

1 **Population trends in northern spotted owls: associations with climate in the Pacific**

2 **Northwest**

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9 **Abstract**

10 We used reverse time capture-mark-recapture models to describe associations between
11 rate of population change (λ) and climate for northern spotted owls (*Strix occidentalis caurina*)
12 at 6 long-term study areas in Washington and Oregon, USA. Populations in three of six areas
13 showed strong evidence of declining populations, while populations in two additional areas were
14 likely declining as well. At 4 areas, λ was positively associated with wetter-than-normal
15 conditions during the growing season, which likely affects prey availability. Lambda was also
16 negatively associated with cold, wet winters and nesting seasons, and the number of hot summer
17 days. The amount of annual variation in λ accounted for by climate varied across study areas (3-
18 85%). Rate of population change was more sensitive to adult survival than to recruitment;
19 however, there was considerable variation among years and across study areas for all
20 demographic rates. While annual survival was more closely related to regional climate
21 conditions, recruitment was often associated with local weather. In addition to climate, declines

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22 in recruitment at four of six areas were associated with increased presence of barred owls.
23 Climate change models predict warmer, wetter winters and hotter, drier summers for the Pacific
24 Northwest in the first half of the 21st century. Our results indicate that these conditions have the
25 potential to negatively affect annual survival, recruitment, and consequently population growth
26 rates for northern spotted owls.

27 *Key-words:* adult survival, barred owl, climate, rate of population change, recruitment, *Strix*
28 *occidentalis caurina*, weather.

29 **1. Introduction**

30 Two decades of research have documented declines in northern spotted owl (*Strix*
31 *occidentalis caurina*) populations across the Pacific Northwest (Anderson and Burnham 1992;
32 Burnham et al. 1994; Anthony et al. 2006; Forsman et al. *in press*). To meet requirements of the
33 Endangered Species Act and National Forest Management Act, federal agencies adopted the
34 Northwest Forest Plan (NWFP) in 1994 (USDA and USDI 1994) as a conservation strategy for
35 the subspecies. Under this plan, conservation efforts for the spotted owl have focused on
36 protection of late-successional forests on federal lands throughout its geographic range. Because
37 of the contentious debate over how best to manage late-successional forests for the spotted owl
38 (*S. o. caurina*, *S.o. occidentalis*), it has become one of the most studied bird species in the world.
39 In addition to numerous reports on population trends, there have also been many studies of
40 habitat use and home range size (Forsman et al. 1984; Forsman et al. 2005; Carey et al. 1990;
41 Glenn et al. 2004), diet (Barrows 1980; Forsman et al. 1984; Forsman et al. 2001; Forsman et al.
42 2004), genetics (Barrowclough et al. 1999), prey ecology (Carey et al. 1992; Rosenberg et al.
43 2003; Forsman et al. 1994; Zabel et al. 1995), and dispersal (Forsman et al. 2002; Blakesley et al.

44 2006). Despite the extensive research, the effectiveness of the NWFP strategy for conserving
45 northern spotted owls remains unclear (Courtney et al. 2004). Populations have shown continued
46 declines since the early 1990s, and specific causes of declines have not been well-identified
47 (Anthony et al. 2006; Forsman et al. *in press*). Conservation efforts have been further
48 complicated by the range expansion of the congeneric barred owl (*Strix varia*) into the range of
49 the northern spotted owl, with negative effects on site occupancy by spotted owls (Olson et al.
50 2005). Furthermore, both annual survival and reproduction have been shown to be affected by
51 density-independent factors such as weather, in addition to habitat conditions (Franklin et al.
52 2000; Olson et al. 2004; Dugger et al. 2005).

53 Although both habitat and local weather have been shown to influence survival and
54 reproduction (Franklin et al. 2000; Olson et al. 2004), effects of environmental variation on λ
55 have not been addressed for this subspecies. Franklin et al. (2000) proposed that even with
56 unchanging habitat conditions, spotted owl populations could decline solely as a consequence of
57 variation in weather. Under a global climate change scenario, potential effects of weather on
58 population growth rate could be much greater, as changes in both the mean and variance of
59 temperature, precipitation, and weather extremes are predicted (Mote et al. 2008). In order to
60 understand the potential effects of climate change on population persistence, we first need to
61 understand effects of naturally-occurring climate fluctuations on spotted owl populations.

62 Our goal was to evaluate hypotheses regarding associations between climate and realized
63 rate of population growth (hereafter λ) of northern spotted owls at 6 study areas in Washington
64 and Oregon that span most of the range of this subspecies. Because population growth rate is a
65 function of both annual survival and recruitment (Nichols and Hines 2002), we modeled

66 relationships between climate and these two demographic rates to assess associations with λ .
67 First, we evaluated hypotheses regarding associations between climate and both annual survival
68 and recruitment. Second, we determined how much annual variation in demographic rates could
69 be accounted for by weather and climate. Third, we determined the relative contributions of
70 annual survival and recruitment to λ . We predicted that climate associations would differ across
71 study areas and among demographic rates; however, we expected recruitment would be more
72 strongly affected by climate than survival while λ would be most sensitive to variation in annual
73 survival.

74 **2. METHODS**

75 **2.1 Study Areas**

76 We examined associations between weather and climate and annual rate of population
77 change (λ) of northern spotted owls at 6 study areas in Washington and Oregon: Olympic
78 peninsula (OLY) (3,289 km²), Cle Elum (CLE) (1,784 km²), H.J. Andrews (HJA) (1,526 km²),
79 Oregon Coast Range (OCR) (3,919 km²), Tyee (TYE) (1,714 km²), and Southern Oregon
80 Cascades (CAS) (3,375 km²). These 6 areas were part of the Monitoring Plan for the northern
81 spotted owl under the NWFP (Lint et al. 1999) and are described in detail in Anthony et al.
82 (2006) and Glenn (2009). OLY, HJA, and CAS were primarily federal lands, while CLE, OCR,
83 and TYE were a mixture of federal, state, and private lands. TYE, OCR, and CAS contained
84 lands administered by the U.S. Bureau of Land Management with an ownership pattern of
85 alternating sections (2.56 km²) of federal and private lands.

86 All study areas were characterized by mountainous terrain, but elevations in the coastal
87 areas in Oregon (OCR, TYE) rarely exceeded 1250m. The remaining areas in the Cascades

88 (CAS, HJA, CLE) and Olympic Peninsula (OLY) had mountain peaks well above timberline.
89 Vegetation was dominated by mesic coniferous forests of Douglas-Fir (*Pseudotsuga menziesii*)
90 and western hemlock (*Tsuga heterophylla*) on the OLY, OCR, HJA and TYE areas, and by
91 mixed-species associations of Douglas-fir, white fir (*A. concolor*), grand fir (*A. grandis*), and
92 various pines (*Pinus ponderosa*, *P. lambertiana*, *P. monticola*, *P. contorta*) on the CLE and CAS
93 areas (Franklin and Dyrness 1973). Forest structure varied widely within and among areas,
94 ranging from young forests on recently planted clear-cuts to unharvested forests that were > 400
95 years old. All study areas contained large amounts of mature (80-200 yrs old) and old-growth
96 (>200 yrs old) forest, but these age classes were most common on the OLY, HJA, and CAS
97 areas, where >35% of the landscape was covered by mature and old-growth forest.

98 Climate also varied across the 6 areas. Areas in the central (HJA, CAS) or eastern
99 Cascades (CLE) were characterized by warm, dry summers and cool winters, with most
100 precipitation occurring as snow during winter months. At OLY and OCR, climate was maritime
101 with most precipitation falling as rain during winter months, although snow was present at higher
102 elevations at OLY. At TYE, climate was similar to OLY and OCR, although summers were
103 warmer and drier than more coastal areas.

104 **2.2 Field Methods**

105 Owls were monitored at the 6 study areas beginning 1985-1991 and continuing through
106 2005 for all areas except OLY, which was monitored through 2003. Field methods followed
107 Franklin et al. (1996), and data collection was standardized across all areas for all years
108 (Anthony et al. 2006). Capture was defined as the physical capture of an individual or visual

109 identification of marked owls with unique color-bands in subsequent years. Capture histories
110 were developed for banded individuals ≥ 1 year old.

111 Because other studies have found that resighting probabilities increased as researchers
112 became more familiar with owls on a study area, we followed the protocol of Anthony et al.
113 (2006) where the first 1-5 years of data were removed from capture history records to reduce
114 potential bias in λ associated with initial location and banding of owls during the first few years
115 of study. Anthony et al. (2006) also determined that territories at our 6 study areas were not
116 initially saturated with owls at the start of the survey period; thus, there was room for expansion
117 in these populations.

118 **2.3 Statistical Methods**

119 We used an information-theoretic approach (Burnham and Anderson 2002) and reverse
120 time capture-mark-recapture (CMR) models for open populations (Nichols and Hines 2002,
121 Pradel 1996) in Program MARK (White and Burnham 1999) to rank *a priori* models
122 representing hypotheses regarding effects of weather and climate on annual survival (ϕ),
123 recruitment (f), and λ . We used the survival-recruitment model parameterization, and estimated
124 year-specific rates for λ , ϕ , f , as well as the relative contributions of ϕ and f to λ (Nichols and
125 Hines 2002). We evaluated goodness-of-fit and obtained estimates of the overdispersion
126 parameter (\hat{c}) for each data set using program RELEASE (Burnham et al. 1987). We used AIC_c
127 or $QAIC_c$ to rank models, AIC_c or $QAIC_c$ weights (w) to assess the likelihood of a given model,
128 and used model-averaged parameter estimates for ϕ , f , and λ (Burnham and Anderson 2002).

129 Our estimates of λ reflected changes in population size due to births, deaths, and
130 movement in or out of the study area. Because juvenile owls have a high probability of

131 emigrating from the study areas, capture histories used in our analyses were restricted to
132 territorial owls that were ≥ 1.0 year old . Therefore, λ refers to the rate of population change of
133 non-juvenile owls on nesting territories in each study area. Additionally, we incorporated a
134 onetime increase in study area boundaries at OLY, HJA, and CAS to include areas surveyed
135 outside the original boundaries incorporated following methods of Anthony et al. (2006).

136 We used a multistep process for evaluating our hypotheses. First, we identified the best
137 model structure for recapture probabilities by evaluating demographic (sex, reproduction
138 (REPROD), and barred owl presence (BO)) and time effects (time-varying, even-odd year, and
139 time trend models) (Supplementary Material 1). Second, we evaluated a small set of models that
140 considered demographic and climate effects on annual survival. We first identified the most
141 important demographic factors and then considered climate factors. This *a priori* set of models
142 was based on previous studies that examined relationships between survival of northern spotted
143 owls and climate (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Glenn 2009) as
144 well as broader research on associations between avian demographic rates and climate. Finally,
145 we modeled recruitment (f), which is defined as the probability of an individual entering the
146 territorial population on a study area. Recruitment is the result of *in situ* reproduction, survival of
147 juvenile owls until they are recruited into the territorial population, and immigration of transient
148 owls from outside the study area. To model recruitment, we considered *a priori* models which
149 contained demographic and climatic factors that we hypothesized might be associated with
150 either reproduction, annual survival, or both.

151 For each demographic rate, we had numerous statistical models representing our *a priori*
152 hypotheses (Supplementary Material 2). We evaluated the set of *a priori* statistical models to

153 identify which hypotheses were most supported and which statistical model best represented a
154 given hypothesis. If models representing more than one hypothesis were supported, we also
155 considered combinations of *a priori* models if they made sense biologically and did not contain
156 redundancies. We also evaluated different combinations of the competing models on survival
157 and recruitment in cases where several models were competitive for survival, recruitment, or
158 resighting rates to identify factors with the strongest association with a particular demographic
159 rate. Our final models represented our *a priori* hypotheses, but also included a small number of
160 *posteriori* models (1-5 per study area).

161 We used the variance components module in Program MARK to compute estimates of
162 temporal process variation (White et al. 2002). Year-specific seniority rates (λ) were
163 calculated from the time-specific estimates of ϕ and λ following methods of Nichols and Hines
164 (2002), and were used to assess the relative contribution of annual survival to λ (Nichols et al.
165 2000, Nichols and Hines 2002).

166 **2.4 Hypotheses Regarding Associations between Climate and Rate of Population Change**

167 Our *a priori* hypotheses addressed associations between climate and both annual survival
168 and recruitment (Supplementary Material 2). We hypothesized that associations between annual
169 survival and climate would be similar to effects reported in earlier studies (Franklin et al. 2000,
170 Olson et al. 2004, Dugger et al. 2005, Glenn 2009), although we anticipated that climate
171 associations would vary among study areas. We developed 4 biological hypotheses regarding
172 potential relationships between weather and annual survival, as follows: (1) survival would be
173 negatively associated with cold, wet, stormy, or snowy winters or nesting seasons as a result of

174 exposure, decreased foraging efficiency, or decreased prey populations (Franklin et al. 2000;
175 Olson et al. 2004, Glenn 2009); (2) survival would be positively associated with wetter
176 conditions during the growing season (May-Oct) as small mammal populations, the primary
177 prey of spotted owls, tend to increase in more mesic conditions (Luoma et al. 2003); (3) survival
178 would be negatively associated with the number of hot days ($\text{DAYS} \geq 32^{\circ}\text{C}$) during summer as
179 spotted owls are better adapted to cold conditions than hot (Weathers et al. 2001), and (4)
180 survival would be associated with regional climate cycles (Southern Oscillation, Pacific Decadal
181 Oscillation) which assess temperature, moisture, and storm conditions at larger temporal and
182 spatial scales (Glenn 2009). For climate cycles, we considered associations with both the
183 current year and prior year (1-year lag). For models containing precipitation, we considered both
184 linear and quadratic relations as we hypothesized that changes in survival may be associated with
185 deviations from average precipitation levels.

186 For modeling recruitment, we hypothesized that climatic factors associated with both
187 reproduction and annual survival would be important. In general, we predicted that survival and
188 reproduction would be similarly affected by weather; however, we hypothesized that cold, wet,
189 or stormy nesting seasons would have a stronger negative effect on reproduction and
190 consequently recruitment than with survival. We also considered lags of up to 3 years with
191 climate factors associated with recruitment, as owls often do not enter the territorial
192 population for several years after fledging (Forsman et al. 2002).

193 **2.5 Demographic and Climatic Data**

194 Demographic covariates in models included gender, proportion of spotted owl territories
195 with barred owl detections in a given year (BO), and mean number of young fledged per pair per

196 year (REPROD) to evaluate associations between reproductive output and survival and increased
197 resighting probabilities in years with high reproduction (Supplementary Information 3). We also
198 evaluated time-varying and time trend models for survival, recapture, and recruitment. In
199 addition, we included an even-odd year effect on recruitment as northern spotted owls have
200 shown an alternating year pattern in reproductive output in many areas of their range (Anthony et
201 al. 2006).

202 We used Parameter Elevated Regression on Independent Slope Models (PRISM) maps
203 (Oregon Climate Service, Oregon State University, Corvallis, OR, USA) to obtain mean monthly
204 minimum temperature ($^{\circ}\text{C}$) (TMIN), mean monthly maximum temperature ($^{\circ}\text{C}$) (TMAX), and
205 monthly precipitation (cm) (PRECIP) data for each study area. Temperature and precipitation
206 data were compiled for each study area for seasonal time periods associated with spotted owl life
207 history stages (Franklin et al. 2000, Olson et al. 2004): early nesting season (EN)(Mar-Apr),
208 late nesting season (LN)(May-Jun), summer (S)(Jul-Aug), dispersal (D)(Sep- Oct), and winter
209 (W)(Nov-Feb), as well as annually (A)(Jul-Jun). We used a GIS (ArcGIS) to combine monthly
210 maps into seasonal and annual maps for our study areas for our time periods of interest.

211 Total annual snowfall (cm) (SNOW), total number of days each year with a maximum
212 daily temperature $> 32^{\circ}\text{C}$ ($\text{DAYS} \geq 32^{\circ}\text{C}$), and numbers of days with stormy conditions during
213 different seasonal periods for the six study areas were obtained using National Climatic Data
214 Center (NCDC) weather station data (NOAA 2008). Each study area contained 4-13 weather
215 stations that consistently recorded SNOW and # $\text{DAYS} \geq 32^{\circ}\text{C}$ for the time periods of interest.
216 We averaged data across stations to obtain a single measure of SNOW and # $\text{DAYS} \geq 32^{\circ}\text{C}$ for
217 each study area for each year. The NCDC Storm Database (NOAA 2008) provided on-line

218 records of days with heavy precipitation, temperature extremes, snow and ice, and high winds
219 and thunderstorms. Storm data were organized by state and county, which enabled us to tally
220 numbers of days with storm events for our time periods separately for each study area.

221 We used the Palmer Drought Severity Index (PDSI) to assess moisture levels during the
222 growing season as an index to primary productivity that has potential to influence abundance of
223 spotted owl prey. The PDSI measures deviations of moisture conditions from normal (30-year
224 mean: 1970-2000) on a standardized scale so comparisons can be made across regions and over
225 time (NOAA 2008). The index was calculated separately for climate regions within each state.
226 Most study areas fell within one climate region. For study areas that included multiple climate
227 regions, we used a weighted average of PDSI values based on the proportion of the study area
228 that fell within each climate region.

229 We used the Southern Oscillation (el Niño) Index (SOI) and the Pacific Decadal
230 Oscillation index (PDO) to assess region-wide climate patterns. We obtained monthly values for
231 the SOI and PDO indices from NOAA/National Weather Service, Climate Prediction Center
232 <http://www.cpc.ncep.noaa.gov/data/indices/>), and Joint Institute for the Study of the Atmosphere
233 and Ocean at the University of Washington (<http://jisao.washington.edu/pdo/PDO.latest>),
234 respectively. Negative SOI values (el Niño) are associated with warmer, drier winters in the
235 Pacific Northwest, while positive SOI values (la Niña) are associated with cold, wet, snowy
236 winters. Positive PDO values (warm phase) are associated with lower rainfall and higher
237 temperatures in the Pacific Northwest, while negative values (cool phase) are associated with
238 higher precipitation and cooler temperatures. We averaged monthly SOI and PDO values to
239 obtain annual (Jul 1- Jun 30) measures for these indices.

240 3. RESULTS

241 Analyses were based on capture histories for 2,110 individual owls on the 6 study areas.
242 OCR had the greatest number of owls (423) while CLE had the least (142) (Supplemental
243 Information 1). TYE and HJA had 15 years of capture history data included in the analyses,
244 while the remaining areas had 13 years. Estimates of overdispersion from Program RELEASE
245 ranged from 1.0 at CLE to 2.52 at OLY. We used AIC_c to rank models at CLE and $QAIC_c$ for
246 remaining areas.

247 3.1 Weather and Climate

248 Weather and climate conditions during our study varied among years and study areas
249 (Supplemental Information 4). Daily mean temperature was highest at OCR ($\bar{0} = 11.84$ °C, SE =
250 0.135) and lowest at CLE ($\bar{0} = 5.58$ °C, SE = 0.127), while mean annual precipitation was
251 highest at OLY ($\bar{0} = 287$ cm, SE=15.04) and lowest at CAS ($\bar{0} = 114$ cm, SE = 7.97). CAS,
252 CLE, and TYE were relatively dry compared to OLY, OCR, and HJA. Although patterns varied
253 by study area, 1996-7 and 1998-9 were generally the wettest years while 1991-2, 1992-4, 2000-1,
254 and 2004-5 were the driest. Similarly, 1991-2 and 2003-4 were warm years; however, there was
255 not a consistent pattern for cold years across study areas. Temperature and precipitation varied
256 seasonally as well as annually, with high precipitation in winter and early nesting season and
257 relatively dry conditions during summer through early fall at all areas.

258 The highest storm frequencies occurred in 1994-1998, which was consistent with the
259 number of years with highest precipitation. The OCR study area, which was the most coastal of
260 the 6 areas, had the greatest number of storm days per year over the duration of the study ($\bar{0} =$

261 20.4, SE = 2.13), while CAS had the fewest ($\bar{0} = 7.52$, SE= 0.73). Snowfall was consistently
262 highest at CLE; variable at HJA, CLE, and OCR; and low at OLY and TYE. Number of DAYS \geq
263 32°C was cyclic at most areas between 1993-1999, where even-numbered years (e.g. 1994) had
264 more # DAYS \geq 32°C and odd-numbered years had fewer. Overall, CAS, HJA, and TYE had the
265 highest # DAYS \geq 32°C, while OCR, CLE, and OLY had relatively few.

266 Drought conditions were recorded at OCR and CAS in 1992, at CLE in 1994, and at CLE
267 and CAS in 2000 and 2001. Unusually wet conditions were recorded at TYE, HJA, OLY, and
268 CAS between 1994-1997. The SOI and PDO indices measured climate conditions at larger
269 spatial scales, reflecting climate conditions across the Pacific region. Thus, SOI and PDO values
270 did not vary by study area. Strong El Niño conditions ($SOI \leq -1.0$) occurred in 1986, 1991, and
271 1997, and moderate El Niño conditions occurred in 1992-1994, 2002, and 2004. Strong La Niña
272 conditions ($SOI \geq 1.0$) occurred in 1988-1989 and 1998-2000. The PDO generally follows a
273 longer cycle than SOI, cycling over decades rather than years. During our study, the PDO
274 remained primarily in the warm phase, but switched to the cool phase in 1988-1990 and 1998-
275 2001.

276 **3.2 Climate Factors Associated with Survival and Recruitment**

277 **3.2.1 Annual Survival**

278 For the Washington study areas (OLY, CLE), the top model contained combinations of 2
279 *a priori* hypotheses for annual survival, while the top models for the Oregon areas represented a
280 single climate hypothesis (Table 1). The growing season moisture hypothesis received most
281 support at OLY, CLE, and OCR (Table 1). At all 3 areas, the covariate that best quantified this
282 association was PDSI. Survival was positively associated with wetter-than-normal growing

283 season conditions at all 3 areas, although at OCR there was also an interaction between PDSI and
284 BO where the positive association between annual survival and wet growing season conditions
285 decreased as the proportion of spotted owl territories with barred owl detections increased (Table
286 2). At OLY, there was also a negative association between annual survival and the number of
287 storms during winter (Table 2). At CLE, there was a quadratic relationship between survival and
288 the number of storms during the nesting period. Survival was lower during years with lower or
289 higher than average numbers of stormy days (Table2). At TYE, the climate cycle hypothesis
290 received the most support. Survival was highest during years when the SOI was in the cool, wet
291 (la Niña) phase and the PDO was in the warm phase (Table 2). At the most southern study area
292 (CAS), survival was negatively associated with hot summer days (Table 2). None of the climate
293 hypotheses received support at HJA (Table 1).

294 **3.2.2 Recruitment**

295 Among the *a priori* hypotheses, the growing season moisture hypotheses had greatest
296 support at OLY, CLE, and CAS (Table1). At OLY, we observed a quadratic relation between
297 recruitment and precipitation during the growing season two years prior (Table 2) where
298 recruitment was higher following years of either lower-than-normal or higher-than-normal
299 precipitation (Table 2). At CLE, recruitment was positively associated with wet growing seasons
300 (PDSI) three years prior, while at CAS, recruitment was positively associated with PDSI two
301 years prior. At OCR, we observed a positive relationship between the PDSI in the previous year
302 in a competing model, but not in the top model (Table 1).

303 The hypothesis representing negative associations with cold/wet/stormy nesting seasons
304 received support at HJA, OCR, and TYE (Table 2). At these three areas, recruitment was

305 negatively associated with precipitation during the early nesting season, although the 95% CI for
306 beta estimate at HJA overlapped zero (Table 2). There was also some support for a positive
307 relation with early nesting season temperature ($\beta = 0.101$, SE = 0.158, 95% CI: -0.210 - 0.411),
308 and a negative association with late nesting season precipitation ($\beta = -0.007$, SE=0.021, 95%CI: -
309 0.048 – 0.034) in competing models at OCR. At CAS, there was support for the winter weather
310 hypothesis, as we observed a quadratic relation between both winter precipitation and winter
311 storms two years prior at CAS (Table 2). At TYE, recruitment was also positively associated
312 with la Niña conditions and the cool, wet phase of the PDO two years prior (Table 2).

313 **3.3 Demographic Factors Associated with Survival, Recruitment, and Resighting**

314 Annual survival was negatively associated with the proportion of spotted owl territories
315 containing barred owl detections at OLY and OCR (Table 2). Survival was higher for male owls
316 at OLY, and was lower at HJA during years of high reproduction. Recruitment was negatively
317 associated with barred owl presence at OLY, HJA, OCR, and TYE, and an even-odd year pattern
318 in recruitment was evident at OLY (Table 2). Resighting probabilities were positively associated
319 with the number of young fledged per pair per year at OLY, CLE, and TYE. Barred owls were
320 negatively associated with resighting at OCR and TYE, but positively associated at HJA.
321 Resighting probabilities were higher for males than females at TYE.

322 **3.4 Annual Rate of Population Change and Climate**

323 Mean estimates of λ were <1.0 at all study areas, but 95% confidence intervals
324 overlapped 1.0 for OLY and TYE (Table 3). Mean λ was highest at TYE ($\lambda = 0.986$, SE = 0.015)
325 and lowest at CLE ($\lambda = 0.920$, SE = 0.016) (Table 3). Year-specific estimates indicated a decline
326 in λ over time at CLE, HJA, and OCR (Figure 1B, C, D). Year-specific estimates of λ were

327 highly variable at OLY (range: 0.63-1.23) and CAS (range: 0.81-1.23) (Figure 1A, F) and least
328 variable at TYE (range: 0.92-1.07) and CLE (range: 0.87 – 1.04) (Figure 1B, E).

329 Associations between λ and climate were a function of the climate associations with
330 survival and recruitment. We observed associations with climate on both survival and
331 recruitment at all areas except HJA, where only recruitment was associated with climate. At
332 OLY, λ was highest when growing season conditions were wetter-than-normal and the number
333 of winter storm days was low, although recruitment was somewhat lower when growing seasons
334 during the previous year had high precipitation. Similarly, λ was highest at CLE when growing
335 seasons were wetter-than-normal and the number of nesting season storm days was moderate. At
336 HJA, λ was negatively related to early nesting season precipitation in the previous year, while
337 λ at OCR was negatively related to nesting season precipitation but also positively related to
338 wetter-than-normal growing season conditions. At TYE, λ was highest following years when the
339 SOI was in the el Niño phase and the PDO was in the cool, wet phase which occurred in 1989-
340 1991 and 1998-1999. Similar to HJA and OCR, λ at TYE was lower following years with high
341 nesting season precipitation. At CAS, λ was highest following years with wetter-than-normal
342 growing seasons, lower amounts of winter precipitation, and fewer DAYS > 32° C.

343 **3.5 Relative contributions of survival and recruitment to λ**

344 Time-specific seniority estimates () indicated that the relative contribution of survival
345 to λ (~0.90) was much greater than recruitment (~0.10) for all areas although relative
346 contributions of survival and recruitment to λ varied over time (range: 0.76–0.99) and among
347 study areas (Figure 2, Supplementary Information 5),. Year-to-year variation in seniority was
348 greatest at OLY and CAS and least at CLE and OCR (Figure 3). Years during which λ >1.0

349 were those during which recruitment was higher than average (Figure 1), particularly for OLY,
350 TYE, and CAS.

351 **3.6 Variance Components**

352 The top models accounted for 30-87% of the temporal process variation in λ , with
353 climate accounting for 8-85% of this variation (Table 4). Climate accounted for the most
354 temporal variation in λ at TYE (85%) and OCR (78%), and least at HJA (3%) and CLE (8%).
355 The top models accounted for 2-100% of the temporal variation in annual survival, with climate
356 accounting for 0-67% (Table 4). Climate accounted for a substantial amount of variation in
357 survival only at OLY (67%), while the combined effects of barred owls and climate accounted
358 for most (~100%) of the temporal process variation in survival at OCR. For recruitment, the top
359 models accounted for 2-92% of the temporal process variation, with climate accounting for 2-
360 51% (Table 4). Climate accounted for 51% at CAS, 48% at OLY, 44% at TYE, and 25% at
361 OCR. Relatively low amounts of variation in recruitment were accounted for by climate for CLE
362 (2%) or HJA (6%).

363 **4. DISCUSSION**

364 This is the first study to examine associations between rate of population change and
365 climate for the northern spotted owl and to consider such associations across a broad geographic
366 range. We established new associations between survival, recruitment and rate of population
367 change and moisture conditions during the growing season, regional climate cycles, and hot
368 summer days not previously reported for this subspecies. While we observed relationships
369 between demographic rates and local weather during the winter and nesting season similar to
370 those of earlier studies (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), these models

371 generally received far less support than those representing regional moisture conditions and
372 climate cycles at most study areas. Although population growth rates were associated with
373 climate at all 6 study areas, the specific climatic factors, the strength of the relationships, and the
374 amount of temporal variation accounted for by climate varied among areas. As predicted, climate
375 accounted for more variability in recruitment than survival, while λ was most sensitive to
376 changes in adult survival. Franklin et al. (2000) suggested that northern spotted owls follow a
377 bet-hedging life history strategy, where selection favors individuals that increase their odds of
378 survival by reproducing only during favorable conditions. Our results were consistent with this
379 hypothesis; however, we found that relative contributions of survival and recruitment to rate of
380 population growth varied geographically and temporally. These differences may reflect variation
381 in prey availability, habitat quality, environmental conditions, or life history strategies across the
382 range of the subspecies.

383 **4.1 Regional Climate**

384 At four study areas, λ was positively associated with wetter than normal conditions
385 during the growing season, either through associations with annual survival, recruitment, or both.
386 Year-specific survival rates were related to moisture conditions during the current year, while
387 recruitment reflected moisture conditions 2-3 years prior, which likely influenced survival of
388 juveniles from prior years' reproduction. Similarly, survival, recruitment, and λ at TYE were
389 associated with the Southern Oscillation and Pacific Decadal Oscillation while at CAS, λ was
390 negatively associated with summer temperature. Our *a priori* hypotheses regarding regional
391 climate cycles, growing season moisture, and to some extent hot summer days postulated that
392 climate affected spotted owl population dynamics by influencing prey abundance rather than

393 through direct effects of weather on owls, and our results supported this hypothesis at OLY,
394 CLE, OCR, TYE and CAS.

395 Both annual survival and reproductive success in raptors has frequently been associated
396 with prey availability (Newton 1979). Population sizes of northern flying squirrels (*Glaucomys*
397 *sabrinus*), deer mice (*Peromyscus maniculatus*), and other mammal species that comprise
398 spotted owl diets are often characterized by large annual variations in population size driven
399 primarily by food availability (Ransome and Sullivan 1997, Waters and Zabel 1998, Gomez et
400 al. 2005). Variation in weather can have substantial influence on food availability for small
401 mammals. Small mammal populations have shown declines during drought (Spevak 1983), and
402 population dynamics have been shown to be associated with regional climate cycles such as the
403 SOI (Lima et al. 2001). Northern flying squirrels feed primarily on hypogeous fungi (Gomez et
404 al. 2005), which are most abundant during mesic conditions particularly during late summer and
405 fall (Luoma et al. 2003). Similar to our results, annual survival and fecundity of Mexican
406 spotted owls (*Strix occidentalis lucida*) were positively associated with precipitation during the
407 previous year (Seamans et al. 2002). Few studies of small mammal population dynamics have
408 been conducted within the range of the northern spotted owl. Rosenberg et al. (2003) found a
409 positive relationship between spotted owl reproduction and abundance of deer mice at HJA and
410 suggested that interactions between small mammal populations and weather may influence prey
411 availability for spotted owls. However, without studies that specifically identify responses of
412 small mammal populations to climate variability at these areas, we can only speculate about the
413 causal mechanisms that may link climate, small mammals, and spotted owl population dynamics.

414 Population growth rate was negatively associated with hot summer temperatures at CAS,
415 which was the southernmost area and had the greatest number of days with temperatures $\geq 32^{\circ}\text{C}$
416 in all years. Although Forsman et al. (1984), Barrows and Barrows (1978), and Weathers et al.
417 (2001) all reported that spotted owls become stressed at temperatures above 28°C , there is no
418 evidence to indicate that they are ever directly killed by temperatures normally encountered
419 within their range because they are able to thermoregulate by seeking out shady roosts in the
420 forest understory on hot days (Forsman et al. 1984; Barrows and Barrows 1978). While the
421 number of days $\geq 32^{\circ}\text{C}$ was a measure of local weather, it is possible that summers with many
422 hot days are associated with reduced prey populations or foraging success, consequently
423 reducing survival and population growth of spotted owls.

424

425 **4.2 Local Weather**

426 Although wetter-than-average conditions during the growing season appeared to be
427 beneficial for spotted owls, heavy precipitation during the early nesting season did not. While
428 annual survival was more closely related to regional climate conditions, recruitment was often
429 associated with local weather. We found negative associations between recruitment and heavy
430 nesting season precipitation at OCR, TYE, and HJA. During this period, owls initiate nesting
431 and incubate eggs (Forsman et al. 1984). Energy demands on adults can be higher during nesting
432 seasons, and severe, winter-like conditions can decrease prey abundance, prey availability, and
433 foraging success (Forsman et al. 1984). We also observed quadratic associations with winter
434 precipitation and storms at CAS. Negative associations between spotted owl survival or
435 reproduction and severe weather during the nesting season or winter have been documented in

436 other studies (Franklin et al. 2000; Olson et al. 2004; Dugger et al.2005; Glenn 2009); however,
437 ours is the first study to suggest similar relationships in the context of λ .

438 **4.3 Barred Owls**

439 We found a negative association between the proportion of spotted owl territories with
440 barred owl detections (BO) and annual survival OLY and OCR. On most study areas, we found
441 that BO was either negatively associated with resighting probabilities (OLY, CLE, OCR, CAS)
442 or not associated with resighting probabilities (TYE). The exception was the HJA study area
443 where the association between BO and resighting probability was positive. Although annual
444 reproduction of northern spotted owls is highly variable (Anthony *et al.* 2006), recruitment of
445 new individuals into the territorial population in our study was less variable. At these six study
446 areas, a negative association between numbers of young fledged per pair per year and the BO
447 covariate was detected only at OLY (Glenn 2009). However, recruitment was negatively
448 associated with BO at OLY, HJA, OCR, and TYE. This suggests that barred owls may have a
449 negative effect on rates of population change of spotted owls primarily by influencing
450 recruitment as opposed to reproduction. These results are consistent with Olson et al. (2005) and
451 Kelly et al (2003), who reported that barred owls were associated with decreased territory
452 occupancy of spotted owls. Olson et al. (2005) also reported that barred owl presence was related
453 to increased local (territory) extinction at TYE and OCR, and also to decreased local
454 colonization probabilities at HJA. Why relationships between barred owls and spotted owl
455 survival, resighting, and recruitment were not consistent among areas is unclear, although it is
456 possible that the covariate we used (% of spotted owl territories with barred owl detections for a
457 study area in a given year) was too coarse to reflect the true impact of barred owls.

458 Documentation of this relationship will require more consistent surveys of barred owls (Bailey et
459 al. 2009) and may be better documented with territory-specific analyses such as those conducted
460 by Olson et al. (2005) and Dugger et al. (2005).

461 **4.4 Conclusions**

462 Our study demonstrated that demographic rates of northern spotted owls are associated with
463 local weather and regional climate, although the specific climatic factors most strongly
464 associated with demographic rates, the relative contributions of survival and recruitment to
465 population growth rate, and the amount of variation in demographic rates accounted for by
466 climate varied among the 6 areas. Additionally, we found a negative association between barred
467 owl presence and recruitment at four areas and barred owls and survival at two areas. This study
468 has helped expanded our understanding of both exogenous and endogenous factors that influence
469 demographic performance of this subspecies. Most northern spotted owl populations have been
470 declining since the mid 1990s (Forsman et al. *in press*). Variation in climate has the potential to
471 strongly influence population dynamics for spotted owls; however, there are numerous other
472 factors including habitat, barred owls, and prey that must be considered as well.

473 Potential consequences of global climate change on Pacific Northwest forests remain unclear.
474 Most models predict warmer, wetter winters and hotter, drier summers for the Pacific Northwest
475 in the first half of the 21st century (Mote et al. 2008). Given the patterns we observed during
476 1990-2005, increased occurrence of drought conditions during the summer has the potential to
477 negatively affect annual survival, recruitment, and population growth rates of northern spotted
478 owls across much of their range. Furthermore, changes in climate resulting from human
479 activities have the potential to cause fundamentally different patterns in weather which may have

480 unpredictable consequences for northern spotted owl populations. Given that natural resource
481 managers cannot control climate variation and barred owls are likely to persist and increase in
482 the range of the northern spotted owl, maintaining sufficient high quality habitat on the
483 landscape remains the most important management strategy for the conservation of this
484 subspecies.

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491

492

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632 Table 1. Top (lowest QAIC_c value) and competing (Δ QAIC_c < 2.0) Pradel reverse-time capture-mark-recapture models for northern
 633 spotted owls at 6 study areas in Washington and Oregon, 1990-2005.

Model ^{ab}	QAIC _c	Δ QAIC _c	QAIC _c w	K	Q Deviance
OLY ($\hat{c} = 1.54$)					
{ ϕ (sex+BO+PDSI+STORMS-W) p (REPROD) f (BO+EO+GPRED)(lag2)}	3080.71	0.00	0.32	12	903.27
{ ϕ (BO+PDSI+STORMS-W) p (REPROD) f (BO+EO+GPRED)(lag2)}	3080.83	0.12	0.30	11	905.42
{ ϕ (sex+ BO+PDSI+ STORMS-W) p (REPROD) f (BO + GPRED (Q)(lag2)}	3081.38	0.67	0.23	11	905.97
CLE ($\hat{c} = 1.00$)					
	AIC _c	Δ AIC _c	AIC _c w	K	Deviance
{ ϕ (PDSI+STORMS-N(Q)) p (REPROD) f (PDSI(lag3))}	1461.86	0.00	0.40	8	432.67
{ ϕ (PDSI+ STORMS-N(Q)) p (REPROD) f (SNOW+PDSI(lag3))}	1462.37	0.51	0.31	9	431.13
HJA ($\hat{c} = 1.56$)					
	QAIC _c	Δ QAIC _c	QAIC _c w	K	Q Deviance
{ ϕ (REPROD) p (BO) f (exp+BO(lag1) +ENPRE(lag1))}	2759.54	0.00	0.19	8	818.72
{ ϕ (REPROD) p (BO) f (exp+BO(lag1)+WTMIN (lag1))}	2760.30	0.76	0.13	8	819.47
{ ϕ (REPROD) p (BO) f (exp+BO(lag1)+WTMIN (lag1)+ENPRE (lag1))}	2760.30	0.76	0.13	9	817.46
{ ϕ (REPROD) p (BO) f (exp+BO(lag1)+ENPRE (lag1)+ENTMIN (lag1)+(ENTMIN*ENPRE)(lag1)}	2760.73	1.19	0.11	10	815.87
{ ϕ (REPROD) p (BO) f (exp+BO(lag1))}	2760.89	1.35	0.10	7	822.09
{ ϕ (REPROD) p (BO) f (exp+BO(lag1)+PDO (lag1)}	2760.92	1.38	0.10	8	820.09

$\{\varphi(\text{REPROD}+\text{ENPRE}) p(\text{BO}) f(\text{exp}+\text{BO}(\text{lag1})+\text{ENPRE}(\text{lag1}))\}$	2761.04	1.50	0.09	9	818.19
OCR ($\hat{c} = 2.52$)					
$\{\varphi(\text{BO}*\text{PDSI}) p(\text{BO}) f(\text{BO}+\text{ENPRE}(\text{lag1}))\}$	1912.83	0.00	0.33	9	410.81
$\{\varphi(\text{BO}*\text{PDSI}) p(\text{BO}) f(\text{BO}+\text{ENPRE}(\text{lag1})+\text{ENTMIN}(\text{lag1}))\}$	1914.43	1.61	0.15	10	410.40
$\{\varphi(\text{BO}*\text{PDSI}) p(\text{BO}) f(\text{BO}+\text{ENPRE}(\text{lag1})+\text{PDSI}(\text{lag1}))\}$	1914.56	1.74	0.14	10	410.53
$\{\varphi(\text{BO}*\text{PDSI}) p(\text{BO}) f(\text{BO}+\text{ENPRE}(\text{lag1})+\text{LNPRE}(\text{lag1}))\}$	1914.73	1.91	0.13	10	410.70
TYE ($\hat{c} = 1.30$)					
$\{\varphi(\text{SOI}(\text{lag1}) + \text{PDO}(\text{lag1})) p(\text{sex}+\text{REPROD}) f(\text{BO}(\text{lag1})+\text{PDO}(\text{lag2})+\text{ENPRE}(\text{lag1})+\text{SOI}(\text{lag1}))\}$	3158.57	0.00	0.44	11	559.45
$\{\varphi(\text{SOI}(\text{lag1})+\text{PDO}(\text{lag1})) p(\text{sex}+\text{REPROD}) f(\text{BO}(\text{lag1})+\text{PDO}(\text{lag2})+\text{ENPRE}(\text{lag1}))\}$	3159.02	0.45	0.35	10	561.92
CAS($\hat{c} = 1.84$)					
$\{\varphi(\text{DAYS} \geq 32^\circ\text{C}) p(\text{T}) f(\text{exp}+\text{WPRES}(\text{Q})(\text{lag2})+\text{STORMS-W}(\text{Q})(\text{lag2})+\text{PDSI}(\text{lag2}))\}$	2283.24	0.00	0.70	11	616.43
$\{\varphi(\text{DAYS} \geq 32^\circ\text{C}) p(\text{T}) f(\text{exp}+\text{PDSI}(\text{lag2}))\}$	2287.96	4.72	0.07	7	629.25

634 ^a (Q): quadratic relation between covariate and survival or recruitment. Lag1 (2,3) indicates a 1-year (2-year, 3-year) lag between the specified
635 climatic condition and the effect on the demographic parameter.

636 ^bCovariates included the following: 1-time expansion of study area boundaries (exp), proportion of spotted owl territories with barred owl
637 detections (BO), mean number of young fledged/pair/year (REPROD), linear time trend (T), Palmer Drought Severity Index (PDSI), growing
638 season precipitation (GPRES), # of days with storm conditions during winter (STORMS-W), winter precipitation (WPRES), early nesting season
639 (Mar-Apr) precipitation (ENPRE), early nesting season (Mar-Apr) mean minimum temperature (ENTMIN), late nesting season (May-Jun)
640 precipitation (LNPRE), late nesting season (May-Jun) mean minimum temperature (LNTMIN), # of days with storm conditions during nesting
641 season (STORMS-N), Southern Oscillation Index (SOI), Pacific Decadal Oscillation Index (PDO), # days with maximum temperature > 32° C
642 (DAYS>32°C), total winter snowfall (SNOW), and winter mean minimum temperature (WTMIN).

643 Table 2. Parameter estimates from top (lowest AIC_c) Pradel reverse-time capture-mark-
 644 recapture models for northern spotted owls at 6 study areas in Washington and Oregon, 1990-
 645 2005.

Parameter ^a	Estimate	SE	95% CI		
			lower	upper	
OLY	ϕ intercept	3.244	0.404	2.453	4.036
	ϕ sex	0.210	0.144	-0.072	0.492
	ϕ BO	-6.368	2.064	-10.414	-2.323
	ϕ PDSI	0.202	0.083	0.039	0.365
	ϕ STORMS-W	-0.061	0.019	-0.099	-0.023
	p intercept	0.657	0.108	0.444	0.869
	p REPROD	0.668	0.166	0.342	0.993
	f intercept	5.571	2.240	1.180	9.962
	f BO	-16.329	4.644	-25.431	-7.226
	f EO	-0.583	0.380	-1.329	0.162
	f GPRE	-0.134	0.047	-0.226	-0.042
	f GPRE ²	0.001	0.000	0.000	0.001
	CLE	ϕ intercept	1.492	0.214	1.072
ϕ PDSI		0.155	0.079	0.000	0.310
ϕ STORMS-N		0.534	0.260	0.023	1.044
ϕ STORMS-N ²		-0.101	0.051	-0.200	-0.001
p intercept		1.624	0.279	1.078	2.171
p REPROD		0.583	0.289	0.016	1.151
f intercept		-2.164	0.136	-2.430	-1.897
f PDSI (3 year lag)		0.216	0.101	0.017	0.415
HJA	ϕ intercept	2.533	0.201	2.139	2.927
	ϕ REPROD	-0.849	0.253	-1.345	-0.352
	p intercept	1.605	0.157	1.297	1.914
	p BO	3.357	1.817	-0.205	6.918
	f intercept	-0.386	0.657	-1.673	0.901
	f exp	1.242	0.436	0.387	2.097
	f BO (lag1)	-25.049	5.157	-35.157	-14.941
	f ENPRE(lag1)	-0.025	0.014	-0.053	0.003
OCR	ϕ intercept	2.263	0.232	1.807	2.718

	ϕ BO	-2.607	1.386	-5.324	0.109
	ϕ PDSI	0.198	0.090	0.022	0.374
	ϕ BO*PDSI	-1.188	0.693	-2.546	0.170
	p intercept	2.328	0.220	1.898	2.759
	p BO	-1.160	0.793	-2.714	0.393
	f intercept	-0.672	0.524	-1.699	0.354
	f BO	-2.894	0.841	-4.543	-1.245
	f ENPRE (lag1)	-0.029	0.012	-0.053	-0.004
TYE	ϕ intercept	1.934	0.089	1.761	2.108
	ϕ SOI lag	0.308	0.122	0.069	0.548
	ϕ PDO lag	0.204	0.116	-0.023	0.431
	p intercept	1.798	0.402	1.010	2.586
	p sex	0.627	0.270	0.098	1.156
	p REPROD	1.299	0.662	0.001	2.598
	f intercept	-0.709	0.361	-1.417	-0.001
	f BO (lag1)	-6.651	1.336	-9.269	-4.033
	f PDO (lag2)	-0.203	0.125	-0.448	0.043
	f ENPRE (lag1)	-0.031	0.014	-0.058	-0.004
	f SOI (lag2)	0.172	0.109	-0.041	0.385
CAS	ϕ intercept	3.410	0.613	2.209	4.611
	ϕ DAYS \geq 32°C	-0.057	0.019	-0.095	-0.019
	p intercept	0.468	0.201	0.074	0.863
	p T	0.128	0.027	0.076	0.181
	f intercept	1.815	1.558	-1.239	4.870
	f expansion year	2.067	0.541	1.006	3.127
	f WPRE (lag2)	-0.177	0.075	-0.324	-0.030
	f WPRE ² (lag2)	0.001	0.001	0.000	0.002
	f STORMS-W (lag2)	0.274	0.192	-0.102	0.649
	f STORMS-W ² (lag2)	-0.010	0.008	-0.027	0.006
	f PDSI (lag2)	0.276	0.087	0.106	0.446

646 ^aCovariates included the following: proportion of spotted owl territories with barred owl
647 detections (BO), mean number of young fledged/pair/year (REPROD), linear time trend (T),
648 Palmer Drought Severity Index (PDSI), growing season precipitation (GPRE), # of days with
649 storm conditions during winter (STORMS-W), winter precipitation (WPRE), early nesting
650 season (Mar-Apr) precipitation (ENPRE), early nesting season (Mar-Apr) mean minimum
651 temperature (ENTMIN), late nesting season (May-Jun) precipitation (LNPRE), late nesting

652 season (May-Jun) mean minimum temperature (LNTMIN), # of days with storm conditions
653 during nesting season (STORMS-N), Southern Oscillation Index (SOI), Pacific Decadal
654 Oscillation Index (PDO), # days with max temperature > 32 C (DAYS >32°C), total winter
655 snowfall (SNOW), winter mean minimum temperature (WTMIN)

656 Table 3 Mean estimates for λ , survival, recruitment, and resighting of northern spotted owls on
 657 6 study areas in Washington and Oregon, 1990-2005. Mean values were obtained from the
 658 random effects models.

	λ		ϕ		f		p	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
OLY	0.966	0.0210	0.869	0.023	0.093	0.022	0.893	0.075
CLE	0.919	0.0155	0.834	0.014	0.079	0.011	0.892	0.033
HJA	0.955	0.0178	0.885	0.009	0.072	0.014	0.916	0.047
OCR	0.961	0.0190	0.878	0.011	0.083	0.012	0.898	0.042
TYE	0.986	0.0149	0.872	0.009	0.120	0.016	0.871	0.046
CAS	0.947	0.0131	0.852	0.012	0.093	0.025	0.887	0.086

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662 Table 4. Estimated variance components for top Pradel survival and recruitment models for northern spotted owls on 6 study areas in
 663 Washington and Oregon, 1990-2005.

	σ^2 temporal process	95% CI	σ^2 model	95% CI	%	σ^2 climate	%	σ^2 demographic factors	%
Variance components for λ									
OLY	0.031	0.009 - 0.070	0.021	0.008-0.068	67	0.012	40	0.0086	28
CLE	0.003	-0.0002-0.013	0.001	0.000-0.006	30	0.0002	8	na	na
HJA	0.005	0.001- 0.017	0.003	0.001-0.010	66	0.0001	3	0.0032	63
OCR	0.003	-0.001 - 0.018	0.003	0.0001-0.014	78	0.003	78	2.8E-06	0
TYE	0.003	0.0005-.010	0.002	0.001-0.007	87	0.002	85	0.0001	3
CAS	0.025	0.009- 0.081	0.013	0.004 - 0.047	53	0.013	53	na	na
Variance components for survival									
OLY	0.007	0.003-0.022	0.005	0.001-0.018	67	0.005	67	2.0E-05	0
CLE	0.006	0.002-0.021	0.0001	0.000-0.004	2	0.0001	2	na	na
HJA	0.003	0.001-0.009	5.0E-05	0.000-0.002	7	na	na	5.0E-05	2
OCR	2.2E-05	-0.001-0.004	2.2E-05	0.000-0.001	100	climate*demog		2.2E-05	100
TYE	3.80E-06	-0.0004-0.003	3.8E-06	0.000-0.0002	1	3.8E-06	1	na	0
CAS	0.006	0.002-0.019	0.0002	0.000-0.004	3	0.0002	3	na	na
Variance components for recruitment									
OLY	0.018	0.002- 0.029	0.013	0.001- 0.030	70	0.009	48	0.0040	22
CLE	0.002	0.001-0.005	2.4E-05	0.000-0.001	2	2.4E-05	2	na	na
HJA	0.002	0.001-0.007	0.002	0.001-0.007	92	1.4E-04	6	0.0020	86
OCR	0.002	0.001-0.009	0.001	0.0001-0.005	32	0.001	26	1.2E-04	6
TYE	0.004	0.002-0.012	0.003	0.001-0.009	63	0.002	44	0.0008	19
CAS	0.013	0.005- 0.044	0.006	0.002-0.024	51	0.006	51	na	na

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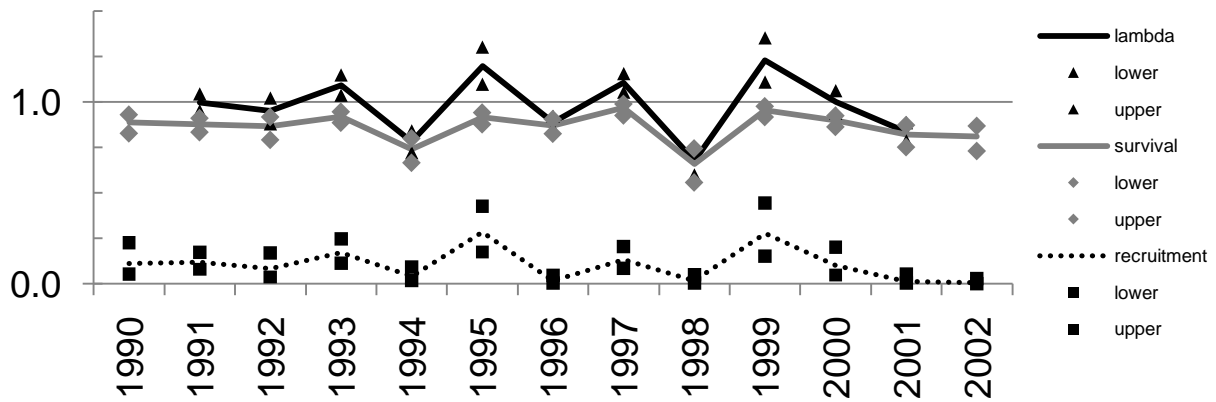
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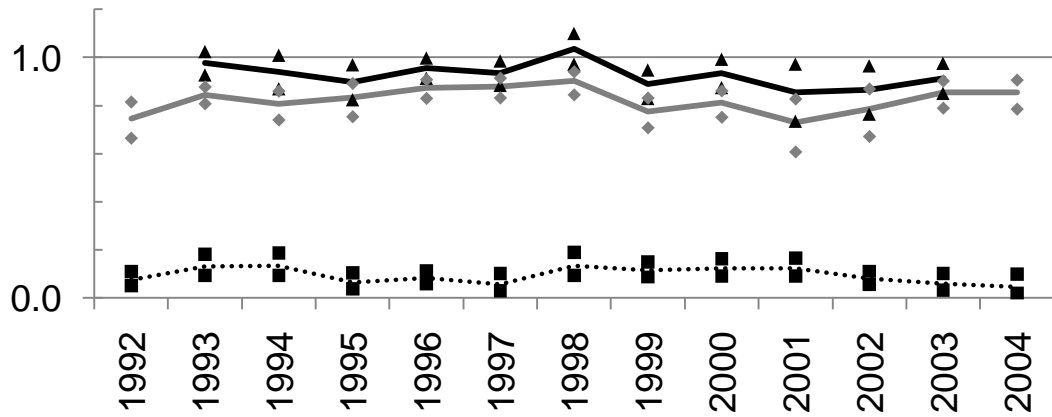
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686 Figure 1. Time-specific estimates of λ , μ , and σ for northern spotted owls on 6 study areas (A-F)
687 in Washington and Oregon, 1990-2005. Upper and lower 95% confidence intervals are indicated
688 for each rate

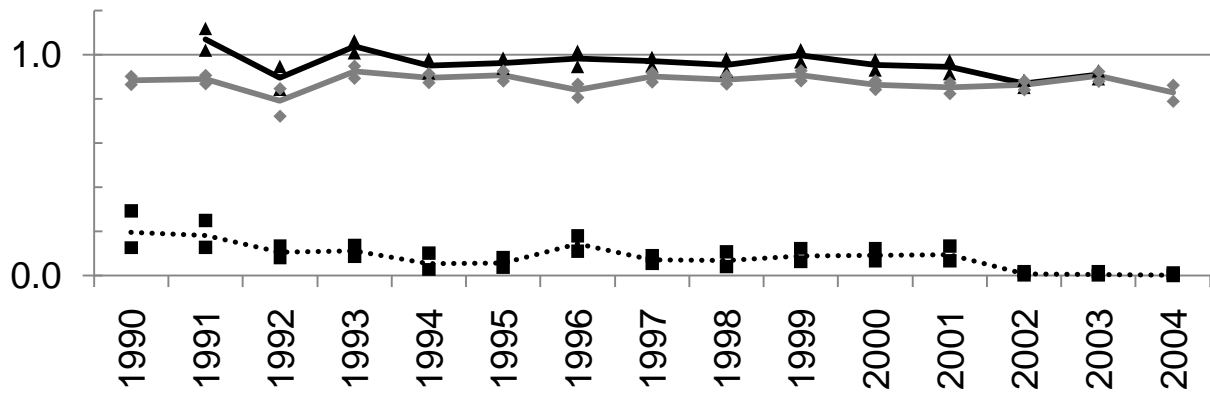
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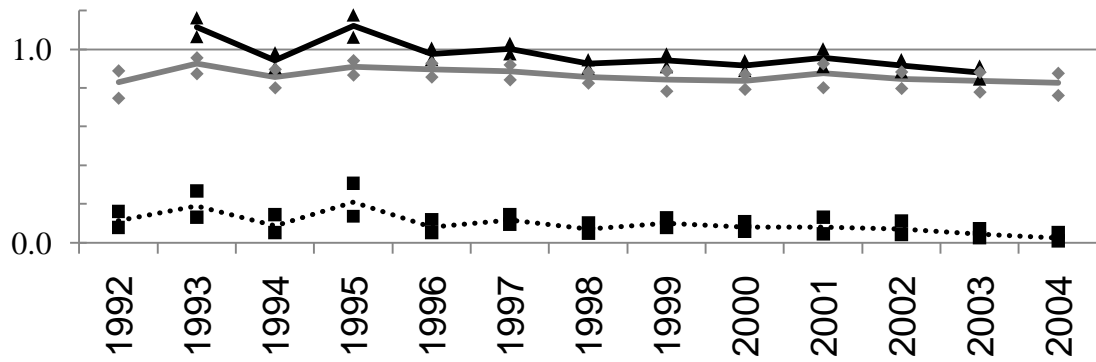
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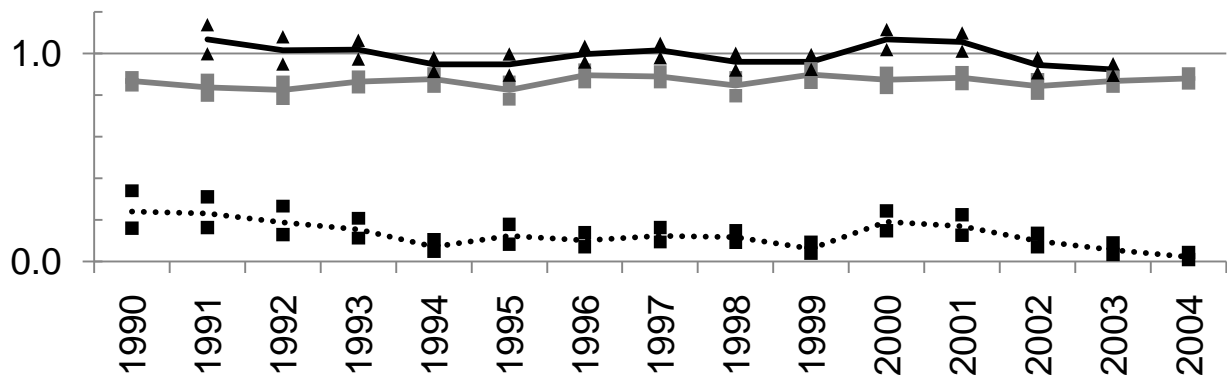
C. HJA



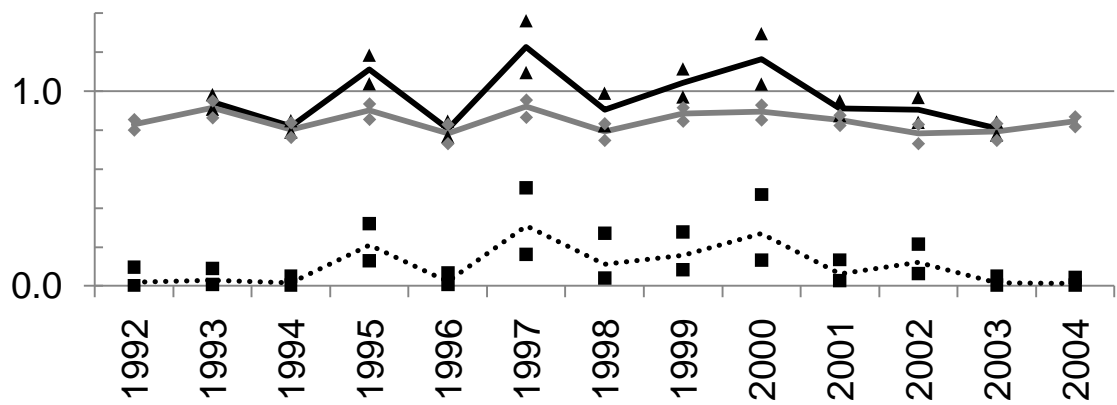
D.OCR



E. TYE



F. CAS



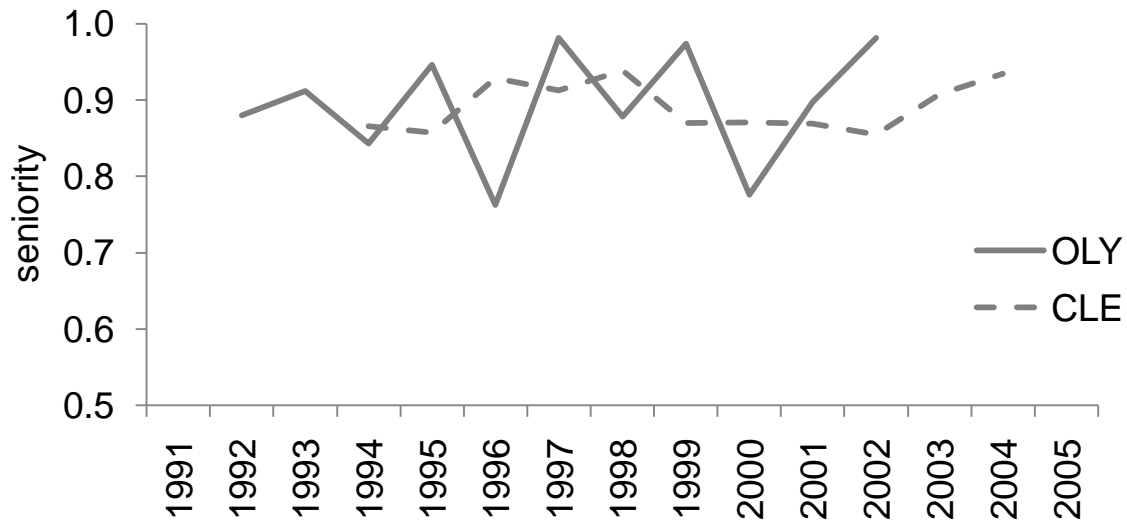
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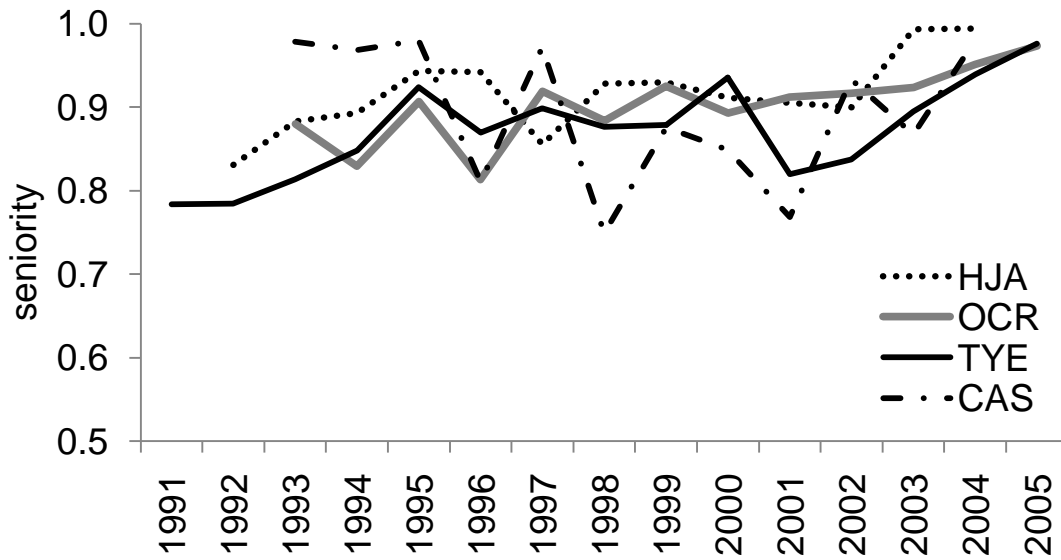
Figure 2. Estimates of seniority for northern spotted owls at 6 study areas in Washington (A) and Oregon (B), 1990-2005.

714 A. Washington study areas



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716 B. Oregon study areas



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