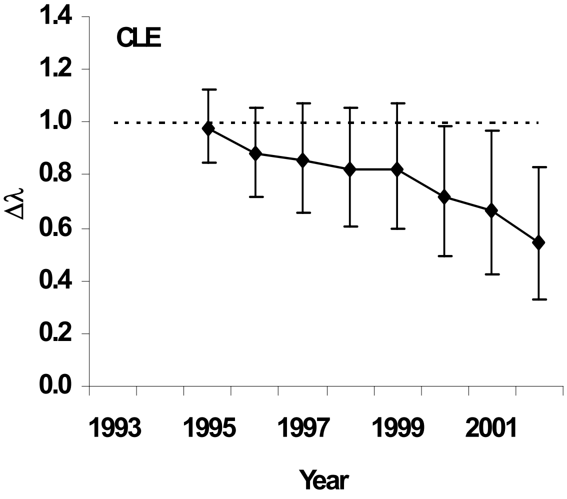
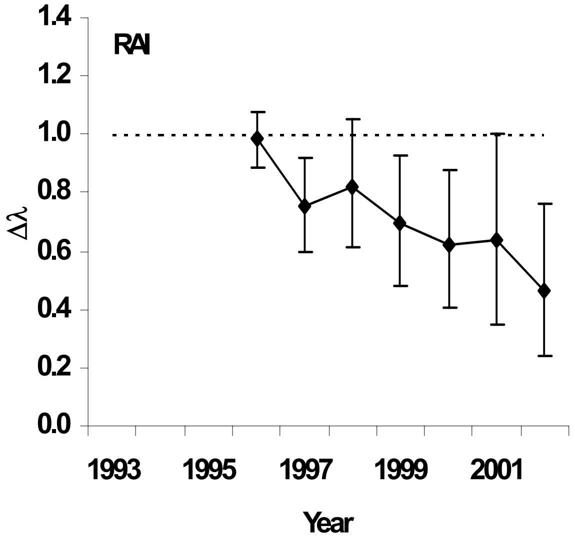


Fig. 9a. The realized change in population size ($\Delta\hat{\lambda}$) with 95% confidence intervals for northern spotted owls in the 4 Density Study Areas (DSA) (study area acronyms in Table 1; Appendix A).


WEN
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Δλ
1993
1995
1997
1999
2001
Year


CLE
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Δλ
1993
1995
1997
1999
2001
Year


RAI
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Δλ
1993
1995
1997
1999
2001
Year

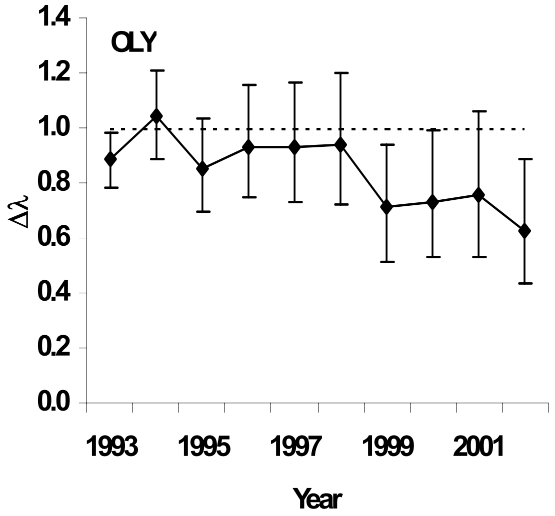
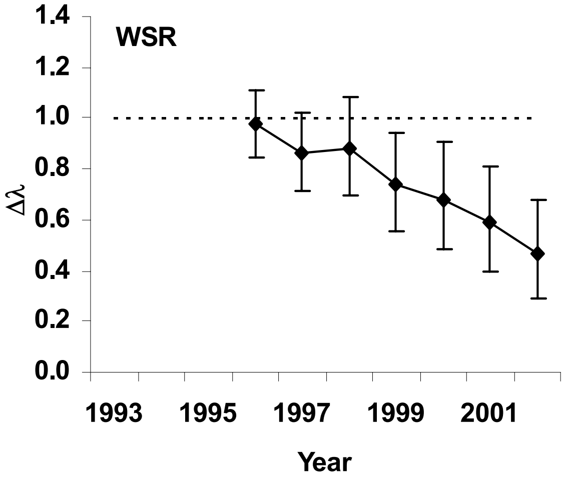
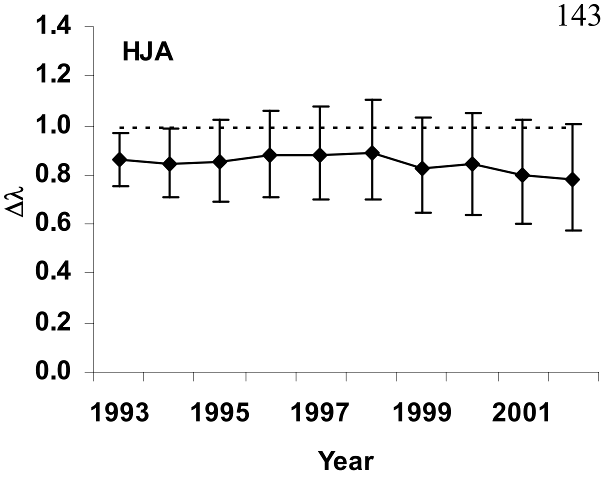
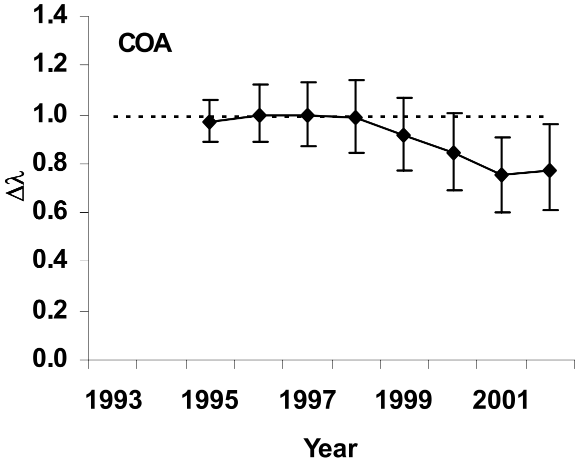
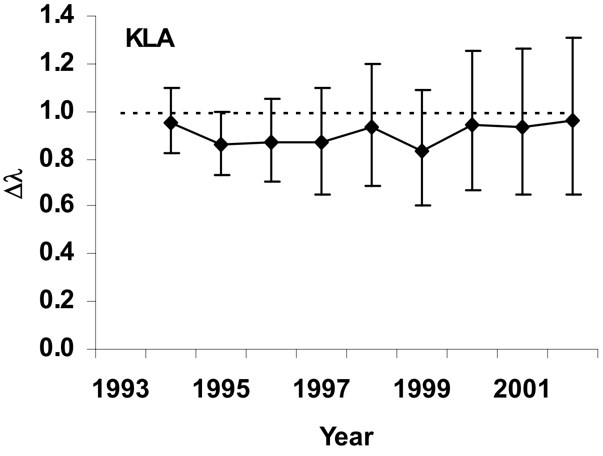

OLY
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Δλ
1993
1995
1997
1999
2001
Year

Fig. 9b. The realized change in population size ($\Delta\hat{\lambda}$) with 95% confidence intervals for northern spotted owls on the 4 Territory Study Areas (TSA) in Washington (study area acronyms in Table 1; Appendix A).


WSR
Δλ
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1993
1995
1997
1999
2001
Year


HJA
Δλ
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1993
1995
1997
1999
2001
Year


COA
Δλ
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1993
1995
1997
1999
2001
Year


KLA
Δλ
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1993
1995
1997
1999
2001
Year

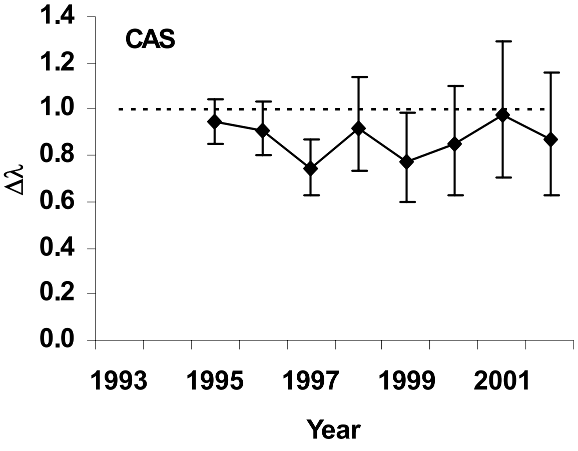
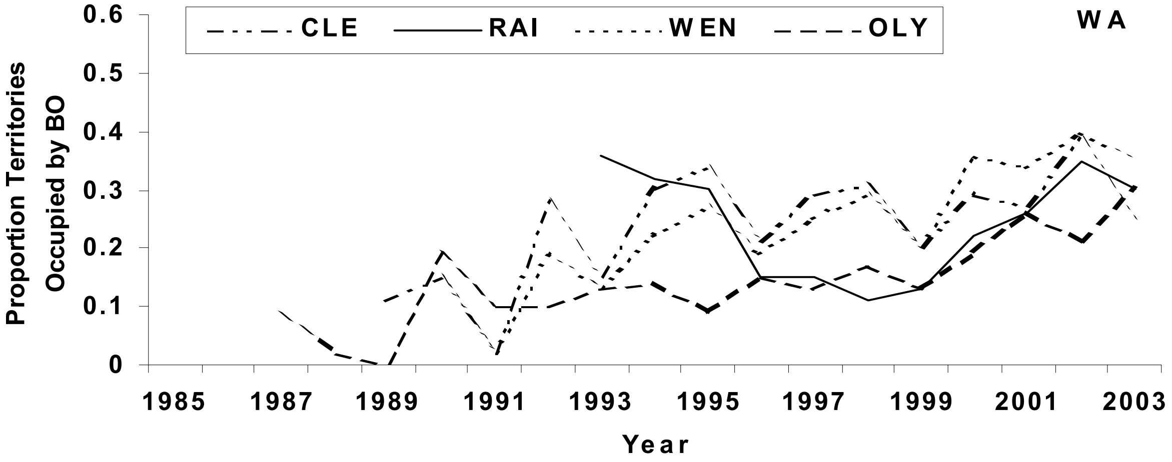
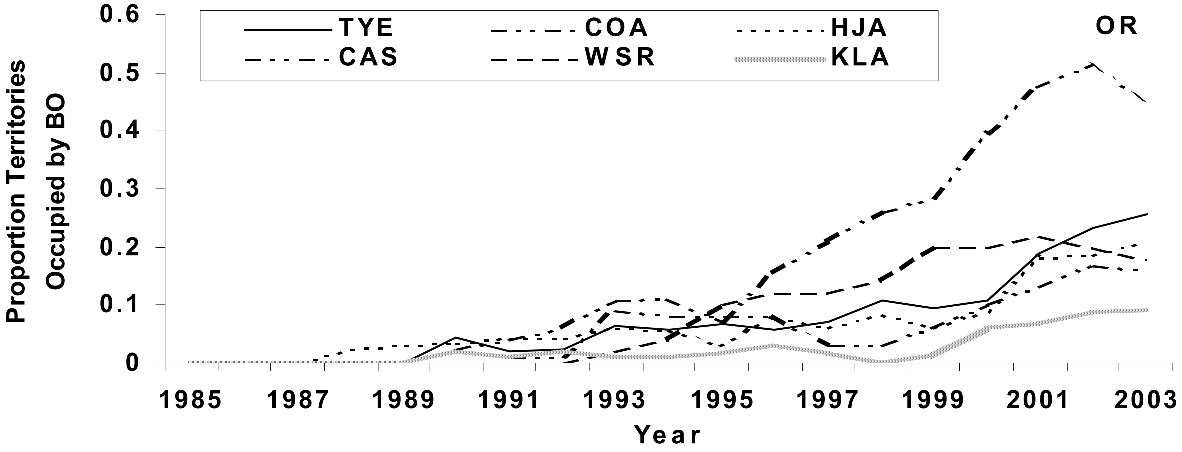
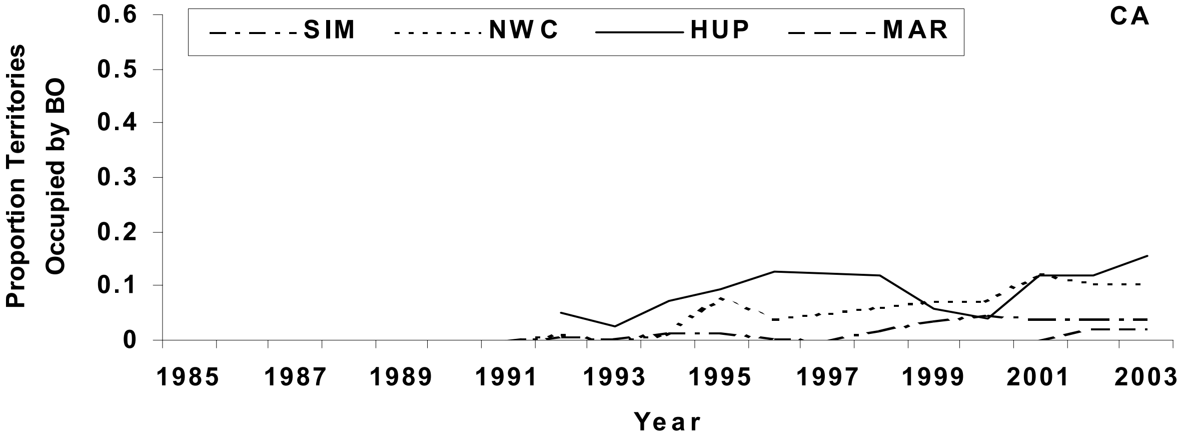

CAS
Δλ
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1993
1995
1997
1999
2001
Year

Fig. 9c. The realized change in population size ($\Delta\hat{\lambda}$) with 95% confidence intervals for northern spotted owls on the 5 Territory Study Areas (TSA) in Oregon (study area acronyms in Table 1; Appendix A).

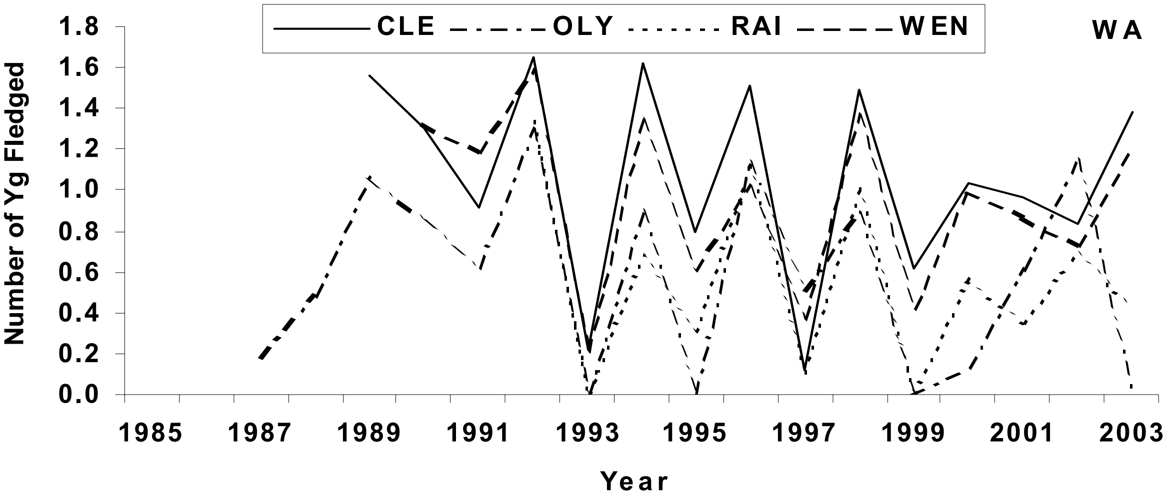
Appendix D. Barred Owl covariate used to model northern spotted owl fecundity, survival and capture probability on 14 study areas in Washington (WA), Oregon (OR), and California (CA) (study area acronyms specified in Table 1; Appendix A).

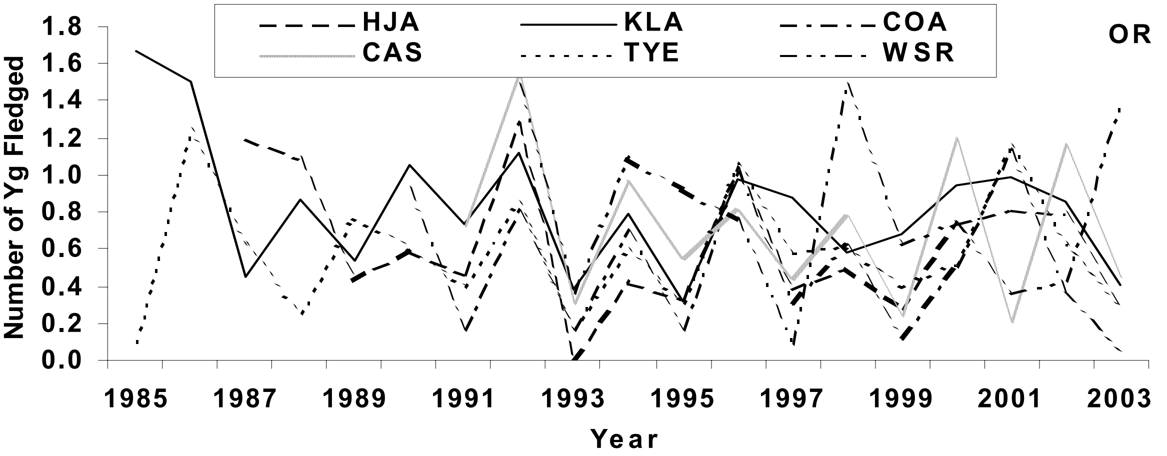

CLE
RAI
WEN
OLY
WA
Proportion Territories Occupied by BO
0.6
0.5
0.4
0.3
0.2
0.1
0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

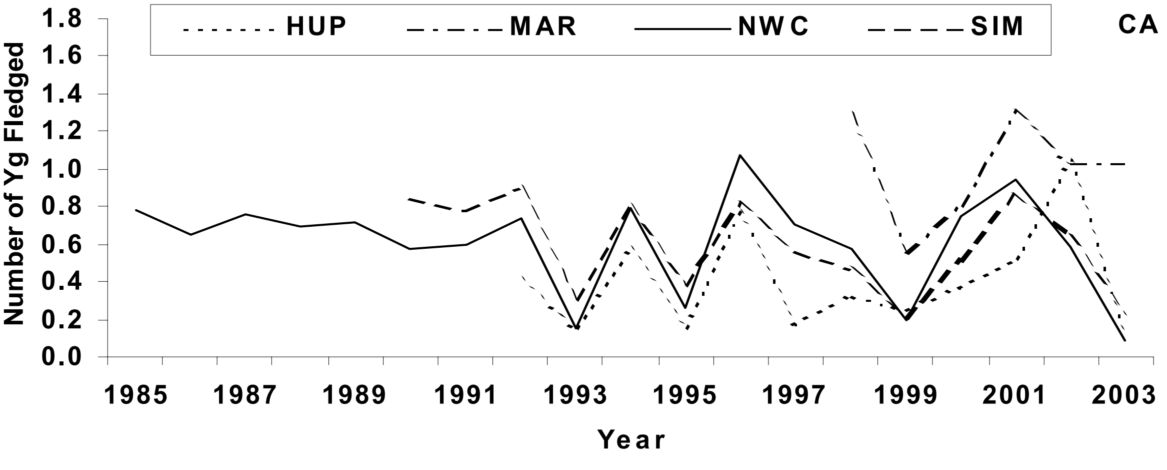

TYE
COA
HJA
CAS
WSR
KLA
OR
Proportion Territories Occupied by BO
0.6
0.5
0.4
0.3
0.2
0.1
0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year


SIM
NWC
HUP
MAR
CA
Proportion Territories Occupied by BO
0.6
0.5
0.4
0.3
0.2
0.1
0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

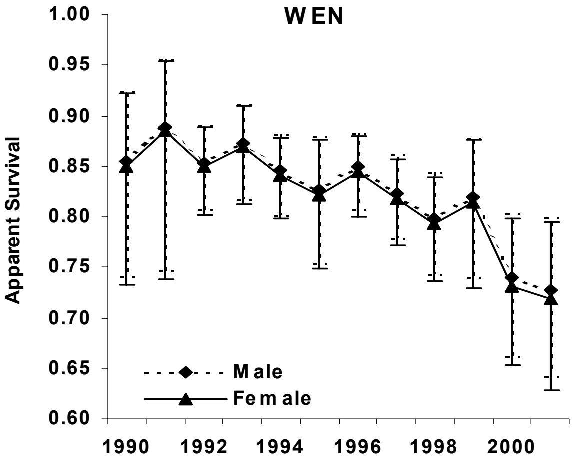
Appendix E. Reproductive covariate (number of young fledged per year) used to model northern spotted owl fecundity, survival and capture probability on 14 study areas in Washington (WA), Oregon (OR), and California (CA) (study area acronyms specified in Table 1; Appendix A).

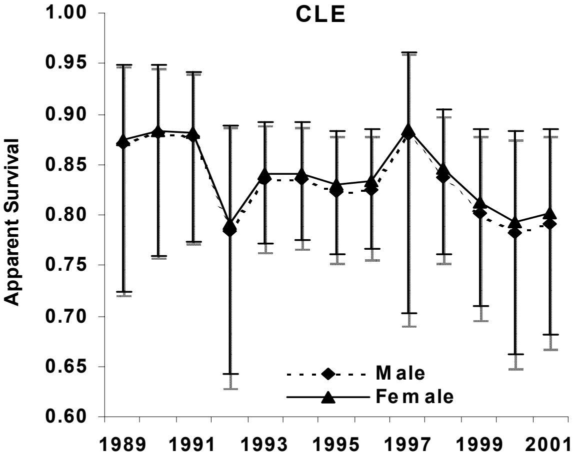

CLE
OLY
RAI
WEN
WA
Number of Yg Fledged
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

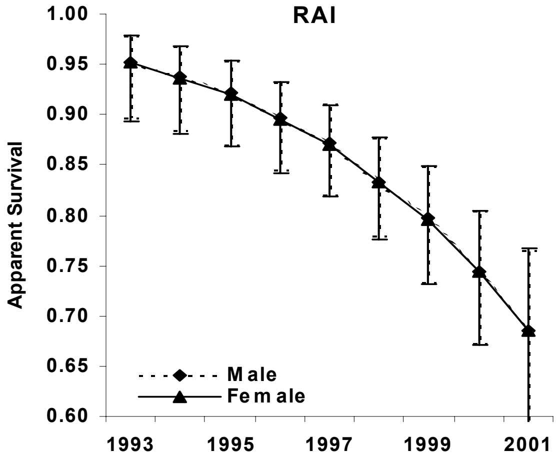

HJA
KLA
COA
CAS
TYE
WSR
OR
Number of Yg Fledged
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

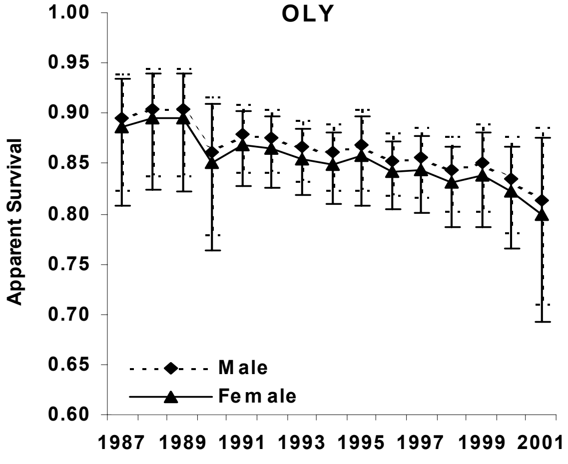

HUP
MAR
NWC
SIM
CA
Number of Yg Fledged
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

Appendix I. Model averaged apparent survival estimates with 95% confidence intervals for male and female northern spotted owls on the 4 study areas in Washington (WEN, CLE, RAI, OLY), 6 study areas in Oregon (COA, HJA, WSR, TYE, KLA, CAS), and 4 study areas in California (NWC, HUP, SIM, MAR). Study area acronyms specified in Table 1; Appendix A.

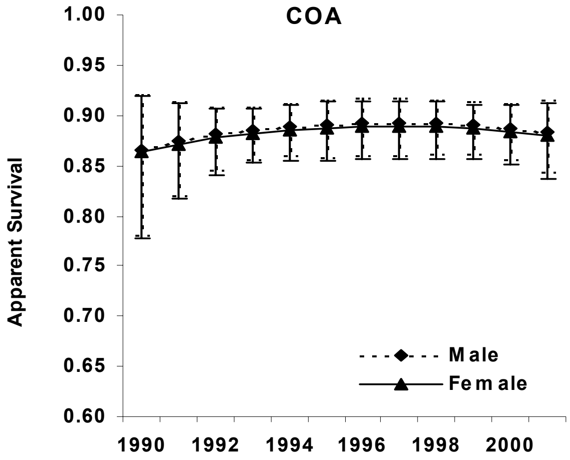

WEN
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1990
1992
1994
1996
1998
2000
Male
Female

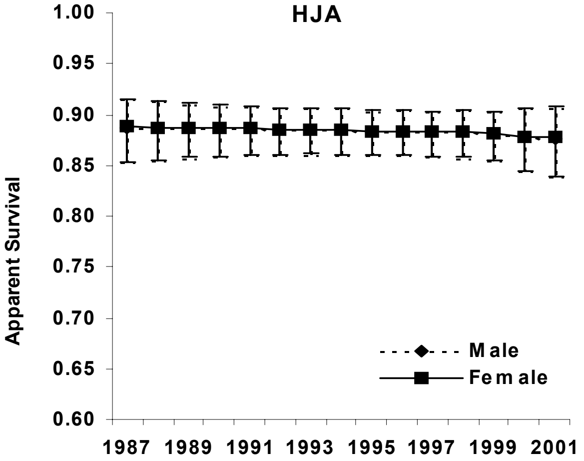

CLE
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1989
1991
1993
1995
1997
1999
2001
Male
Female

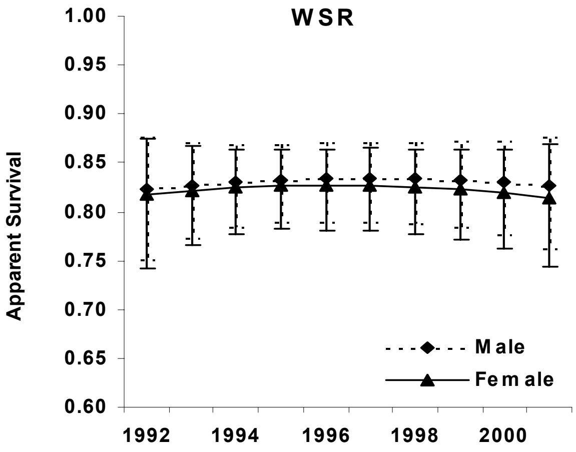

RAI
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1993
1995
1997
1999
2001
Male
Female

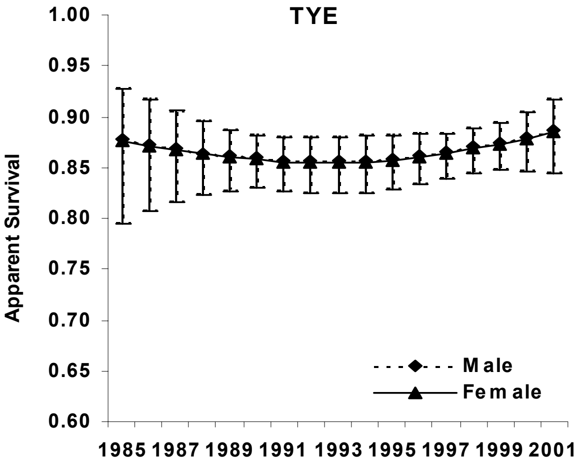

OLY
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1987
1989
1991
1993
1995
1997
1999
2001
Male
Female

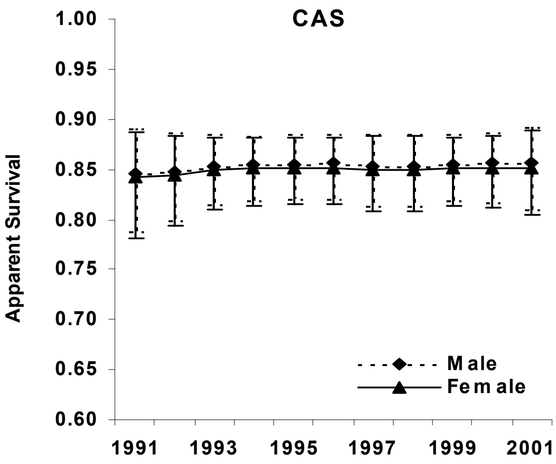
Appendix I cont.

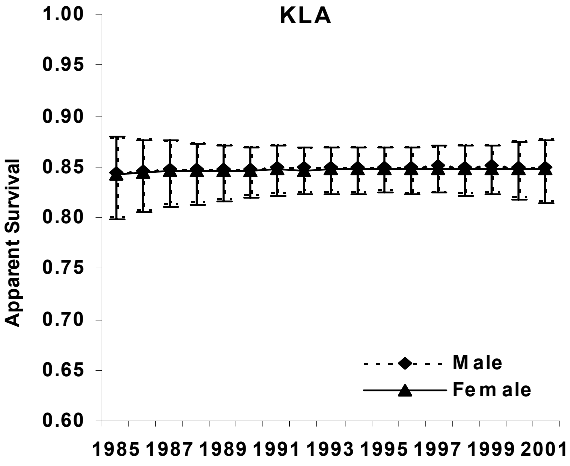

COA
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1990
1992
1994
1996
1998
2000
Male
Female

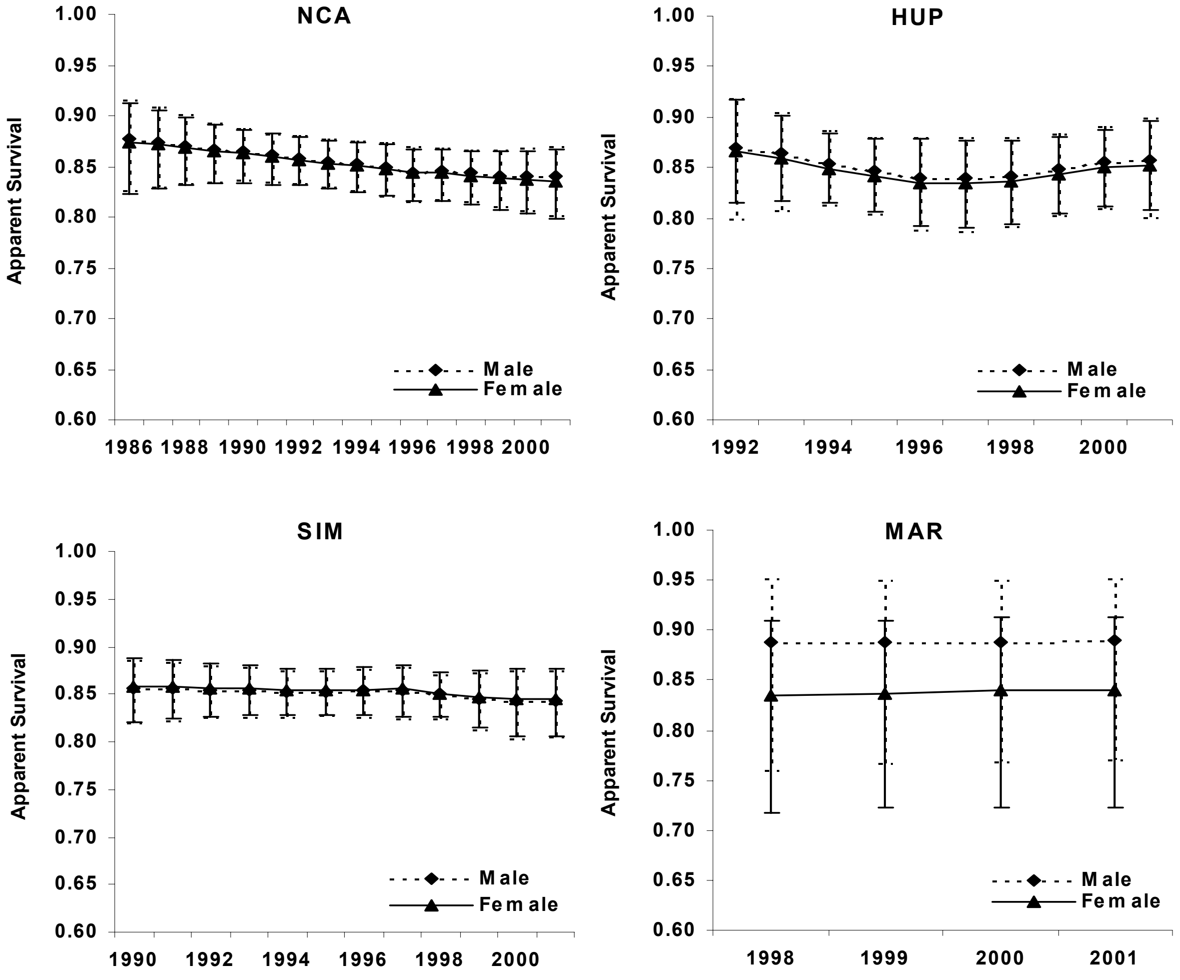

HJA
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1987
1989
1991
1993
1995
1997
1999
2001
Male
Female


WSR
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1992
1994
1996
1998
2000
Male
Female


TYE
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1985
1987
1989
1991
1993
1995
1997
1999
2001
Male
Female


CAS
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1991
1993
1995
1997
1999
2001
Male
Female


KLA
Apparent Survival
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
1985
1987
1989
1991
1993
1995
1997
1999
2001
Male
Female



Appendix I cont.

Appendix A. Study areas included in the January 2004 analysis of demographic trends of northern spotted owls.[a]

Study area	Study area code	Study area type[b]	Start year[c]	8_{RJS} start year[d]	Expansion year[e]	Land Owner[f]	Region	Latitude
Washington								
Wenatchee	WEN	TSA	1990	1992	1994	Mixed	Washington Mixed-Conifer	46.996
Cle Elum	CLE	TSA	1989	1992	none	Mixed	Washington Mixed-Conifer	47.195
Rainier	RAI	TSA	1992	1993	1998	Mixed	Washington Douglas-fir	47.041
Olympic	OLY	TSA	1987	1990	1994	Federal	Washington Douglas-fir	47.800
Oregon								
Coast Ranges	COA	TSA	1990	1992	none	Mixed	Oregon Coastal Douglas-fir	44.381
Tyee	TYE	DSA	1985	1990	none	Mixed	Oregon Coastal Douglas-fir	43.468
HJ Andrews	HJA	TSA	1987	1990	2000	Federal	Oregon Cascades Douglas-fir	44.213
Warm Springs	WSR	TSA	1992	1993	none	Tribal	Oregon Cascades Douglas-fir	44.938
South Cascades	CAS	TSA	1991	1992	1998	Federal	Oregon Cascades Douglas-fir	42.695
Klamath	KLA	TSA	1985	1991	1998	Mixed	Oregon/California Mixed-Conifer	42.736
California								
NW California	NWC	DSA	1985	1985	none	Federal	Oregon/California Mixed-Conifer	40.848
Hoopa	HUP	DSA	1992	1992	none	Tribal	Oregon/California Mixed-Conifer	41.051
Simpson	SIM	DSA	1990	1993	none	Private	California Coast	41.122
Marin	MAR	TSA	1998	1998	none	Federal	California Coast	37.994

[a] We analyzed data through 2003 on all study areas, except that we only analyzed 8_{RJS}. on the Wenatchee Study Area through 2002, because that study area was not completely surveyed in 2003.

[b] TSA = study area in which a sample of owl territories was surveyed each year; DSA = density study area in which the entire study area was sampled each year.

[c] Year that mark-recapture study was started.

[d] First year that data were used for analysis of 8_{RJS}.

[e] Year that study area size was increased, if any, for analysis of 8_{RJS}.

[f] Federal = Forest Service, Bureau of Land Management, National Park Service. Mixed = federal lands mixed with inclusions of private or state lands. Tribal and private study areas were lumped together for analyses of ownership.

Appendix B. List of participants at the workshop on analysis of demographic rates for the northern spotted owl held 4-11 January 2004 in Corvallis, Oregon.

BIOLOGISTS WITH DEMOGRAPHIC DATA (listed by study area and state)

Cle Elum (Washington)

Stan Sovern	Oregon Cooperative Wildlife Research Unit, Oregon State University
Eric Forsman	U.S. Forest Service, Pacific Northwest Research Station

Olympic Penninsula (Washington)

Scott Gremel	U.S. National Park Service, Olympic National Park
Patti Happe	U.S. National Park Service, Olympic National Park
Brian Biswell	U.S. Forest Service, Pacific Northwest Research Station
Eric Forsman	U.S. Forest Service, Pacific Northwest Research Station

Rainier (Washington)

Dale Herter	Raedeke Associates
Lorin Hicks	Plum Creek Timber Company
Jim Schaberl	U.S. National Park Service, Mount Rainier National Park

Wenatchee (Washington)

Tracy Flemming	National Council for Air & Stream Improvement
Larry Irwin	National Council for Air & Stream Improvement

Oregon Coast Range (Oregon)

Peter Loschl	Oregon Cooperative Wildlife Research Unit, Oregon State University
Tom Snetsinger	Oregon Cooperative Wildlife Research Unit, Oregon State University
Chris McAfferty	Oregon Cooperative Wildlife Research Unit, Oregon State University
Eric Forsman	U.S. Forest Service, Pacific Northwest Research Station

H. J. Andrews (Oregon)

Steve Ackers	Oregon Cooperative Wildlife Research Unit, Oregon State University
Sheila Turner-Hane	Oregon Cooperative Wildlife Research Unit, Oregon State University
Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University

Roseburg BLM - Klamath (Oregon)

Robert Horn	U.S. Bureau of Land Management, Roseburg District Office

Roseburg BLM - Tyee (Oregon)

Janice Reid	U.S. Forest Service, Pacific Northwest Research Station
Eric Forsman	U.S. Forest Service, Pacific Northwest Research Station

Southern Cascades (Oregon)

Steve Andrews	Oregon Cooperative Wildlife Research Unit, Oregon State University
Frank Wagner	Oregon Cooperative Wildlife Research Unit, Oregon State University

Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University

Warm Springs Tribal Lands (Oregon)

Rick Gearhart	Private Consultant (NEED COMPANY NAME??)

Hoopa Tribal Lands (California)

Mark Higley	Hoopa Tribal Forestry
Peter Carlson	Hoopa Tribal Forestry

Simpson Resource Company (California)

Lowell Diller	Simpson Resource Company, Redwood Division
Joel Thompson	Simpson Resource Company, Redwood Division
Keith Hamm	Simpson Resource Company, Redwood Division

NW California (California)

Alan Franklin	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University
Tammy Hamer	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University

Marin (Point Reyes) (California)

Katie Fehring	Point Reyes Bird Observatory

ANALYSTS

David Anderson	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University
Jennifer Blakesley	Sustainable Ecosystems Institute
Kenneth Burnham	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University
Mary Conner	Utah State University

Sarah Converse	Department of Fishery & Wildlife Biology, Colorado State University
Steven Dinsmore	Department of Wildlife and Fisheries, Mississippi State University
Paul Doherty	Department of Fishery & Wildlife Biology, Colorado State University
Vicky Dreitz	Colorado Division of Wildlife
Katie Dugger	Oregon Cooperative Wildlife Research Unit, Oregon State University
Alan Franklin	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University
James Hines	Patuxent Wildlife Research Center, U.S. Geological Survey
Paul Lukacs	Department of Fishery & Wildlife Biology, Colorado State University
Brett McClintock	Department of Fishery & Wildlife Biology, Colorado State University
Trent McDonald	Western Ecosystems Technologies, Inc.
Jim Nichols	Patuxent Wildlife Research Center, U.S. Geological Survey
Gail Olson	Oregon Cooperative Wildlife Research Unit, Oregon State University

Eric Rexstad	Institute of Arctic Biology, University of Alaska - Fairbanks
Carl Schwarz	Department of Statistics and Actuarial Science, Simon Fraser University
Mark Seamans	Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota
Gary White	Department of Fishery and Wildlife Biology, Colorado State University
Guthrie Zimmerman	Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota.

OTHER ATTENDEES

Betsy Glenn	Oregon State University
Karl C. Halupka	U.S. Fish and Wildlife Service
Gina King	Yakama Tribe
Joe Lint	Bureau of Land Management

Jim Thrailkill	U.S. Fish and Wildlife Service

ORGANIZERS

Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University
Eric Forsman	U.S. Forest Service, Pacific Northwest Research Station
Gail Olson	Oregon Cooperative Wildlife Research Unit, Oregon State University
Katie Dugger	Oregon Cooperative Wildlife Research Unit, Oregon State University
Pete Loschl	Oregon Cooperative Wildlife Research Unit, Oregon State University
Tom Snetsinger	Oregon Cooperative Wildlife Research Unit, Oregon State University
David Anderson	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University
Kenneth Burnham	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University
Alan Franklin	Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University

Gary White	Department of Fishery and Wildlife Biology, Colorado State University

Appendix F. Model selection results from analysis of productivity of northern spotted owls (number of young produced) based on analysis of means.

Study area	Model [a]	-2log ‹	*K* [b]	AICc	) AICc	Akaike weight
Washington						
Wenatchee (WEN)						
	A+EO	35.30	5	47.37	0.00	0.31
	A+EO+BO	33.55	6	48.55	1.17	0.17
	A+EO+T	33.70	6	48.70	1.33	0.16
	A+EO+TT	31.41	9	49.56	2.19	0.11
	A	40.63	4	49.97	2.59	0.09
	A+T	39.04	5	51.11	3.74	0.05
	A*EO	33.82	7	51.97	4.60	0.03
	A+TT	36.99	6	51.99	4.62	0.03
	A+BO	40.26	5	52.33	4.96	0.03
	A*EO+T	32.43	8	53.97	6.60	0.01
	A*EO+TT	30.11	9	55.31	7.94	0.01
	A*BO	40.09	7	58.24	10.86	0.00
	Constant	59.11	2	63.48	16.11	0.00
	BO	58.22	3	65.00	17.62	0.00
	A+t	9.79	17	79.79	32.41	0.00
Cle Elum (CLE)						
	A+EO	74.94	5	86.70	0.00	0.36
	A+EO+T	72.46	6	87.01	0.31	0.31
	A+EO+BO	74.69	6	89.24	2.53	0.10
	A+EO+TT	72.25	7	89.75	3.05	0.08
	A	81.80	4	90.95	4.24	0.04
	A+T	79.54	5	91.30	4.60	0.04

	A*EO	74.89	7	92.39	5.69	0.02
	A*EO+T	72.43	8	93.08	6.37	0.01

Appendix F. (continued).

Study area	Model [a]	-2log‹	*K* [b]	AICc	) AICc	Akaike weight
	A+BO	81.61	5	93.37	6.67	0.01
	A+TT	79.16	6	93.70	7.00	0.01
	Constant	91.69	2	96.02	9.31	0.00
	A*EO+TT	72.21	9	96.21	9.50	0.00
	BO	91.44	3	98.11	11.41	0.00
	A*BO	80.71	7	98.21	11.50	0.00
	A+t	54.16	18	122.74	36.03	0.00
Rainier (REI)						
	A*EO	-20.18	7	3.15	0.00	0.89
	A*EO+T	-20.40	8	8.69	5.53	0.05
	A+EO	-4.47	5	9.81	6.66	0.03
	A+EO+BO	-4.61	6	13.85	10.70	0.00
	A+EO+T	-4.56	6	13.90	10.75	0.00
	A*EO+TT	-20.42	9	15.58	12.42	0.00
	A	6.63	4	17.29	14.14	0.00
	A+EO+TT	-5.10	7	18.22	15.07	0.00
	A+BO	6.18	5	20.46	17.31	0.00
	A+T	6.58	5	20.87	17.72	0.00
	Constant	18.11	2	22.82	19.66	0.00
	A+TT	6.18	6	24.64	21.49	0.00
	BO	17.72	3	25.22	22.07	0.00
	A*BO	5.72	7	29.05	25.90	0.00
	A+t	-13.66	14	98.34	95.19	0.00

Appendix F. (continued).

Study area	Model [a]	-2log‹	*K* [b]	AICc	) AICc	Akaike weight
Olympic Peninsula (OLY)						
	A+EO	21.60	5	34.00	0.00	0.55
	A+EO+BO	20.25	6	35.75	1.74	0.23
	A+EO+T	21.44	6	36.94	2.94	0.13
	A*EO	20.32	7	39.19	5.19	0.04
	A+EO+TT	20.38	7	39.25	5.25	0.04
	A*EO+T	20.19	8	42.74	8.74	0.01
	A	34.59	4	44.12	10.12	0.00
	Constant	39.74	2	44.17	10.17	0.00
	BO	38.14	3	45.03	11.03	0.00
	A*EO+TT	19.17	9	45.74	11.73	0.00
	A+BO	33.70	5	46.10	12.10	0.00
	A+T	34.40	5	46.80	12.80	0.00
	A+TT	32.20	6	47.70	13.70	0.00
	A*BO	33.30	7	52.17	18.17	0.00
	A+t	-16.95	20	107.05	73.05	0.00
Oregon Study Areas						
Coast Ranges (COA)						
	A+EO	2.50	5	14.81	0.00	0.43
	A+EO+T	0.98	6	16.34	1.53	0.20
	A+EO+BO	1.35	6	16.71	1.91	0.16
	A*EO	-0.91	7	17.76	2.95	0.10
	A+EO+TT	0.96	7	19.63	4.83	0.04
	A*EO+T	-2.47	8	19.79	4.99	0.04
	A	12.02	4	21.50	6.69	0.01

	A+T	9.74	5	22.04	7.24	0.01
	A+BO	10.71	5	23.02	8.21	0.01
	A*EO+TT	-2.51	8	23.67	8.86	0.01
	A+TT	9.73	6	25.09	10.28	0.00
	A*BO	9.11	7	27.78	12.97	0.00
	Constant	25.09	2	29.50	14.69	0.00

Appendix F. (continued).

Study area	Model [a]	$-2\log \mathcal{L}$	K [b]	AICc	ΔAICc	Akaike weight
	BO	23.51	3	30.37	15.56	0.00
	A+t	-27.75	17	49.96	35.16	0.00
H.J. Andrews (HJA)						
	A+EO+TT	26.92	7	44.42	0.00	0.89
	A*EO+TT	26.91	9	50.91	6.49	0.03
	A+EO	39.66	5	51.42	7.00	0.03
	A+EO+T	37.54	6	52.09	7.67	0.02
	A+TT	38.56	6	53.11	8.69	0.01
	A+EO+BO	39.48	6	54.02	9.60	0.01
	A+T	44.88	5	56.65	12.23	0.00
	A	47.59	4	56.74	12.32	0.00
	A*EO	39.51	7	57.01	12.59	0.00
	A*EO+T	37.35	8	58.00	13.58	0.00
	A+BO	46.94	5	58.71	14.29	0.00
	Constant	55.71	2	60.03	15.62	0.00
	BO	54.72	3	61.38	16.97	0.00
	A*BO	44.01	7	61.51	17.09	0.00
	A+t	10.87	20	95.08	50.67	0.00
Warm Springs Reservation (WSR)						

	A	25.08	4	35.58	0.00	0.36
	A+EO	22.71	5	36.71	1.13	0.20
	Constant	32.57	2	37.23	1.66	0.16
	A+BO	24.93	5	38.93	3.36	0.07
	A+T	25.02	5	39.02	3.44	0.06
	BO	32.55	3	39.96	4.39	0.04
	A+EO+T	22.34	6	40.34	4.76	0.03
	A*EO	22.51	6	40.51	4.93	0.03

Appendix F. (continued).

Study area	Model [a]	-2log ‹	*K* [b]	AICc	) AICc	Akaike weight
	A+EO+BO	22.70	6	40.70	5.12	0.03
	A+TT	24.18	6	42.18	6.61	0.01
	A+EO+TT	21.01	7	43.62	8.05	0.01
	A*EO+T	22.20	7	44.82	9.24	0.00
	A*BO	23.23	7	45.85	10.27	0.00
	A*EO+TT	20.95	8	48.95	13.38	0.00
	A+t	-18.93	15	107.07	71.50	0.00
Tyee (TYE)						
	A+T	27.31	5	38.62	0.00	0.31
	A	30.80	4	39.65	1.03	0.18
	A+BO	29.23	5	40.53	1.92	0.12
	A+EO+T	27.10	6	40.97	2.35	0.10
	A+TT	27.27	6	41.14	2.52	0.09
	A+EO	30.61	5	41.91	3.30	0.06
	A+EO+BO	28.99	6	42.86	4.24	0.04
	A*EO+T	23.57	8	42.92	4.31	0.04
	A+EO+TT	27.07	7	43.62	5.00	0.03

	A*EO	27.28	7	43.83	5.22	0.02
	A*BO	27.97	7	44.52	5.90	0.02
	A*EO+TT	23.56	9	45.84	7.23	0.01
	Constant	49.82	2	54.07	15.45	0.00
	BO	49.15	3	55.65	17.03	0.00
	A+t	-1.55	22	77.34	38.73	0.00
Klamath (KLA)						
	A+EO	30.20	5	41.59	0.00	0.22
	A	32.73	4	41.64	0.05	0.22
	A*EO	26.69	7	43.42	1.83	0.09

Appendix F. (continued).

Study area	Model [a]	$-2\log\mathcal{L}$	K [b]	AICc	ΔAICc	Akaike weight
	A+BO	32.07	5	43.47	1.88	0.09
	A+EO+BO	29.67	6	43.67	2.08	0.08
	A+T	32.58	5	43.98	2.38	0.07
	A+EO+T	30.07	6	44.07	2.48	0.06
	A+EO+TT	27.53	7	44.26	2.67	0.06
	A+TT	30.70	6	44.70	3.11	0.05
	A*EO+T	26.48	8	46.08	4.49	0.02
	A*EO+TT	23.55	9	46.17	4.58	0.02
	A*BO	30.08	7	46.81	5.22	0.02
	Constant	60.93	2	65.19	23.60	0.00
	BO	60.90	3	67.44	25.84	0.00
	A+t	-12.52	22	70.41	28.81	0.00
Southern Cascades (CAS)						
	A+EO+T	31.92	6	46.72	0.00	0.36
	A+EO	35.84	5	47.78	1.06	0.21

	A+EO+TT	30.85	7	48.71	1.99	0.13
	A+EO+BO	34.67	6	49.47	2.76	0.09
	A*EO+T	28.37	8	49.51	2.79	0.09
	A*EO	32.97	7	50.83	4.11	0.05
	A*EO+TT	26.74	9	51.40	4.69	0.03
	A+T	41.82	5	53.75	7.04	0.01
	A	45.18	4	54.43	7.71	0.01
	A+BO	43.96	5	55.90	9.18	0.00
	A+TT	41.49	6	56.29	9.58	0.00
	Constant	55.60	2	59.95	13.24	0.00
	BO	54.38	3	61.11	14.39	0.00
	A*BO	43.72	7	61.58	14.86	0.00

Appendix F. (continued).

Study area	Model [a]	-2log ‹	*K* [b]	AICc	) AICc	Akaike weight
	A+t	15.13	16	74.33	27.61	0.00
California Study Areas						
Northwest California (NWC)						
	A+T	51.40	5	62.68	0.00	0.27
	A+BO	52.66	5	63.93	1.25	0.14
	A	55.22	4	64.05	1.37	0.13
	A+TT	50.30	6	64.13	1.45	0.13
	A+EO+T	51.14	6	64.97	2.29	0.08
	A+EO	54.95	5	66.23	3.55	0.04
	A*EO+T	46.98	8	66.25	3.57	0.04
	A+EO+TT	49.86	9	66.35	3.67	0.04
	A+EO+BO	52.56	6	66.38	3.70	0.04
	A*EO	51.20	7	67.69	5.01	0.02

	A*EO+TT	45.69	9	67.88	5.20	0.02
	A*BO	52.03	7	68.52	5.83	0.01
	Constant	65.27	2	69.51	6.83	0.01
	BO	63.18	3	69.67	6.99	0.01
	A+t	23.91	22	101.64	38.96	0.00
Hoopa Reservation (HUP)						
	A+EO+T	-7.99	6	7.83	0.00	0.32
	A+EO+BO	-7.47	6	8.35	0.53	0.25
	A+EO	-3.73	5	8.88	1.06	0.19
	A+EO+TT	-8.09	7	11.24	3.42	0.06
	A*EO+T	-11.51	9	11.69	3.86	0.05
	A*EO	-7.43	7	11.90	4.07	0.04
	A	2.44	4	12.11	4.28	0.04
	A+T	0.47	5	13.08	5.25	0.02

Appendix F. (continued).

Study area	Model [a]	-2log ℒ	*K* [b]	AICc	ΔAICc	Akaike weight
	A+BO	1.24	5	13.84	6.02	0.02
	A*EO+TT	-11.73	9	15.74	7.92	0.01
	A+TT	0.28	6	16.10	8.28	0.01
	Constant	15.35	2	19.81	11.98	0.00
	A*BO	0.92	7	20.25	12.42	0.00
	BO	15.10	3	22.06	14.23	0.00
	A+t	-27.43	15	39.50	31.67	0.00
Simpson Resources Company (SIM)						
	A+EO	-0.66	5	11.01	0.00	0.42
	A+EO+T	-1.76	6	12.64	1.64	0.19
	A+EO+BO	-1.46	6	12.94	1.93	0.16

	A	5.71	4	14.79	3.79	0.06
	A+EO+TT	-1.89	7	15.40	4.39	0.05
	A+T	4.10	5	15.76	4.76	0.04
	A*EO	-1.00	7	16.29	5.28	0.03
	A+BO	4.93	5	16.60	5.59	0.03
	A*EO+T	-2.11	8	18.26	7.25	0.01
	A+TT	3.98	6	18.38	7.37	0.01
	A*BO	2.61	7	19.91	8.90	0.00
	A*EO+TT	-2.25	9	21.38	10.37	0.00
	Constant	25.42	2	29.73	18.72	0.00
	BO	24.94	3	31.57	20.56	0.00
	A+t	-13.03	17	46.47	35.46	0.00
Marin (MAR)						
	Constant	34.34	2	39.20	0.00	0.52
	BO	32.46	3	40.30	1.10	0.30
	A	31.84	4	43.18	3.98	0.07

Appendix F. (continued).

Study area	Model [a]	-2log‹	K [b]	AICc	) AICc	Akaike weight
	A+EO	29.08	5	44.54	5.34	0.04
	A+BO	29.47	5	44.92	5.72	0.03
	A+EO+BO	26.56	6	46.96	7.76	0.01
	A+T	31.74	5	47.20	8.00	0.01
	A+TT	28.03	6	48.43	9.23	0.01
	A+EO+T	28.53	6	48.93	9.72	0.00
	A+EO+TT	23.19	7	49.64	10.44	0.00
	A*BO	24.43	7	50.88	11.68	0.00
	A*EO	27.30	7	53.75	14.55	0.00

A*EO+T	26.81	9	60.81	21.61	0.00
A+t	17.13	9	60.85	21.64	0.00
A*EO+TT	19.88	9	63.59	24.39	0.00

[a] Model notation indicates additive (+) or interactive (*) effects of owl age (A), even-odd years (EO), linear time (T), quadratic time (TT) or barred owls (BO). "Constant" indicates models with no structure.

Appendix G. Estimates of annual recapture probabilities ($\hat{p}$) of banded northern spotted owls in 14 demographic study areas in Washington, Oregon and California. Estimates are from the best AICc model for each study area. Study areas that had a sex effect on *p* include separate columns for males and females.

	WEN		CLE%%		CLE&&		RAI		OLY	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1988									0.600	0.163
1989									0.793	0.096
1990			0.899	0.017	0.844	0.021			0.818	0.060
1991	0.625	0.050	0.886	0.017	0.826	0.021			0.781	0.055
1992	0.643	0.042	0.909	0.019	0.859	0.025			0.813	0.047
1993	0.660	0.034	0.860	0.027	0.790	0.034			0.729	0.052
1994	0.676	0.028	0.908	0.019	0.858	0.025	1.000	0.000	0.764	0.049
1995	0.693	0.023	0.882	0.018	0.821	0.022	0.895	0.056	0.669	0.056
1996	0.708	0.020	0.905	0.018	0.853	0.024	0.890	0.051	0.784	0.048
1997	0.724	0.020	0.856	0.029	0.785	0.038	0.652	0.083	0.749	0.048
1998	0.738	0.021	0.904	0.018	0.852	0.023	0.883	0.053	0.774	0.049
1999	0.753	0.025	0.876	0.020	0.812	0.024	0.560	0.076	0.296	0.053
2000	0.766	0.029	0.890	0.017	0.832	0.020	0.635	0.078	0.746	0.058
2001	0.780	0.032	0.888	0.017	0.829	0.020	0.733	0.079	0.763	0.055
2002	0.792	0.036	0.884	0.017	0.823	0.021	0.789	0.090	0.843	0.056
2003	0.804	0.040	0.901	0.017	0.848	0.022	0.988	0.189	0.698	0.082

	COA		HJA		WSR		TYE%%		TYE&&	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1986							0.857	0.031	0.805	0.038
1987							0.867	0.027	0.819	0.033

1988			0.846	0.043			0.876	0.023	0.831	0.029
1989			0.829	0.035			0.886	0.020	0.843	0.025

Appendix G (continued).

	COA		HJA		WSR		TYE%%		TYE&&	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1990			0.813	0.029			0.894	0.017	0.854	0.022
1991	0.863	0.012	0.800	0.023			0.902	0.015	0.864	0.019
1992	0.863	0.012	0.790	0.021			0.909	0.013	0.874	0.016
1993	0.863	0.012	0.784	0.021	0.903	0.033	0.916	0.012	0.883	0.015
1994	0.863	0.012	0.781	0.022	0.934	0.020	0.923	0.011	0.892	0.013
1995	0.863	0.012	0.783	0.022	0.892	0.019	0.929	0.010	0.900	0.013
1996	0.863	0.012	0.788	0.022	0.865	0.019	0.934	0.009	0.908	0.012
1997	0.863	0.012	0.797	0.020	0.795	0.042	0.939	0.009	0.915	0.012
1998	0.863	0.012	0.809	0.019	0.906	0.027	0.944	0.009	0.921	0.012
1999	0.863	0.012	0.825	0.018	0.772	0.033	0.948	0.009	0.927	0.012
2000	0.863	0.012	0.842	0.019	0.786	0.032	0.952	0.009	0.933	0.012
2001	0.863	0.012	0.860	0.023	0.707	0.049	0.956	0.009	0.938	0.012
2002	0.863	0.012	0.880	0.026	0.745	0.037	0.960	0.009	0.943	0.012
2003	0.863	0.012	0.899	0.030	0.873	0.034	0.963	0.009	0.947	0.012

	KLA		CAS		NWC		MAR%%		MAR&&	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1986	0.669	0.227			0.765	0.041				
1987	0.609	0.147			0.765	0.041				
1988	0.581	0.102			0.917	0.009				
1989	0.731	0.077			0.917	0.009				
1990	0.851	0.050			0.917	0.009				

1991	0.851	0.043			0.917	0.009
1992	0.791	0.042	0.878	0.040	0.917	0.009
1993	0.757	0.046	0.832	0.035	0.872	0.020
1994	0.858	0.036	0.788	0.029	0.917	0.009

Appendix G (continued).

	KLA		CAS		NWC		MAR%%		MAR&&	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1995	0.772	0.043	0.754	0.027	0.872	0.020				
1996	0.732	0.046	0.734	0.030	0.917	0.009				
1997	0.748	0.049	0.730	0.031	0.917	0.009				
1998	0.859	0.035	0.745	0.030	0.917	0.009				
1999	0.882	0.033	0.775	0.027	0.872	0.020	0.996	0.007	0.981	0.027
2000	0.881	0.032	0.816	0.025	0.917	0.009	0.989	0.013	0.956	0.040
2001	0.950	0.022	0.862	0.027	0.917	0.009	0.940	0.059	0.786	0.097
2002	0.953	0.021	0.906	0.027	0.917	0.009	0.976	0.024	0.905	0.048
2003	0.897	0.041	0.942	0.025	0.872	0.020	0.976	0.024	0.905	0.048

	HUP		SIM %%		SIM &&	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1991			0.859	0.017	0.819	0.019
1992			0.859	0.017	0.819	0.019
1993	0.868	0.039	0.859	0.017	0.819	0.019
1994	0.861	0.027	0.859	0.017	0.819	0.019
1995	0.861	0.024	0.859	0.017	0.819	0.019
1996	0.867	0.025	0.859	0.017	0.819	0.019
1997	0.879	0.025	0.859	0.017	0.819	0.019
1998	0.895	0.022	0.859	0.017	0.819	0.019

1999	0.914	0.019	0.859	0.017	0.819	0.019
2000	0.933	0.017	0.859	0.017	0.819	0.019
2001	0.950	0.017	0.859	0.017	0.819	0.019
2002	0.965	0.017	0.859	0.017	0.819	0.019
2003	0.977	0.016	0.859	0.017	0.819	0.019