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Review

Range-wide declines of northern spotted owl populations in the Pacific Northwest: A meta-analysis

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ABSTRACT

The northern spotted owl (*Strix occidentalis caurina*) inhabits older coniferous forests in the Pacific Northwest and has been at the center of forest management issues in this region. The immediate threats to this federally listed species include habitat loss and competition with barred owls (*Strix varia*), which invaded from eastern North America. We conducted a prospective meta-analysis to assess population trends and factors affecting those trends in northern spotted owls using 26 years of survey and capture-recapture data from 11 study areas across the owls' geographic range to analyze demographic traits, rates of population change, and occupancy parameters for spotted owl territories. We found that northern spotted owl populations experienced significant declines of 6–9% annually on 6 study areas and 2–5% annually on 5 other study areas. Annual declines translated to ≤35% of the populations remaining on 7 study areas since 1995. Barred owl presence on spotted owl territories was the

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primary factor negatively affecting apparent survival, recruitment, and ultimately, rates of population change. Analysis of spotted and barred owl detections in an occupancy framework corroborated the capture-recapture analyses with barred owl presence increasing territorial extinction and decreasing territorial colonization of spotted owls. While landscape habitat components reduced the effect of barred owls on these rates of decline, they did not reverse the negative trend. Our analyses indicated that northern spotted owl populations potentially face extirpation if the negative effects of barred owls are not ameliorated while maintaining northern spotted owl habitat across their range.

1. Introduction

The northern spotted owl (*Strix occidentalis caurina*; NSO) inhabits coniferous forests in the Pacific Northwest of the U.S., extending from British Columbia through Washington and Oregon and into northern California (Gutiérrez et al., 1995). This subspecies has been at the nexus of forest management issues in the Pacific Northwest since the 1970s because of its strong association with older forests coupled with relatively large home ranges. In 1990, the NSO was listed as threatened under the Endangered Species Act (U. S. Fish and Wildlife Service, 1990) and protection of older forests for NSO and other old-forest obligates reduced timber harvest (Dixon and Juelson, 1987). Multiple management strategies and plans were developed by federal agencies on whose lands the bulk of NSO populations were found. Most of these management plans were litigated, especially after the owl was federally listed (Marcot and Thomas, 1997). In 1994, the Northwest Forest Plan (NWFP) was adopted, which attempted to balance maintenance of forests for NSO populations with economically viable timber harvest on federal lands throughout the owls' range; current forest management continues under this plan (U. S. Department of Agriculture and U. S. Department of the Interior, 1994).

One component of the NWFP required long-term monitoring of NSO populations (Lint et al., 1999). This monitoring scheme utilized eight existing NSO demographic studies that were established as early as 1985. Additional demographic studies were also initiated outside the NWFP population monitoring framework and, at one point, there were 15 demographic studies distributed across the range of the NSO (Franklin et al., 1999). These studies were alike in that all utilized similar field methods to estimate demographic parameters using primarily capture-recapture estimators (Franklin et al., 1996).

Collectively, the demographic studies of the NSO were considered as meta-replicates, where the study area was the unit of replication (Johnson, 2002, 2006). This allowed for a prospective meta-analysis (Seidler et al., 2019) of NSO demographic studies, where study area selection, hypotheses, and analyses were specified before the meta-analysis was conducted (e.g., Anthony et al., 2006). Although rare, prospective meta-analyses are useful for addressing high-priority research questions in situations where new studies are expected to emerge (Seidler et al., 2019).

We provide here the results from the seventh meta-analysis on population trends in NSOs (Table 1). This meta-analysis continued the tradition of earlier meta-analyses in addressing two key questions of concern to forest and wildlife managers: *What are the range-wide population trends in NSO populations?* and *Are management activities or other factors affecting these trends?* We addressed the first broad question by examining a number of more specific questions, including: *What are the trends in life history traits, such as fecundity, survival, and recruitment?* and *What are the annual rates of population change?* To address the second broad question, hypotheses about range-wide factors, such as habitat, climate, and invasive species, are addressed in the meta-analysis, especially those factors previously identified as threats to population recovery (e.g., Dugger et al., 2016; Forsman et al., 2011). Threats to NSO populations have changed since the first several meta-analyses (Table 1) with habitat loss and fragmentation considered the primary threats in the 1980s and 1990s (U. S. Fish and Wildlife Service, 1990). Since the adoption of the NWFP, timber harvesting declined on federal lands, which slowed the threat of alteration and removal of suitable forest for NSO on federal lands. Concurrently, barred owls (*Strix varia*; BO) from the eastern U. S. began expanding their distribution and increasing in numbers throughout the Pacific Northwest (Kelly et al., 2003; Long and Wolfe, 2019). In the last two decades, BOs have been considered a primary threat to NSO populations (U. S. Fish and Wildlife Service, 2011, 2020), through both interference and exploitative competition (Lesmeister et al., 2018; Van Lanen et al., 2011; Wiens et al., 2014). Relative to NSO, congeneric BOs are larger, use smaller home ranges, and have a broader (generalist) diet that includes numerous small mammalian prey important to NSO (Gutiérrez et al., 2007; Hamer et al., 2001; Wiens et al., 2014). BOs are also behaviorally dominant to NSO during territorial confrontations (Van Lanen et al., 2011), and where the two species co-occur they exhibit a high degree of overlap in patterns of habitat selection at nesting sites and foraging areas (Long and Wolfe, 2019; Wiens et al., 2014). This combination of exploitation and interference competition, coupled with rapidly increasing numbers of BOs in older forests throughout the Pacific Northwest, has exacerbated NSO population declines historically triggered by habitat loss.

In the last meta-analysis, BOs were identified as a primary influence negatively affecting life history traits, territory occupancy rates, and, ultimately, rates of population change in NSOs (Dugger et al., 2016). Recently, the U.S. Fish and Wildlife Service determined that the NSO was warranted for uplisting to endangered, but this re-classification was precluded by other higher priority listings (U. S. Fish and Wildlife Service, 2020). This, coupled with the recent elimination of 14,050 km^2 of critical habitat for the NSO (U. S. Fish and Wildlife Service, 2021), makes it imperative to understand current population trends and the factors affecting those trends for this species.

The meta-analysis presented here follows the same general guidelines as preceding meta-analyses on NSO populations to objectively evaluate trends in population parameters and competing hypotheses representing different effects that can influence those trends (Anderson et al., 1999). We used rigorous analytical methods, such as random effects, and approaches that accounted for imperfect detectability, such as capture-recapture and occupancy modeling. In keeping with previous meta-analyses, we also incorporated recent innovations in statistical analyses to provide a rigorous analytical approach.

Table 1
History of meta-analyses to estimate range-wide population trends in northern spotted owls.

Year	No. of study areas	No. of participants[a]	Source
1991	5	12	Anderson and Burnham (1992)
1993	14	47	Forsman et al. (1996b)
1998	15	44	Franklin et al. (1999)
2004	14	44	Anthony et al. (2006)
2009	11	43	Forsman et al. (2011)
2014	11	38	Dugger et al. (2016)
2020	11	40	Current study

[a] Number of participants at the analytical workshops.

2. Methods

2.1. Study areas

We used 11 study areas where demographic data were collected on

NSOs (3 in Washington, 5 in Oregon, and 3 in California) through 2018 (Table 2, Fig. 1). Although the duration of these studies ranged from 27 to 34 years, we used 1993 as the starting year for all the study areas because it provided a common time period for analyses and allowed for comparisons among study areas that began in different years (Fig. 2; 26 years: 1993–2018). Eight of the 11 study areas (OLY, CLE, COA, HJA, TYE, KLA, CAS, NWC) were part of the NWFP Effectiveness Monitoring Program (Lint et al., 1999). Of these eight study areas, the OLY, HJA, CAS, and NWC study areas were primarily on federal public lands while the CLE, COA, TYE, and KLA study areas were on a mixture of federal and private lands. The 3 study areas not included in the NWFP Monitoring Program were on lands owned by Green Diamond Resource Company (GDR) and the Hoopa Tribe Reservation (HUP), both in California. Also, the RAI study area in Washington included lands managed by Weyerhaeuser Company, the National Park Service, the U.S. Forest Service, and Hancock Forest Management. The study areas were large (356–3922 km^2; Table 2) and were distributed across the range of the NSO, which encompassed different climatic, topographic, vegetative, and elevation regimes (Fig. 1, Table 2; see Anthony et al. (2006) for study area details). Since the last meta-analysis (Dugger et al., 2016), the CAS study area was reduced from 3377 to 2372 km^2 because areas surveyed for spotted owls by the Bureau of Land Management (BLM) and National Park Service (NPS) were reduced or discontinued after 2013 and subsequently eliminated from the CAS data. Thus, the CAS data were reduced in spatial and temporal scope during this current meta-analysis. In addition, Green Diamond Resource Company discontinued monitoring spotted owls on 100 km^2 of the GDR study area since the last meta-analysis, which eliminated about 30 NSO territories that were included in the previous meta-analysis. For the analyses described below, we included the data associated with those owls and territories until monitoring was discontinued.

The 11 study areas in our analysis were not selected randomly (see Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 1996), but this collection of study areas sampled most of the geographic provinces within the range of the NSO (Fig. 1, Table 2). Combined, these study areas covered about 8% (18,683 km^2/230,690 km^2) of the range of the NSO, and the percentages of suitable NSO habitat on the study areas were similar to those of the surrounding landscape of federal lands (Appendix F in Anthony et al., 2006). These three lines of evidence suggest that habitat conditions within the study areas on federal lands were representative of forest and general conditions on federal lands within the geographic range of the owl. The GDR and HUP were on non-federal lands, where forests were actively managed while maintaining protections for NSOs and their forested habitat.

Since the last meta-analysis (Dugger et al., 2016), active BO removals occurred on portions of the CLE, COA, and HUP study areas as part of a removal experiment estimating the effects of BOs on NSO populations (U. S. Fish and Wildlife Service, 2013; Wiens et al., 2019, 2020). BO removals occurred on the GDR study area from 2009–2014. Data from areas where BOs were removed were censored from our meta-analysis beginning in the year of first removal and including all subsequent years, regardless of whether removals were later discontinued (e.g., GDR; Fig. 2). BOs were removed over the entire HUP study area starting in late 2013, so NSO demographic data collected from 2014–2018 were not included in our analyses (Fig. 2). Both CLE and COA were split into control and removal areas starting in 2016 (Fig. 2). While both control and removal areas were surveyed for BOs and NSOs in 2016–2018, only the control portions of these study areas were included in the meta-analysis, with a study area contraction starting the first field season after removals began. The area of the GDR involved in a BO removal experiment from 2009–2014 (Diller et al., 2016) was excluded from analyses after 2009 to remove any possible carryover effects from BO removals (Fig. 2). We excluded areas with BO removal from our meta-analysis because 1) our goal was to examine population trends in NSO for the NWFP monitoring program without experimental manipulations, and 2) analyses specific to the effects of BO removal on NSO populations are presented elsewhere (Wiens et al., 2021).

Within each study area, NSO territories were delineated using Thiessen polygons, which were defined as "*a landscape patch that represented the cumulative area of use by an owl, or pair of owls, during the study period*" (Dugger et al., 2016). Thiessen polygons were delineated around each territory using the total number of annual locations of owls collected across all years, which were prioritized based on nests, fledged young, roosts, and, rarely, nocturnal detections (see Field methods section). Thus, Thiessen polygons were static for the study period of 1993–2018 (i.e., did not change from year to year). Within each study area, Thiessen polygons were used to define range-wide covariates at the territory scale, summarize data for territory occupancy-based analyses, and merged to form boundaries for the development of covariates at the study area scale (Fig. 3).

2.2. Meta-analysis format

We followed the philosophy and protocols of previous meta-analyses of NSO demographic data (Anderson and Burnham, 1992; Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Forsman et al., 1996b; Franklin et al., 1999). Although we followed the protocol established by Anderson et al. (1999), the structure of the meta-analysis described here differed from the previous efforts in that the analysis was not completed in a 7–10 day in-person workshop because the complexity of the data and analyses had grown beyond what could be completed

Table 2
Characteristics of 11 study areas used to study demography of northern spotted owls from 1993 through 2018 in Washington, Oregon and California, USA.

Study area	Acronym	Area (km^2)	Number banded S2 and adult owls	Landowner	Ecological region	Mean annual precipitation (cm)
Washington						
Cle Elum	CLE	1784	218	Mixed	WA mixed conifer	136
Rainier	RAI	2167	194	Mixed	WA Douglas-fir	215
Olympic	OLY	2230	377	Federal	WA Douglas-fir	282
Oregon						
Coast Ranges	COA	3922	580	Mixed	OR coastal Douglas-fir	212
H.J. Andrews	HJA	1604	690	Federal	OR Cascades Douglas-fir	201
Tyee	TYE	1026	426	Mixed	OR coastal Douglas-fir	126
Klamath	KLA	1422	630	Mixed	OR-CA mixed conifer	116
South Cascades	CAS	2372[a]	555	Federal	OR Cascades Douglas-fir	119
California						
NW California	NWC	460	459	Federal	OR-CA mixed conifer	154
Hoopa	HUP	356	234	Tribal	OR-CA mixed conifer	176
Green Diamond Resources	GDR	1340	803	Private	CA coast	187
Totals		18,683	5166			

[a] Study area size was 3377 km^2 in 2014 meta-analysis.

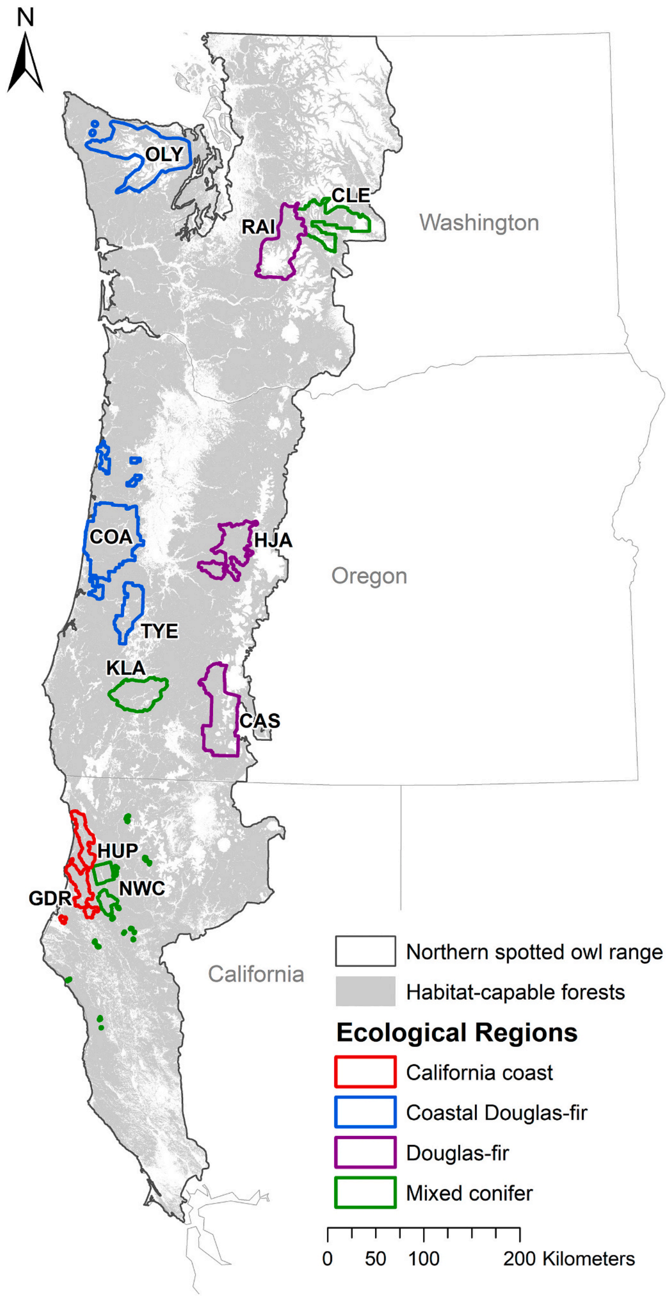

Fig. 1. Location of 11 study areas used in the northern spotted owl demographic meta-analysis.

within the short time frame of previous workshops. Rather, we structured this meta-analysis with an introductory workshop where all participants gathered to decide on the research questions of interest and how data would be analyzed. A written protocol describing each analysis was developed (Appendix A), and participants separated into working groups that subsequently analyzed data remotely. Several months later, we held a series of webinars where participants reviewed and commented on results from the working groups, ultimately resulting in the final synthesis of results (see Fig. 1 in Appendix A Supplementary Materials). Data combined across all study areas in a meta-analysis framework provided more power to evaluate trends and identify important associations between environmental factors and NSO demographics.

We analyzed fecundity from reproductive survey data, and apparent survival, recruitment rates, and rates of population change from capture-recapture data. We also analyzed detection/non-detection data for both NSOs and BOs using two-species occupancy models to estimate occupancy, local extinction rates, and colonization rates of NSO territories for both species. We used a random effects approach for all analyses except the occupancy analysis and used an information-theoretic approach for model selection and inference.

2.3. *Field methods*

Field methods were similar across all study areas and have been described in detail elsewhere (Appendix B in Dugger et al., 2016; Franklin et al., 1996; Reid et al., 1999). Study areas were surveyed for NSOs each year to locate territorial individuals, which were initially captured and banded with a uniquely numbered USGS aluminum band and a unique color-band combination (Forsman et al., 1996a). Banded owls were subsequently identified as individuals by re-sighting color-band combinations. Each year, reproductive output of individuals was determined using established methods (Franklin et al., 1996) where the number of fledged young (including 0 young) was estimated. The surveys of study areas were designed to estimate whether individuals were present and, if so, their unique identity and how many young they fledged. NSOs are strongly territorial, have high site fidelity, and are detectable even when they are not breeding (Franklin et al., 1996; Reid et al., 1999). Thus, we assumed that the birds sampled during an entire breeding season were not biased towards those that reproduced, and that the sample of owls used in our analyses was representative of the territorial population on the study areas. Owls that were visually detected were assigned to 1 of 3 discrete age classes based on their plumage characteristics when first captured as a territorial bird (S1 = 1-year old, S2 = 2-year old, Adults ≥ 3 years old) (Forsman, 1981; Franklin et al., 1996; Moen et al., 1991).

2.4. *Development of range-wide covariates*

We developed range-wide covariates to incorporate in the meta-analysis that reflected extrinsic factors previously associated with NSO demographics. These covariates included ecological region, reproductive effort, BO presence, climate descriptors, habitat components, and disturbance to habitat components (Table 3, Appendix B). We generated estimates of annual reproductive effort (R) from the analysis of fecundity (see below), which was used solely in the subsequent analysis of rates of population change. BO, climate, and habitat covariates are described in more detail in Appendix B and summarized in Table 3.

2.5. *Analytical approach*

Our meta-analysis differed from the previous meta-analyses in that we did not conduct analyses on individual study areas. Instead, study areas were treated as one level of sampling unit, with estimates and evaluation of covariate effects conducted in meta-analyses with data from all study areas combined.

We used random effects in two different analyses. First, to assess annual process variation, the method-of-moments random effects approach (Burnham, 2019; Burnham and White, 2002; Appendix F in Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2002) was used to examine trends in annual survival, fecundity, recruitment, and rates of population change of NSOs and associations between these vital rates and the covariates described above. In this random effects approach, process variation (σ^2) is treated as the conceptual unexplained ("random") variation in the true, unknown, set of parameters, such as annual survival, which is considered a random variable rather than a fixed constant. The random effects approach correctly uses the maximum-likelihood estimates for inference on structural parameters in population-level models while also being robust to over-dispersion (Appendix F in Dugger et al., 2016). The random effects here were the annual estimates of parameters within study areas. A second random

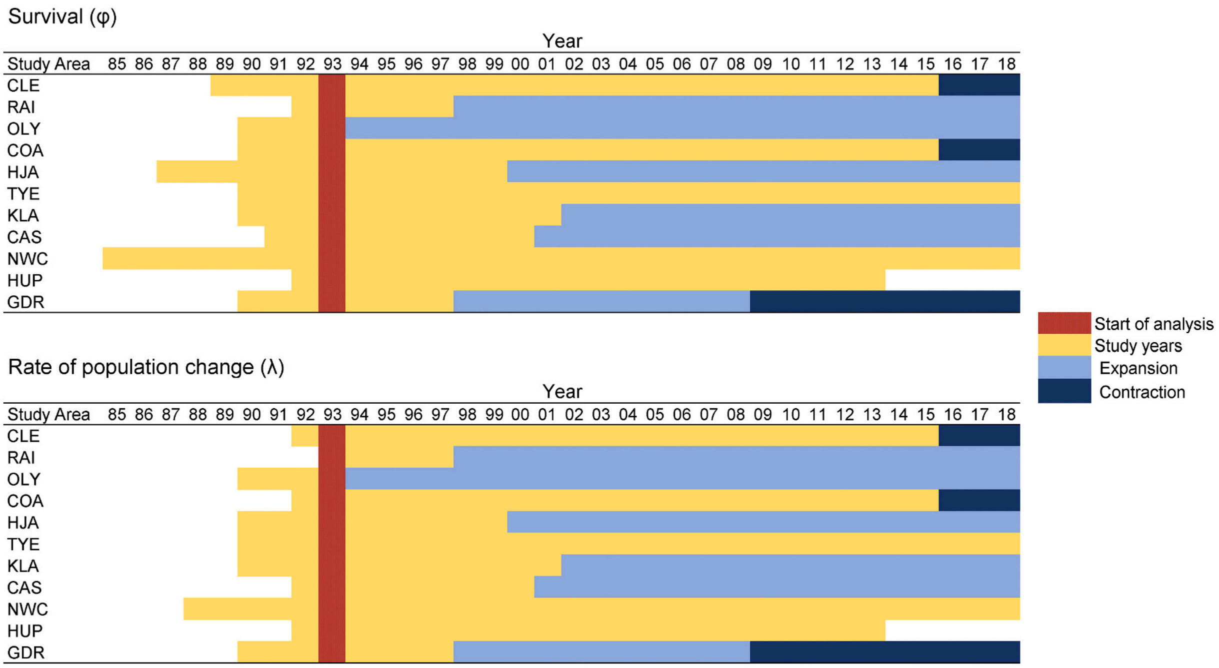

Fig. 2. Timelines for analyses of northern spotted owl demographic parameters on 11 study areas showing expansions (blue) and contractions (black). Brown line indicates common start year across all study areas for all analyses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

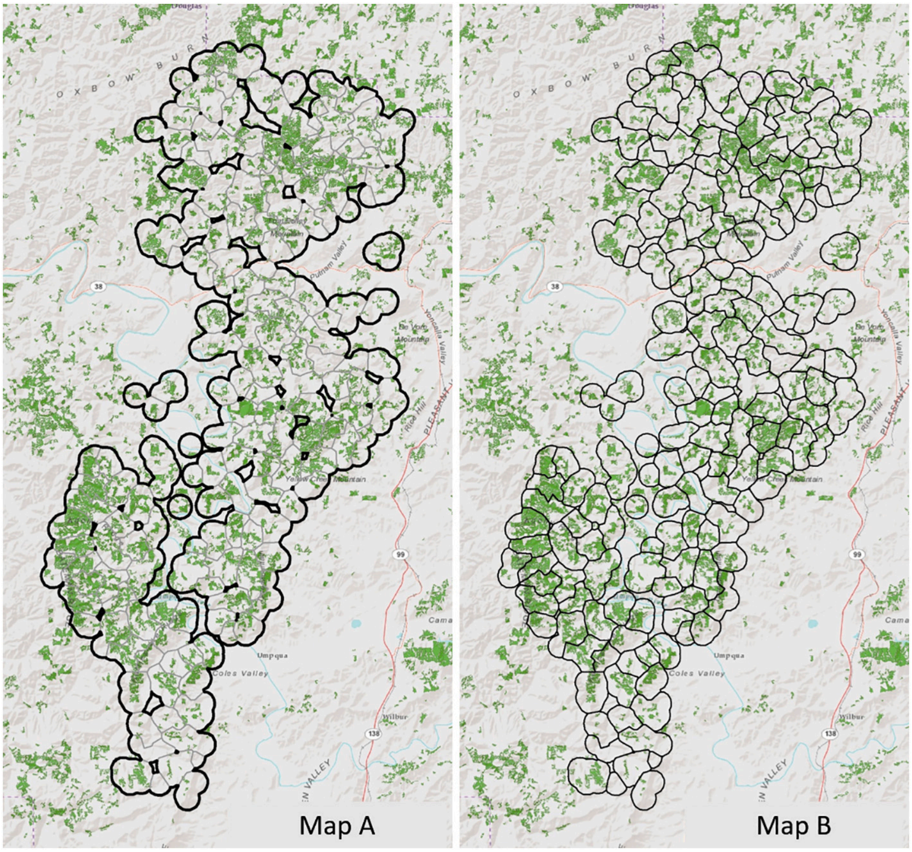

Fig. 3. Examples of study area (Map A) and territory (Thiessen polygon) scales (Map B) used to calculate covariates. Study area scales in Map A were generated from the fusion of Thiessen polygons in Map B. For fecundity, survival, and rates of population analyses, study-area scales (Map A) were used to generate covariates while for the occupancy analyses, territory scales (Map B) were used to generate territory-specific covariates.

Table 3
Definitions of covariates used in meta-analyses of northern spotted owl (NSO) demographic data from 1993–2018.

Covariate	Acronym	Description
Spatial		
Study area	AREA	Individual study area (see acronyms in Table 2)
Ecological region	ECO	Ecological region categories which incorporated geographic location (state) and major forest type, to which each study area was assigned: • WA Douglas Fir (RAI, OLY) • WA Mixed-Conifer (CLE) • OR Coastal Douglas Fir (COA, TYE) • OR Cascade Douglas Fir (HJA, CAS) • OR/CA Mixed-Conifer (KLA, NWC, HUP) • CA Coast (GDR)
Temporal		
Year	YEAR	Year when surveys and sampling occurred
Linear time trends	T	Year as a continuous linear variable, such as 1 = 1993, 2 = 1994, etc.
Quadratic time trends	TT	Year as continuous quadratic variable with T and T^2.
Even-odd year trend	EO	Year as a categorical variable to indicate oscillating time trends, where 1993 = 1 (Odd), 1994 = 0 (Even), 1995 = 1 (Odd), etc.
Spline time trends	SPLINE	A 7-df cubic spline time model with four interior nodes spaced 5 years apart.
Autoregression trend	AR1	Autoregression covariance structure on residuals of year, with a lag of 1 year.
Climate		
Pacific decadal oscillation	PDO	Mean of monthly values over the year (June–June) for sea level pressure at Tahiti minus sea level pressure at Darwin, Australia divided by SD of that quantity (http://research.jisao.washington.edu/pdo/pdo.latest).
Southern oscillation index	SOI	Mean of monthly values over the year (June–June) for the spatial average of monthly sea surface temperatures of the Pacific Ocean north of 20° N (https://www.cpc.ncep.noaa.gov/data/indices/soi).
Winter minimum temperature	WMT	Annual mean minimum monthly temperature (°C), as a spatial average of all values within the boundaries of each study area, from PRISM data (https://prism.oregonstate.edu/explorer/) for the months November–February.
Winter precipitation	WP	Annual total precipitation (cm), as a spatial average of all values within the boundaries of each study area, from PRISM data (https://prism.oregonstate.edu/explorer/) for the months November–February.
Miscellaneous		
Barred owl	BO	Annual estimate that a spotted owl territory (defined by Thiessen polygons) is occupied by ≥1 barred owls as estimated from a single species occupancy model.
Reproductive effort	R	Annual mean number of young fledged per female (NYF) generated from the fecundity analysis.
Sex	SEX	Sex of individual owls
Northern spotted owl habitat components[a]		
Suitable habitat without recruitment (proportion)	HABp	Annual proportion of the forest cover type used by NSOs for nesting and roosting in each study area each year, which included only losses and did not include recruitment of the forest cover type. This is the same covariate as used in Dugger et al. (2016). Used in the study area analyses.
Suitable habitat without recruitment (amount)	HABa	Annual amount (ha) of the forest cover type used by NSOs for nesting and roosting in each spotted owl territory each year, which included only losses and did not include recruitment of the forest cover type. This is the same covariate as used in Dugger et al. (2016). Used in the territory within study area analyses.
Relative habitat suitability (index)	RHS	Annual index representing a structural/composition gradient of forest cover. Index ranges from 0–1, with lower values having forest cover dissimilar to what NSOs use to nest and roost in, while higher values have higher degree of similarity to nesting/roosting cover type (Davis et al., 2016). Calculated as a mean value for study area or territory and includes recruitment of cover types used by NSOs for nesting and roosting
Edge (proportion)	EDGEp	Annual proportion of nesting/roosting cover type that occurs along 30 m wide edges of nesting/roosting cover patches or is contiguous with a patch and interfused with other cover types. Used in the analyses specific to study areas.
Edge (amount)	EDGEa	Annual amount (ha) of nesting/roosting cover type that occurs along 30 m wide edges of nesting/roosting cover patches or is contiguous with a patch and interfused with other cover types. Used in the territory-specific analyses.
Moderate-high disturbance (proportion)	DISThi-p	Annual proportion of moderate to high severity forest disturbance in each study area during the 3-yr interval prior to each survey year.
Moderate-high disturbance (amount)	DISThi-a	Annual amount (ha) of moderate to high severity forest disturbance in each spotted owl territory during the 3-yr interval prior to each survey year.
Low disturbance (proportion)	DISTlo-p	Annual proportion of low severity forest disturbance in each study area during the 3-yr interval prior to each survey year.
Low disturbance (amount)	DISTlo-a	Annual amount (ha) of low severity forest disturbance in each spotted owl territory during the 3-yr interval prior to each survey year.
Barred owl habitat components		
Elevation of NSO territory	ELEV	Mean elevation of forest capable pixels within NSO Thiessen polygons.
Topographic position index of NSO territory	TPI	Mean topographic position index of NSO Thiessen polygons based on the relationship between the elevation of the center pixel and mean elevation of the surrounding pixels for varying radii. Positive numbers indicate higher slope positions and ridge tops, negative index numbers indicate lower slope positions and valley bottoms.

[a] All habitat component covariates are calculated within forest capable lands.

effects analysis was a mixed model approach to construct models of individual heterogeneity of detection probabilities (p) (Gimenez and Choquet, 2010). Variance across individuals in p was estimated as σ_p.

We used an information-theoretic approach (Burnham and Anderson, 2002) and Akaike's information criterion corrected for small sample sizes (AIC_c) to determine the best model(s) from a priori model sets generated for each analysis. We generally selected the model with the lowest AIC or AIC_c values and highest Akaike weights as our best model, but other models with similar Akaike weights were considered competitive (Burnham and Anderson 2002). When evaluating models, we also examined $-2\ln L$ or deviance values to ensure that ΔAIC_c values were not solely the result of adding an additional, uninformative covariate (Arnold, 2010). We evaluated the strength of evidence for specific effects in competing models based on the degree to which 95% confidence intervals (95% CIs) for slope coefficients (β's) overlapped zero (Forsman et al., 2011). Covariates that occurred in competitive models with 95% CIs that did not overlap zero were considered to provide the strongest evidence of an effect. Covariates in competitive models with 95% CIs that overlapped zero with <10% of the interval ("slightly" overlapping) were considered to have less evidence of an effect compared to covariates with CIs that did not overlap zero. Covariates with confidence limits with >10% of the interval above or below zero ("widely" overlapping) were considered to have little support for the importance of the effect.

2.6. Analysis of fecundity

We analyzed only data for adult (≥3-years old) NSOs because fecundity estimated for younger birds from previous analyses (e.g., Dugger et al., 2016) was much lower than fecundity of adult owls and there were very few birds that bred as S1 or S2 owls. The effect of individual owl and NSO territory were very small (Dugger et al., 2016), so we ignored those effects. To be consistent with previous meta-analyses, we analyzed the number of young produced per territorial female per year (NY) as fecundity, which was calculated as NYF = NY/2 because the sex ratio of juvenile owls at hatching was approximately 1:1 (Franklin et al., 2020).

We used the annual means for each study area as the basis for analysis in a mixed-model regression with PROC MIXED in SAS (SAS Institute Inc., 2015). This weighted all years equally regardless of the number of owls sampled within a year. For each site, the models were of the form:

$$\overline{F} = f(\text{covariates})$$

(using a standard model notation) where $\overline{F}$ was the average fecundity for a study area within a year and f(covariates) depended on the model in the model set. The use of a linear model on the yearly averages rather than a generalized linear mixed model on the individual fecundity values follows McDonald and White (2010). Analyzing the mean fecundity also makes the study area-year the experimental unit (matching the level of the covariates) and avoids the need to include a random year-effect in a generalized linear mixed model to account for year-specific effects not captured by the covariates that operate on all birds on a study area-year simultaneously.

We developed an a priori model set (see protocol in Appendix A) and used a linear mixed model approach to investigate patterns of variation and hypothesized relationships between time trends and covariates with NYF. Time-trend models included annual time variation (YEAR), and linear (T), quadratic (TT), even-odd (EO), and spline (SPLINE) trends in annual NYF (Table 3). The EO trend hypothesized that years of high NYF alternated with years of low NYF but required consistent changes in NYF, which may be unrealistic. Therefore, we also fit a model where annual fluctuations in NYF around the long-term average followed an autoregressive 1-year lag process (AR1) as a covariance structure. In this model, a strict EO process was relaxed to allow longer or irregular increases and decreases in NYF. Additional models included the BO and ECO covariates, the HABp, RHS, DISThi-p, DISTlo-p, DISTtot, and EDGEp covariates, and the PDO and SOI climate covariates (Table 3). Because PDO and SOI were correlated ($r = -0.74$), these two covariates did not appear together in the same model. In addition, we removed models with high collinearity, where covariates had substantial covariances.

2.7. Analysis of apparent survival

We used the capture-recapture data and Cormack-Jolly-Seber open population capture-recapture models (Lebreton et al., 1992) in program MARK (White and Burnham, 1999) to estimate capture probabilities (p) and annual apparent survival probabilities (ϕ) of territorial, second-year subadult (S2) and adult (A) owls combined, where apparent survival rate was the probability that a bird in the sampled population of territory holders during sampling in year t was alive and present as a territory holder in year t+1. Following Dugger et al. (2016), captures of first-year subadults (S1) were not included because data for S1 owls were generally sparse, and S1 individuals were more likely to emigrate from study areas (Forsman et al., 2002). Annual estimates of survival were estimated roughly from 15 June in year t to 14 June in year t+1, which was the approximate mid-point of the annual field season during which capture-recapture data were collected from March through August (Dugger et al., 2016). In keeping with previous meta-analyses on NSO demographics (Dugger et al., 2016; Forsman et al., 2011), we did not estimate juvenile survival rates because high rates of permanent emigration of juvenile NSOs negatively bias estimates of apparent survival for juveniles (Burnham et al., 1996). We assumed no extra-binomial variation (overdispersion) in ϕ; we used $\widehat{c} = 1$ because this was very close to the mean $\widehat{c}$ across all study areas in previous analyses (Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011). In addition, regression inferences about covariate effects on parameters such as ϕ and λ are robust to over-dispersion when random effects models are used (Burnham and White, 2002).

Similar to Dugger et al. (2016), we used a hierarchical strategy to develop model sets, (Doherty et al., 2012). We first modeled detection probabilities (p) to determine the best structure on p. We examined interactive combinations of SEX, AREA, and YEAR on p while using two structures on ϕ, ϕ(SEX*AREA*YEAR) and ϕ(AREA*YEAR). We also included an additive random effect of individual heterogeneity (σ_p) on p (Gimenez and Choquet, 2010), while fixing a constant σ_ϕ to zero ($\sigma_\phi(.) = 0$) because the original model of Gimenez and Choquet (2010) included ϕ. In doing so, we assumed most of the individual heterogeneity was in p and little heterogeneity was in ϕ. One issue in incorporating σ_p to model p is that these models require considerable optimization time (>24 h), particularly given that the default in program MARK for these models is to use 101 nodes for the Gauss-Hermite numerical integration. To reduce this optimization time, we reduced the number of nodes for integration to 15. This only had a reduction of <0.002% on the value of $-2\log L$. Therefore, the random effects models considered here were based on 15 nodes in program MARK. Although only 12 models were initially specified in the meta-analysis protocol (Appendix A), additional intermediate models were required to provide starting values for the more complex initial models. Of this set of models, the model with the lowest AIC$_c$ provided the structure on p used in further modeling ϕ.

After selecting an appropriate structure for p, we then ran random effects models on ϕ in Program MARK (White et al., 2001) to investigate the effect of covariates and time trends on apparent survival, always excluding the last confounded estimate of survival (ϕ_{K-1}) (Burnham, 2019; Burnham and White, 2002). In the meta-analysis of survival, we included AREA and BO effects, T and SPLINE as time effects, PDO and SOI as regional climate effects, and HABp, RHS, DISThi-p, DISTlo-p, DISTtot, and EDGEp as effects of different habitat components (Table 3). Estimates and model selection results were generated using the Method of Moments random effects module in Program MARK (White and Burnham, 1999) from a fixed effect global model, which was either the ϕ(SEX*AREA*YEAR) or ϕ(AREA*YEAR) model that was selected during the initial modeling of p.

2.8. Annual rates of population change

We estimated the annual finite rate of population change (λ) across all the study areas using the temporal symmetry modeling approach of Pradel (1996), as implemented in program MARK (Franklin, 2001; White and Burnham, 1999) using RMark (Laake, 2013). Expansions or contractions of areas surveyed on some study areas (Fig. 2) were dealt with through changes in the design matrix (see Appendix C), such that all study areas had estimates of λ that reflected changes in owl numbers that were not confounded with changes in areas sampled or with BO removal experiments. We used all territorial S2 and adult birds, combined and treated as a single age class. Data from 1993 through 2018 were used for all study areas except HUP, for which data extended only through 2013 when BO removals began over the entire study area.

Initial modeling retained general structures for apparent survival, ϕ(AREA*YEAR), and recruitment rate, *f*(AREA*YEAR), and focused on obtaining a good structure for capture probability, *p*. Recruitment rate was defined as the expected number of new owls in the territorial population in the sampling period of year $t+1$ per owl in the territorial population in the sampling period of year *t*. Four different structures for capture probability were tested: *p*(AREA*YEAR), *p*(YEAR), $\sigma_p(.)\ p(.)$, and $\sigma_p(.)$ *p*(AREA*YEAR). The $\sigma_p(.)\ p(.)$ structure models capture probability among individuals as a random effect. This model assumed a common distribution of capture probabilities for all individuals across all study areas and years, with the σ notation indicating the standard deviation of the capture distribution on the logit scale (Gimenez and Choquet, 2010). The $\sigma_p(.)$ *p*(AREA*YEAR) structure again modeled capture probability among individuals as a random effect, permitting heterogeneity that was characterized by a different distribution for each area during each year.

Using the selected model for capture probability, and retaining the general model structure for survival and recruitment, we estimated $\lambda_{a,t}$ (where *a* denotes AREA and *t* is YEAR) as a derived parameter:

$$\widehat{\lambda}_{\mathrm{a,t}} = \widehat{\phi}_{\mathrm{a,t}} + \widehat{f}_{\mathrm{a,t}}$$

For general models with time-specific capture and survival probabilities, the first and last estimates of rate of population change (λ_1, λ_{k-1}) are confounded with other parameters, and the 2nd estimate (λ_2) is frequently biased (Hines and Nichols, 2002). Thus, we present no estimates of λ for 1993, 1994 or 2017. As a summary statistic characterizing the entire study period, we computed the geometric mean of the estimated annual rates of λ for each study area. Standard errors for the geometric mean summary statistics, and, thus, approximate 95% confidence intervals, were computed based on the variance-covariance matrix of the survival and recruitment parameter estimates with the delta method.

Based on the general model used to estimate λ, we then developed models for recruitment rate using a random effects approach based on the fixed effect model, ϕ(AREA*YEAR) *f*(AREA*YEAR) $\sigma_p(.)$ *p*(AREA*YEAR). The random effects approach postulates a distribution of recruitment rates that is characterized with a different mean for each AREA*YEAR combination, but equal variances across all years and areas. The different means are based on linear-logistic models using the covariates that correspond to the specific area and year. These models were designed to test the relevance of a set of covariates to recruitment rate (see protocol in Appendix A). These covariates (Table 3) for $f_{a,t}$ included BO (predicted lower recruitment in years with higher BO occupancy), R lagged by one year (predicted to be positively associated with recruitment rate because NSO can acquire a breeding territory at the end of their first year), HABp (predicted to be positively associated with recruitment), EDGEp (expected to have variable effects), DISThi-p and DISTlo-p (hypothesized to be negatively associated with recruitment rate), WMT and WP (predicted to have negative effects on recruitment rate), and PDO (predicted to positively influence recruitment rate) (Dugger et al., 2016).

We used the methods described in Franklin et al. (2004), to convert estimates of λ_t to estimates of realized population change ($\widehat{\Delta}_t$). This method provides a visual portrayal of the population trajectory ($\Delta_t = N_t/N_x$) in each year (N_t) of the study relative to population size in the first year (N_x) that λ_t was estimated. Annual estimates of realized population change ($\widehat{\Delta}_t$) on each study area were computed as:

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

Approximate 95% confidence intervals for the estimates of realized population change were computed using a parametric bootstrap that incorporated both sampling variation of the parameter estimates and demographic stochasticity characterizing the birth-death process of population dynamics (see Appendix C for details).

2.9. *Analysis of two-species occupancy*

The co-occurrence dynamics of NSOs and BOs were based on 26 years of detection/non-detection data for both species (1993–2018) in 10 study areas and 21 years of detection data in the HUP study area (1993–2013). In 3 study areas (CLE, COA, and GDR) the number of monitored territories declined in recent years because we excluded data from territories where BOs were removed during the removal period. Sampling periods occurred from 1 March through 31 August each year and each sampling period was divided into 12 subsampling occasions corresponding to the first and second half of each month. We created detection histories that signified whether 1) no owls were detected, 2) BOs only were detected, 3) NSOs only were detected, or 4) both species were detected in each subsampling occasion in each year and in each study area. We applied these data to the multi-season (robust design) extension of the conditional, 2-species occupancy model (MacKenzie et al., 2018) following (Yackulic et al., 2014) and (Dugger et al., 2016) and used program R-PRESENCE (https://www.mbr-pwrc.usgs.gov/software/presence.html) to estimate occupancy parameters and model selection results. We did not use any random effects to model NSO occupancy dynamics using two-species occupancy modeling because of the complexity of the analysis and the extent of the data.

Model parameters included initial occupancy (ψ_1), colonization (γ_i), extinction (ε_i), and detection probabilities (p_{ij}) for both species as potential functions of presence of the other species. For initial occupancy, we used the parameterization of Richmond et al. (2010) and assumed that BOs were the dominant species (coded as "A") and that the NSO was the subordinate species (coded as "B"). The primary parameters of interest were: (1) initial probability of occupancy by NSOs when BOs were absent (ψ_1^B) and when BOs were present (ψ_1^{BA}), (2) the probability that a territory unoccupied by a NSO in year *i* was occupied by a NSO the following year (i.e. colonization) when BOs were present (γ_i^{BA}) and when BOs were absent (γ_i^B), (3) the probability that a territory occupied by a NSO in year *i* was unoccupied the following year (i.e. local extinction) when BOs were present (ε_i^{BA}) and when BOs were absent (ε_i^B), and (4) annual probability of territory occupancy by NSOs when BOs were present (ψ_i^{BA}) and when BOs were absent (ψ_i^B), which was derived using the best-supported model structure for detection, extinction, and colonization rates using a forward conditional approach (Yackulic et al., 2020). While of secondary importance, we also examined patterns in occupancy, colonization, and extinction probabilities for BOs.

Given the large number of parameters and hypothesized structures, we defined a fixed structure for detection of both species informed by past studies. Specifically, each species was allowed to have study area-specific seasonal variation in detection described by a quadratic function, and an interspecific interaction effect and a trap response that was shared across study areas. We then employed a 'build-up' modeling strategy (Morin et al., 2020) to limit the number of models fit while identifying factors influencing the occupancy dynamics of the two owl species. Our build-up strategy consisted of five initial stages with no study area effects, followed by five stages in which we considered study area-specific responses. Specifically, our stages were defined by hypotheses, and each stage considered the top model from prior stages and all models with $\Delta\mathrm{AIC} < 10$ in stage 5 and all subsequent stages (Table 4). In all cases, we excluded models with uninformative parameters (Arnold, 2010).

3. Results

3.1. *Fecundity*

Estimates of fecundity were based on 11,117 observations of the number of young produced by territorial adult females. Estimation of spatial (territory), temporal (annual), and residual variance on the territory-specific data indicated that the proportion of variance in number of young fledged attributable to territories and/or individual

Table 4
Modeling stages used in strategy to model two-species occupancy dynamics of northern spotted and barred owls on 11 study areas in Washington, Oregon, and California from 1993–2018.

Stage	Modeling description
1	Interspecific interactions on dynamic rates (i.e., colonization and extinction) of both species.
2	Species-specific covariates of habitat components on initial occupancy and dynamic rates of both species (HABa and RHS for spotted owls, and ELEV and TPI for barred owls).
3	Trend effects on colonization and extinction of both species, as well as on barred owl detection as was commonly observed in past studies (e.g., Dugger et al., 2016).
4	Effects of two climate variables (SOI and PDO) on dynamic rates for both species.
5	All combinations based on models with ΔAIC $<$10 in the first 4 stages, excluding models with uninformative parameters (sensu Arnold, 2010).
6	Study area specific intercepts.
7	Study area specific climate effects.
8	Study area specific trends.
9	Study area specific effects of habitat components.
10	Study area specific interspecific interactions.

owls was generally low (<5%; Table 5). The proportion of variance attributable to fluctuations over time was usually in the range of 6–25%, while the proportion of unexplained variation (residual) was generally very high (>74%; Table 5). Consequently, the explainable variation in fecundity by time and by territory was overwhelmed by unexplained, residual variation.

The meta-analysis of fecundity produced three competitive models (Table 6). The best model included the additive fixed effects of ecological region (ECO), quadratic relationship of time (TT), BO, the even-odd effect (EO), and with a lagged auto-regressive covariance structure (AR1) (Table 6). In the meta-analysis, collinearity between BO and TT was not considered a problem because BO varied across years and study areas, but the annual trend was common for all study areas (e.g., some study areas had no BO and some had BO in the same year). The biennial pattern of high reproduction in even years and low reproduction in odd years seen in the previous analyses continued (Fig. 4a–c) for most study areas. In all cases, the estimated autocorrelation term is negative (Table 7) indicating that years with higher reproductive output tend to be followed by years with lower reproductive output.

Table 5
Variance components (percent of total) of the number of young fledged by adult 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 variability is the random effects estimate of year variability.

Study area	Spatial	Temporal	Residual	Total estimate
Washington				
CLE[a]	3%	16%	80%	0.907
OLY	1%	24%	74%	0.466
RAI	0%	12%	87%	0.502
Oregon				
CAS	2%	21%	75%	0.766
COA[a]	2%	15%	81%	0.538
HJA	0%	21%	78%	0.716
KLA	2%	7%	90%	0.665
TYE	2%	13%	83%	0.631
California				
GDR	1%	6%	92%	0.645
HUP[a]	5%	11%	83%	0.603
NWC	0%	8%	91%	0.699

[a] Includes only territories where no barred owl removals took place.

Table 6
Model selection results from the 10 top-ranked models based on AIC_c for the meta-analysis of the number of young fledged by adult female northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018. Model selection results for all models are listed in Appendix D.

Model[a]	K[b]	$-2\ln L$	AIC_c	ΔAIC_c[c]	Akaike weights
ECO+BO+TT+EO+AR1	12	212.40	237.60	0.0	0.47
ECO+BO+T+EO+AR1	11	215.60	238.70	1.1	0.28
ECO+BO+EO+AR1	10	219.30	240.20	2.6	0.13
ECO+PDO+TT+EO+AR1	12	216.90	242.00	4.5	0.05
ECO+DISTlo-p+T+EO+AR1	11	221.80	244.80	7.2	0.01
ECO+DISTlo-p+TT+EO+AR1	12	220.50	245.70	8.1	0.01
ECO+DISTlo-p+SPLINE+AR1	16	211.80	245.90	8.3	0.01
ECO+TT+EO+AR1	11	224.20	247.20	9.7	0.00
ECO+T+EO+AR1	10	226.90	247.80	10.2	0.00
ECO+PDO+T+EO+AR1	11	224.90	247.90	10.3	0.00

[a] Model notation indicates structure for fixed effects of ecological region (ECO), linear time (T), quadratic time (TT), even-odd years (EO), barred owls (BO), Pacific Decadal Oscillation (PDO), spline time trends (SPLINE) and autoregressive effects of time lagged by 1 year (AR1) as a covariance structure.

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

[c] $\Delta AIC_c =$ difference between the model listed and best AIC_c model.

The three models with highest support (Table 6) included the BO covariate and the estimates of the coefficient for the BO effect for these models were negative, similar in magnitude, and different from zero, based on 95% confidence intervals (Table 7), suggesting fecundity decreased with increased proportion of territories where BOs were detected. No covariates describing habitat components or climate were supported (Table 6, Appendix D). Thus, fecundity varied by time with an oscillating pattern, but in parallel across regions (Fig. 4d), with evidence for an additional BO effect. Average fecundity was substantially higher for the mixed-conifer region in Washington but similar for all other ecological regions (Fig. 5).

3.2. Apparent survival

In the first step to identify a base model for ϕ from which to run the random effects models, all the σ_p models that provided an individual random effect for p were ranked higher than the model without an individual random effect on p (Table 8), including even the simplest σ_p models (e.g., without year or study area effects). Within the models without an individual random effect on p, the top model was an additive model ϕ(AREA+YEAR) p(SEX+AREA+YEAR). However, this model was not appropriate for use in the random effects models for covariates because of the additive constraint. Therefore, the model ϕ(AREA*YEAR) σ_p(.) p(AREA*YEAR) was used to generate the random effects models for covariates. The estimate of σ_p was 1.568 (SE $=$ 0.057) on a logit scale, which demonstrated considerable individual variation in p (Fig. E1 in Appendix E). This estimate of σ_p was across all 11 study areas, while p was YEAR and AREA specific. Under the distribution in Fig. E1, the mean p on the real scale was 0.783 with 50% of the values >0.860, and a mode of 0.984. As the median value of p shifted towards 0.5, the distribution flattened out whereas, when the median p value shifted towards 1, the distribution became even more peaked.

The annual estimates of ϕ from model $\sigma_\phi(.) = 0$ ϕ(AREA*YEAR) σ_p(.) p(AREA*YEAR) were used for the random effects models, except for 2017 where ϕ was confounded with p. In addition, data from 2013–2017 were removed for the HUP study area because BOs were removed from the entire study area during that period. Estimates from 2008 and 2013 for CLE and 2005 for OLY were also removed because the estimates were 1.0 with SE $=$ 0 due to small sample sizes. In this situation, the zero standard errors would have forced shrinkage estimates to be 1, and hence no shrinkage would be allowed.

In the random effects models, the only covariate models that demonstrated any important AIC_c weight were SPLINE, T, and BO (Table 9). These 3 covariates were in all models that received any

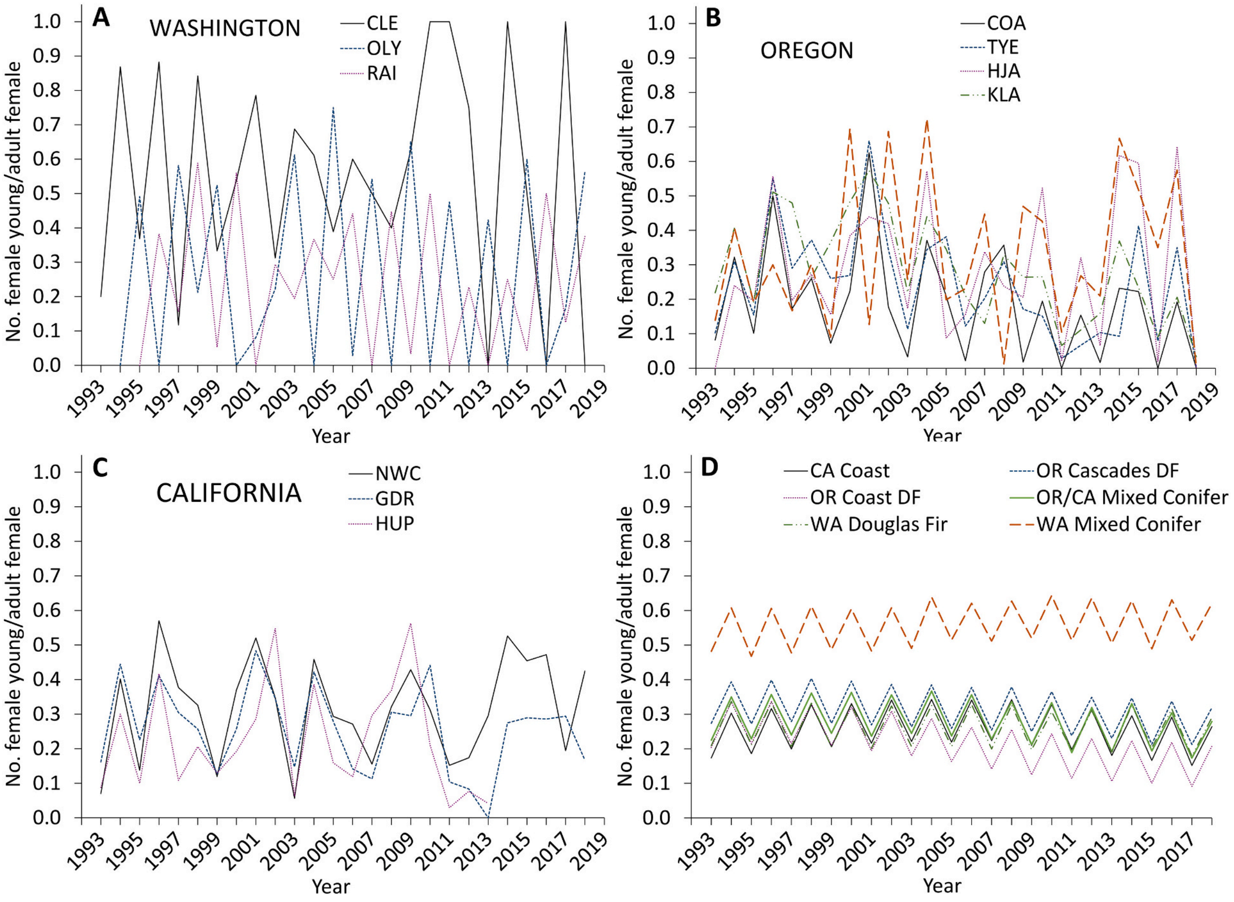

Fig. 4. Mean fecundity (mean number of young fledged per adult female) of northern spotted owls on 11 study areas. Raw estimates are shown for individual study areas in (A) Washington, (B) Oregon, and (C) California during 1993–2018. Top model ECO+BO+TT+EO+AR1 from the meta-analysis of mean fecundity is shown in (D).

Table 7

Parameter estimates ($\widehat{\beta}$) and 95% confidence intervals for fixed effects from the three top-ranked random effects models of fecundity for adult northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018.

Effect	Model 1[a]		Model 2		Model 3	
	$\widehat{\beta}$	95% CI	$\widehat{\beta}$	95% CI	$\widehat{\beta}$	95% CI
Intercept	1.419	1.274, 1.564	1.401	1.257, 1.545	1.349	1.213, 1.484
ECO (CACOA)[b]	−0.731	−0.894, −0.569	−0.728	−0.891, −0.566	−0.667	−0.818, −0.514
ECO (ORCAS)	−0.475	−0.602, −0.349	−0.476	−0.602, −0.350	−0.484	−0.612, −0.356
ECO (ORCOA)	−0.563	−0.707, −0.420	−0.566	−0.710, −0.423	−0.625	−0.758, −0.493
ECO (ORCAMC)	−0.578	−0.697, −0.457	−0.575	−0.695, −0.454	−0.568	−0.690, −0.446
ECO (WADF)	−0.468	−0.613, −0.323	−0.471	−0.616, −0.326	−0.533	−0.665, −0.400
ECO (WAMC)	–	–	–	–	–	–
BO	−0.595	−0.930, −0.260	−0.581	−0.915, −0.246	−0.294	−0.459, −0.130
T	0.016	0.004, 0.027	0.009	−0.001, 0.018	–	–
TT	−0.001	−0.001, 0.000	–	–	–	–
EO	−0.247	−0.372, −0.123	−0.248	−0.374, −0.121	−0.252	−0.377, −0.126
AR1[c]	−0.342	–	−0.350	–	−0.338	–

[a] Model 1 = ECO+BO+TT+EO+AR1; Model 2 = ECO+BO+T+EO+AR1; Model 3 = ECO+BO+EO+AR1.

[b] CACOA = California Coast; ORCAS = Oregon Cascades Douglas Fir; ORCOA = Oregon Coastal Douglas Fir; ORCAMC = Oregon/California Mixed Conifer; WADF = Washington Douglas Fir; WAMC = Washington Mixed Conifer.

[c] Covariance parameter.

weight. None of the models with covariates just describing habitat components or climate contributed weight on their own, and these covariates only appeared in models that incorporated BO as part of the 4 additional models in the protocol that incorporated covariates with BO (Table 9). We did not include time trend effects, such as T and SPLINE, with the BO effect in the same model because all three covariates explained trends across years and were therefore correlated. While the models including T and SPLINE effects provided only trends, models with BO effects provided a potential mechanism that explained those trends. Thus, in the top 5 ranked models (Table 9), the models with the

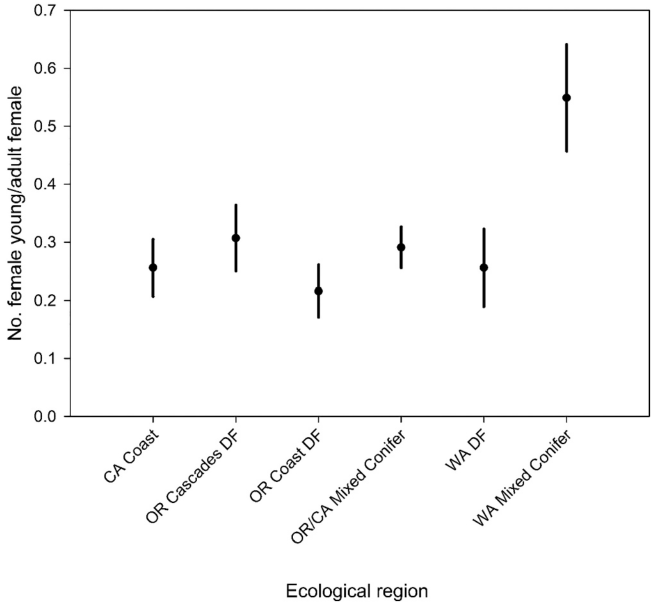

Fig. 5. Estimates of mean annual fecundity (number female young per adult female) of northern spotted owls for 6 ecological regions. Error bars are 95% confidence intervals.

BO effect can be considered separately from the time trend models. In addition, we chose random effects model ϕ(AREA+BO) for inferences about the effects of BOs on apparent survival because it had a nearly identical AIC_c value with model ϕ(AREA+BO+SOI).

In the top-ranked random effects model ϕ(AREA+SPLINE), there was a period of gradual decline since 1993 that was followed by a notable steep decline in apparent survival after 2011 (Table 10, Fig. 6a). Based on random effects model ϕ(AREA+BO), there was also a strong negative effect of BO on apparent survival (BO) (Table 11, Fig. 6b). This varied by study area but only in the starting values of apparent survival in 1993; the trends were the same across all study areas because of the additive BO effect.

3.3. *Annual rates of population change*

Estimates of rates of population change (λ) were based on capture histories of 4429 S2 and adult birds marked and resighted from 1993 through 2018 on the 11 study areas. Our initial investigation of models for capture probability (p) provided strong evidence ($\Delta\text{AIC} > 100$) for models that included variation associated with year and study area, as well as heterogeneity among individuals within each area by year category (denoted as σ_p(.) p(AREA*YEAR), see below).

Rates of population change were estimated as derived parameters based on general model ϕ(AREA*YEAR) f(AREA*YEAR) σ_p(.) p(AREA*YEAR). Area- and time-specific λ was then estimated as the sum of ϕ and f estimates (see Methods). Estimated geometric mean λ for HJA, TYE, CAS, NWC and HUP (where mean corresponded to 1995–2012) were between 0.95 and 0.98, whereas means for all other areas fell between 0.91 and 0.95 for the period 1995–2017 (Fig. 7). In all cases, 95% confidence intervals did not overlap 1, indicating that estimates were indicative of declining populations. Thus, NSO populations were significantly declining by 5–9% annually on 6 study areas and by 2–5% annually on the other 5 study areas.

For all the study areas combined, the arithmetic mean $\widehat{\lambda}$ was 0.944 (SE = 0.020, 95% CI = 0.905, 0.983) and 0.947 (SE = 0.018, 95% CI = 0.912, 0.982) if HUP was excluded because it had a shorter time interval than the other study areas. In both cases, arithmetic mean $\widehat{\lambda}$ was substantially lower than 1.

Table 8
Model selection results for base models used to select an appropriate structure on recapture probabilities (p) for the meta-analysis of apparent survival (ϕ) for northern spotted owls on 11 study areas in Washington, Oregon, California from 1993–2018.

Model[a]	K[b]	$-2\log L$	AIC_c	ΔAIC_c[c]	Akaike weights
ϕ(AREA*YEAR), σ_p(.), p(AREA*YEAR)	530	39683.30	40765.54	0.00	1.00
ϕ(AREA*YEAR), σ_p(.), p(AREA)	287	40389.78	40970.25	204.70	0.00
ϕ(AREA*YEAR), σ_p(.), p(SEX*AREA)	298	40371.67	40974.65	209.11	0.00
ϕ(YEAR), σ_p(.), p(YEAR)	50	40967.76	41067.96	302.42	0.00
ϕ(AREA*YEAR), σ_p(.), p(SEX*AREA*YEAR)	800	39421.49	41072.67	307.13	0.00
ϕ(SEX+AREA*YEAR), σ_p(.), p(SEX*AREA*YEAR)	801	39420.79	41074.10	308.56	0.00
ϕ(AREA*YEAR), σ_p(.), p(YEAR)	296	40549.33	41148.22	382.68	0.00
ϕ(YEAR), σ_p(.), p(.)	27	41095.58	41149.64	384.09	0.00
ϕ(AREA*YEAR), σ_p(.), p(.)	272	40677.36	41227.17	461.62	0.00
ϕ(.), σ_p(.), p(.)	3	41316.31	41322.31	556.76	0.00
ϕ(AREA+YEAR), p(SEX+AREA+YEAR)	70	41943.37	42083.75	1318.21	0.00
ϕ(SEX+AREA+YEAR), p(SEX+AREA+YEAR)	71	41943.40	42085.76	1320.21	0.00
ϕ(AREA*YEAR), p(SEX+AREA*YEAR)	530	41018.48	42100.72	1335.18	0.00
ϕ(SEX+AREA*YEAR), p(SEX+AREA*YEAR)	531	41018.47	42102.80	1337.25	0.00
ϕ(AREA+YEAR), p(AREA+YEAR)	69	41969.28	42107.66	1342.11	0.00
ϕ(SEX+AREA+YEAR), p(AREA+YEAR)	70	41969.13	42109.51	1343.97	0.00
ϕ(AREA*YEAR), p(AREA*YEAR)	529	41044.32	42124.47	1358.93	0.00
ϕ(SEX+AREA*YEAR), p(AREA*YEAR)	530	41044.15	42126.39	1360.85	0.00
ϕ(AREA+YEAR), p(SEX*AREA*YEAR)	548	41066.36	42186.15	1420.61	0.00
ϕ(AREA*YEAR), p(SEX*AREA*YEAR)	799	40779.03	42428.08	1662.54	0.00
ϕ(SEX+AREA*YEAR), p(SEX*AREA*YEAR)	800	40779.03	42430.21	1664.67	0.00
ϕ(SEX*AREA*YEAR), p(AREA*YEAR)	799	40826.29	42475.35	1709.81	0.00
ϕ(SEX*AREA*YEAR), p(SEX*AREA*YEAR)	1058	40580.10	42786.54	2020.99	0.00
ϕ(YEAR), p(YEAR)	49	42703.10	42801.29	2035.75	0.00
ϕ(SEX*YEAR), p(SEX*YEAR)	98	42638.51	42835.27	2069.72	0.00
ϕ(AREA*YEAR), p(YEAR)	294	42286.25	42881.04	2115.50	0.00
ϕ(.), p(.)	2	43176.45	43180.45	2414.91	0.00

[a] Model notation: ϕ = apparent survival; p = capture probability; σ_ϕ = individual heterogeneity for ϕ; σ_p = individual heterogeneity for p. Covariates are described in Table 3. No models were fit with individual heterogeneity on ϕ by fixing $\sigma_\phi(.) = 0$. Models with no individual heterogeneity on either ϕ or p do not include σ_ϕ and σ_p terms. Additive models are constructed as additive terms, e.g., SEX+AREA. Interaction models are constructed as multiplicative terms, e.g., AREA*YEAR. The dot (.) notation means no variation of the parameter in the model being estimated.

[b] Number of estimable parameters.

[c] ΔAIC_c = difference between the model listed and best AIC_c model.

3.4. *Realized population change*

The analysis of realized population change (Δ_t) included the period 1995–2017 because the first 2 years and the last year of λ estimates were either biased or confounded and therefore eliminated. The annual estimates of Δ_t (Fig. 8) provide a depiction of the cumulative consequences of the annual estimates of λ, expressed relative to an initial population in

Table 9

Model selection results from random effects models used to examine the effects of covariates on apparent survival of northern spotted owls from 1993–2018 on 11 study areas in Washington, Oregon, and California.

Model[a]	K[b]	$-2\log L$	AIC_c	ΔAIC_c[c]	Akaike weights
AREA+SPLINE	432.05	39761.02	40639.86	0.00	0.73
AREA+T	434.53	39759.23	40643.19	3.33	0.14
Intercept+SPLINE	436.79	39756.58	40645.22	5.36	0.05
AREA+BO+SOI	437.54	39757.14	40647.32	7.46	0.02
AREA+BO	437.86	39756.89	40647.75	7.89	0.01
Intercept+T	438.68	39755.20	40647.75	7.90	0.01
AREA+BO+RHS	438.11	39756.98	40648.34	8.48	0.01
AREA+BO+BO^2	438.61	39756.10	40648.50	8.64	0.01
AREA+BO+PDO	438.53	39756.36	40648.60	8.74	0.01
AREA+BO+EDGEp	438.74	39756.21	40648.87	9.01	0.01
AREA*BO	443.10	39752.71	40654.41	14.55	0.00
Intercept+BO+DISTtot	447.74	39747.95	40659.26	19.41	0.00
Intercept+BO+DISThi-p	448.59	39747.55	40660.62	20.76	0.00
AREA+EDGEp	448.49	39749.58	40662.43	22.57	0.00
Intercept+BO+SOI	450.29	39746.97	40663.57	23.71	0.00
Intercept+BO	451.10	39746.34	40664.60	24.75	0.00
AREA+RHS	448.87	39750.96	40664.62	24.76	0.00
Intercept+BO+PDO	451.30	39746.30	40664.99	25.13	0.00
AREA+DISThi-p	450.81	39747.74	40665.41	25.55	0.00
Intercept+BO+BO^2	451.68	39745.95	40665.42	25.56	0.00
Intercept+DISTtot	450.93	39747.90	40665.80	25.94	0.00
Intercept+DISThi-p	451.17	39747.78	40666.19	26.34	0.00
AREA+DISTtot	451.86	39746.92	40666.76	26.90	0.00
AREA+HABp	452.09	39746.82	40667.13	27.27	0.00
Intercept+DISTlo-p	452.24	39746.98	40667.62	27.77	0.00
Intercept+RHS	451.41	39749.31	40668.22	28.36	0.00
AREA+SOI	452.37	39747.38	40668.29	28.43	0.00
Intercept+SOI	452.51	39747.24	40668.43	28.57	0.00
Intercept+PDO	453.69	39746.62	40670.24	30.39	0.00
AREA+PDO	453.71	39746.66	40670.34	30.48	0.00
Intercept	453.93	39746.32	40670.44	30.58	0.00
AREA+DISTlo-p	454.48	39745.33	40670.61	30.75	0.00
AREA	454.22	39745.98	40670.71	30.85	0.00
Intercept+EDGEp	454.42	39745.94	40671.09	31.23	0.00
Intercept+HABp	454.52	39745.79	40671.14	31.28	0.00
Base model[d]	530.00	39683.30	40765.54	125.69	0.00

[a] Model notation: Covariates used in the linear random effects models are described in Table 3 with BO^2 being BO squared. Models including Area have area-specific intercepts, whereas Intercept models have the same intercept for all study areas in the linear model.

[b] Number of estimable parameters.

[c] ΔAIC_c = difference between the model listed and best AIC_c model.

[d] Model ϕ(AREA*YEAR), σ_p(.), p(AREA*YEAR) from Table 8.

1995. Annual estimates >1 indicate population size for those years was greater than the starting population size in 1995, and estimates <1 indicate that estimated population size was less than in 1995. Despite some fluctuations with estimates >1 during early and middle portions of the time series for some areas, all estimates were <1 for all study areas after 2010 (Fig. 8).

In Washington state, estimated population sizes in 2017 had declined by >80% relative to those in 1995 for the OLY and CLE study areas and almost 75% for the RAI study area. In Oregon, all study areas declined by >60%, with COA and KLA declining by >75%. In California, NWC declined by about 50%, HUP by about 30% (by 2012), and GDR had declined by >60%. These estimates (Fig. 8) differed from the previous meta-analysis (Dugger et al., 2016) because the initial year used for previous estimates varied across the analyses. Final realized change estimates can also be viewed as the percentage of the NSO population that remained in 2017 on the 10 study areas relative to initial populations in 1995. Seven of the study areas had ≤35% of their populations remaining with the other three study areas having ≤50% of their populations (Fig. 8).

Table 10

Parameter estimates ($\widehat{\beta}$), standard errors (SE), and 95% confidence intervals from the random effects model of apparent survival ϕ(AREA+SPLINE) with the lowest AIC for adult northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018. Estimates are real and not logit-transformed.

Effect	$\widehat{\beta}$	SE	95% confidence interval	
			Lower	Upper
Intercept (CAS)	0.872	0.015	0.842	0.903
Intercept (CLE)	0.839	0.018	0.803	0.875
Intercept (COA)	0.895	0.015	0.866	0.924
Intercept (GDR)	0.864	0.015	0.834	0.893
Intercept (HJA)	0.892	0.015	0.862	0.921
Intercept (HUP)	0.868	0.018	0.833	0.902
Intercept (KLA)	0.864	0.015	0.834	0.894
Intercept (NWC)	0.862	0.016	0.831	0.893
Intercept (OLY)	0.863	0.017	0.830	0.896
Intercept (RAI)	0.877	0.018	0.842	0.911
Intercept (TYE)	0.890	0.015	0.860	0.920
Spline-linear	−0.002	0.026	−0.053	0.048
Spline-quadratic	−0.012	0.020	−0.051	0.028
Spline-cubic (1994)	−0.010	0.022	−0.054	0.034
Spline-cubic (1999)	−0.064	0.024	−0.112	−0.016
Spline-cubic (2005)	−0.032	0.029	−0.089	0.025
Spline-cubic (2011)	−0.142	0.028	−0.196	−0.088

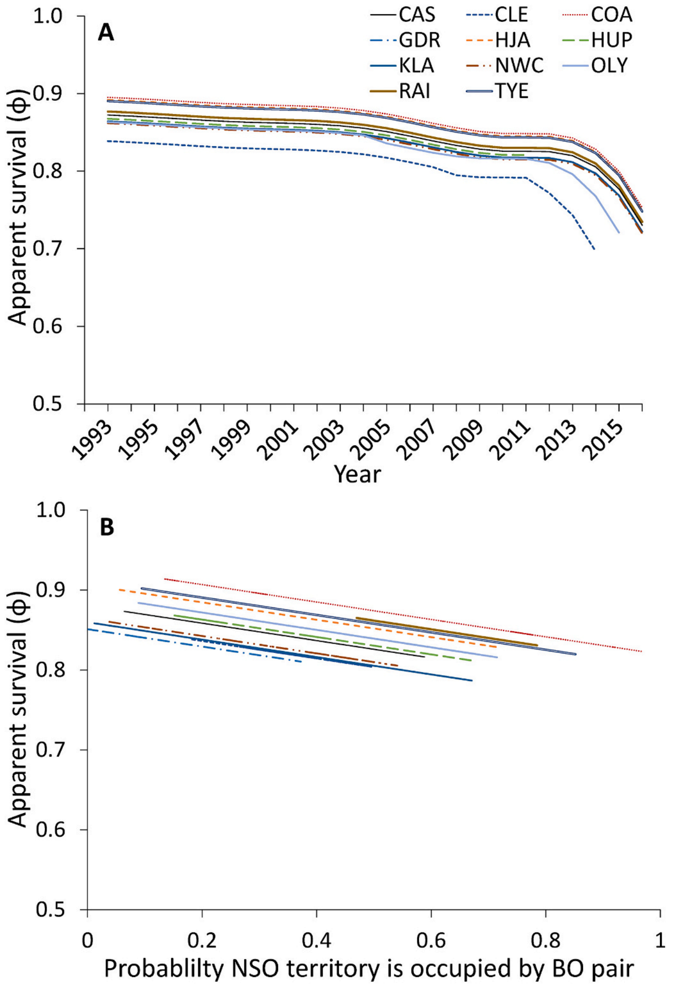

Fig. 6. Trends in apparent survival from 1993–2017 for northern spotted owls on 11 study areas in Washington, Oregon, and California based on (A) time from random effects model ϕ(AREA+SPLINE), and (B) effects of barred owl presence from random effects model ϕ(AREA+BO). Length of the lines in graph B are determined by the range of values in the x-axis for each study area.

Table 11

Parameter estimates ($\widehat{\beta}$), standard errors (SE), and 95% confidence intervals from the random effects model of apparent survival ϕ(AREA+BO) with the effect of barred owls on adult northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018.

Effect	$\widehat{\beta}$	SE	95% confidence interval	
			Lower	Upper
Intercept (CAS)	0.880	0.011	0.859	0.902
Intercept (CLE)	0.858	0.015	0.828	0.888
Intercept (COA)	0.929	0.012	0.904	0.953
Intercept (GDR)	0.851	0.009	0.833	0.869
Intercept (HJA)	0.906	0.011	0.885	0.928
Intercept (HUP)	0.885	0.014	0.857	0.912
Intercept (KLA)	0.860	0.010	0.840	0.879
Intercept (NWC)	0.864	0.011	0.842	0.886
Intercept (OLY)	0.894	0.014	0.866	0.921
Intercept (RAI)	0.916	0.017	0.883	0.949
Intercept (TYE)	0.912	0.012	0.889	0.936
BO	−0.109	0.017	−0.143	−0.075

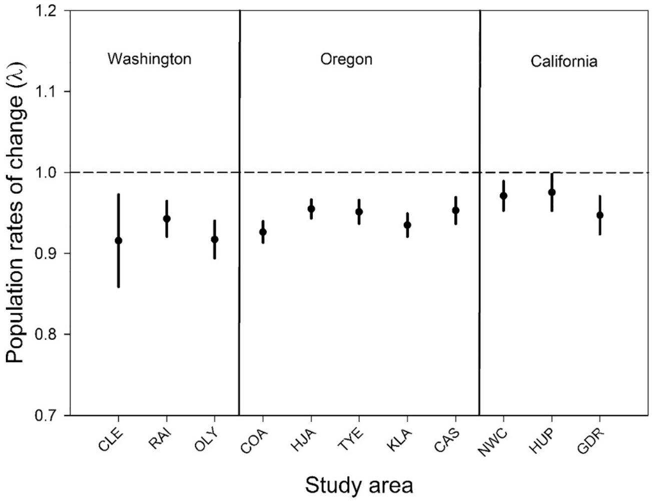

Fig. 7. Estimates of geometric mean rates of population change (λ) and approximate 95% confidence intervals for northern spotted owls on 11 study areas in Washington, Oregon, and California. Means were estimated from 1995–2017 for all study areas except for the HUP study area, which included only data from 1995–2012.

3.5. Recruitment rate

All the random effects modeling of recruitment rate was based on estimates from the general model ϕ(AREA*YEAR) f(AREA*YEAR) σ_p(.) p (AREA*YEAR), the same model used to produce the rates of population change and realized change estimates (e.g., Figs. 7 and 8). There was substantial uncertainty associated with model selection, but only 5 models showed non-negligible Akaike weights $\geq$0.01 (Table 12). All of these low-AIC$_c$ models included the covariate BO, and the $\widehat{\beta}$ for this covariate was negative in all models, with a confidence interval that did not overlap zero (Table 13). The negative relationship followed our predictions, and our analyses thus provided strong evidence that recruitment rates between years t and t+1 declined as the proportion of NSO territories occupied by BOs in year t increased.

Recruitment model RE f(BO+Lag1R) was one of the top models, and the $\widehat{\beta}$ for Lag1R was positive with confidence intervals that did not overlap zero (Table 13). The Lag1R covariate was the average number of young produced per pair of NSOs in the breeding season of year t−1. The positive relationship between reproduction in year t−1 indicates that some of the young fledged in year t−1 returned to recruit into the territorial population in subsequent years. The other three models receiving Akaike weights >0.01 (Table 13) included covariates HABp, EDGEp, and DISThi-p, but all $\widehat{\beta}$ had confidence intervals that broadly overlapped 0 (Table 13). HABp and EDGEp were both predicted to influence recruitment positively, and the $\widehat{\beta}$ were consistent with these predictions. DISThi-p was predicted to be a negative influence on recruitment, and its $\widehat{\beta}$ was consistent with this prediction. However, other than the strong negative BO effect, none of the models provided strong evidence for effects of the covariates describing habitat components. Finally, we note that none of the models with climate covariates received any support, all having AIC$_c$ weights <0.01.

3.6. Two-species occupancy

The top model included a mixture of effects specific to study areas as well as effects shared across study areas, including interspecific interactions and trends on all dynamic rates, effects of habitat components (HABa and ELEV) on three of the four vital rates, and climate impacts on NSO local extinction rates only (Table 14). According to the top model identified through our model selection process, NSO territory occupancy has declined substantially in all study areas coincident with increasing BO occupancy in all study areas (Fig. 9). We found strong and consistent effects of BO presence on colonization and extinction of NSO territories across study areas (Fig. 10). Colonization of NSO territories was positively affected by HABa but colonization still had a negative trend across most study areas (Fig. 10). Extinction of NSO territories was similar across study areas and showed a negative association with HABa and a positive association with BO presence, climate (SOI), and exhibited an overall increasing trend (Fig. 10). BO colonization increased through time in all study areas and was positively associated with the presence of NSOs and lower elevations in most study areas (Fig. 10). In contrast, BO extinction was clearly higher in territories co-occupied with NSOs, while any trend in extinction was inconsistent across study areas. The positive relationship of NSO presence to both BO colonization and extinction was probably due to either habitat conditions not represented by our covariates (i.e., BO are selecting similar conditions to NSO) or behavioral attraction (i.e., BOs are attracted by NSO territorial vocalizations).

4. Discussion

Since the last meta-analysis (Dugger et al., 2016), we found that NSO populations continued to experience dramatic declines on study areas distributed across the species' geographic range. Evidence that the presence of BOs was a primary causative factor for those declines is stronger, and BO presence was found to negatively affect every demographic trait we estimated for NSO (Fig. 11). These declines and effects were reinforced by analyzing two types of data, capture-recapture data to estimate demographic traits and rates of population change, and detection/non-detection data to estimate two-species territory occupancy. Both data sets corroborated each other by documenting declines in NSO populations and identifying BO presence as the primary factor associated with those declines.

Substantial evidence has accumulated showing that interspecific interactions and competition for space, habitat, and food with rapidly expanding populations of invasive BOs has negatively affected the population viability of NSO (Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Long and Wolfe, 2019). The underlying mechanisms by which BO negatively impact NSO is likely through a combination of exploitation competition for shared habitat and prey resources and interference competition via interspecific exclusion from breeding territories (Gutiérrez et al., 2007; Hamer et al., 2007; Hamer et al., 2001; Wiens et al., 2014). Our study provides range-wide evidence that the negative consequences of interspecific competition with BO have increasingly overwhelmed dwindling populations of NSO since the last meta-analysis reported by Dugger et al. (2016).

Although BOs were the dominant negative effect on NSO

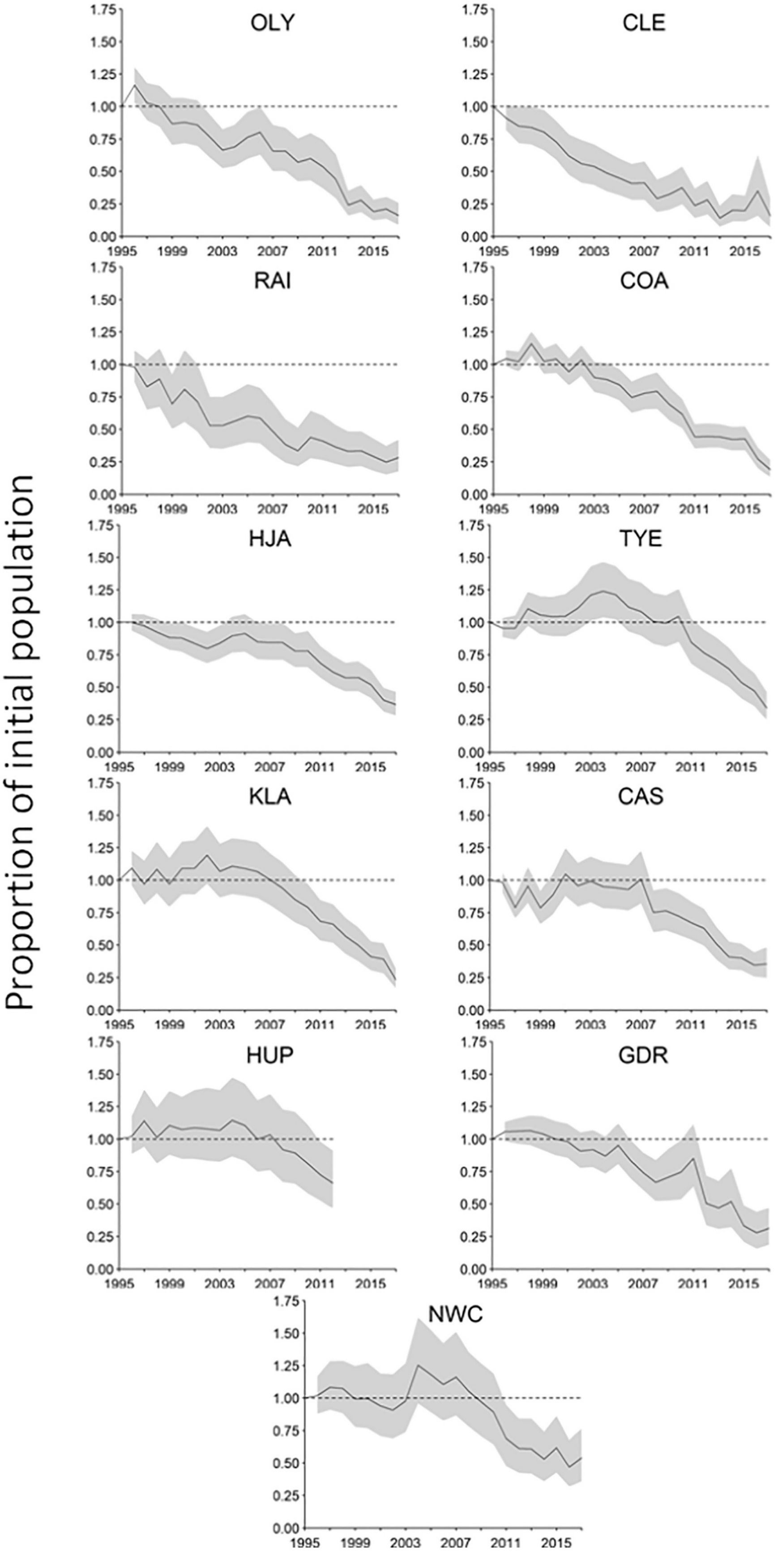

Fig. 8. Annual estimates of realized population change with approximate 95% confidence intervals (shaded area) for northern spotted owls on 11 study areas in Washington, Oregon, and California from 1995–2017.

Table 12

Model selection results for random effects (RE) modeling of recruitment rate, based on the general model ϕ(AREA*YEAR) *f*(AREA*YEAR) σ_p(.) *p*(AREA*YEAR) for northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018.

Model[a]	*K*[b]	$-2\ln L$	AIC$_c$[c]	ΔAIC$_c$	Akaike weights
σ_p(.) *p*(AREA*YEAR), RE BO+HABp	728.10	63312.20	64816.75	0.00	0.35
σ_p(.) *p*(AREA*YEAR), RE BO+EDGEp	727.97	63312.60	64816.88	0.13	0.33
σ_p(.) *p*(AREA*YEAR), RE BO+Lag1R	724.23	63321.30	64817.60	0.85	0.23
σ_p(.) *p*(AREA*YEAR), RE BO+DISThi-p	727.98	63315.71	64820.01	3.26	0.07
σ_p(.) *p*(AREA*YEAR), RE BO	727.77	63320.92	64824.77	8.02	0.01
σ_p(.) *p*(AREA*YEAR), RE Lag2R+DISThi-p	736.26	63303.61	64825.59	8.84	0.00
σ_p(.) *p*(AREA*YEAR), RE WMT+WP	738.17	63302.77	64828.84	12.09	0.00
σ_p(.) *p*(AREA*YEAR), RE DISThi-p	737.85	63305.15	64830.53	13.78	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag1R+EDGEp	733.33	63316.15	64831.87	15.12	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag2R+DISTlo-p	737.66	63307.12	64832.10	15.35	0.00
σ_p(.) *p*(AREA*YEAR), RE WP	738.04	63306.86	64832.65	15.9	0.00
σ_p(.) *p*(AREA*YEAR), RE DISTlo-p	737.77	63307.46	64832.67	15.92	0.00
σ_p(.) *p*(AREA*YEAR), RE BO+DISTlo-p	728.58	63327.75	64833.33	16.58	0.00
σ_p(.) *p*(AREA*YEAR), RE WMT+PDO	738.2	63307.43	64833.56	16.81	0.00
σ_p(.) *p*(AREA*YEAR), RE EDGEp	737.43	63310.49	64834.97	18.22	0.00
σ_p(.) *p*(AREA*YEAR), RE BO+Lag2R	728.3	63330.85	64835.84	19.09	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag2R+HABp	737.26	63311.82	64835.94	19.19	0.00
σ_p(.) *p*(AREA*YEAR), RE WP*PDO	738.89	63308.98	64836.58	19.83	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag2R	737.23	63314.32	64838.38	21.63	0.00
σ_p(.) *p*(AREA*YEAR), RE WMT*WP	738.33	63312.61	64839.02	22.27	0.00
σ_p(.) *p*(AREA*YEAR), RE HABp	737.65	63314.21	64839.16	22.41	0.00
σ_p(.) *p*(AREA*YEAR), RE WP+PDO	738.37	63313.38	64839.88	23.13	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag1R+DISTlo-p	733.87	63324.88	64841.76	25.01	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag1R+DISThi-p	733.13	63333.33	64848.63	31.88	0.00
σ_p(.) *p*(AREA*YEAR), RE PDO	737.93	63327.42	64852.97	36.22	0.00
σ_p(.) *p*(AREA*YEAR), RE WMT*PDO	738.05	63327.45	64853.26	36.51	0.00
σ_p(.) *p*(AREA*YEAR), RE WMT	737.73	63330.20	64855.33	38.58	0.00
σ_p(.) *p*(AREA*YEAR), RE Lag2R+EDGEp	737.08	63342.03	64865.77	49.02	0.00
σ_p(.) *p*(AREA*YEAR), RE Intercept	737.64	63342.8	64867.73	50.98	0.00
σ_p(.) *p*(AREA*YEAR)	797	63282.24	64934.35	117.6	0.00
p(AREA*YEAR, π)	836	63344.61	65080.66	263.91	0.00
σ_p(.) *p*(.)	554	64168.79	65304.57	487.82	0.00
p(.,π)	555	64303.63	65441.52	624.77	0.00
p(AREA*YEAR)	830	64315.72	66038.84	1222.09	0.00
p(YEAR)	576	65544.81	66726.88	1910.13	0.00
p(.)	553	65790.03	66923.72	2106.97	0.00

[a] Covariates are described in Table 3, except for Lag1R and Lag2 R, which are Reproductive Effort (R) lagged by 1 and 2 years, respectively. Model *p* (AREA*YEAR, π) indicates a different 2-point finite mixture model for capture probability for each study area and year; σ_p(.) *p*(.) indicates a heterogeneous capture probability model in which there is a single distribution over all areas and years; *p*(.,π) indicates a heterogeneous capture probability model based on a single 2-point finite mixture which is the same for all areas and years; *p*(YEAR) indicates a single year-specific capture probability parameter for all areas; and *p* (.) indicates a single capture probability for all areas and years. Models in which the capture probability notation is not followed by RE indicate the base ϕ(AREA*YEAR) *f*(AREA*YEAR) model with no random effects modeling of recruitment. The notation following "RE" denotes the covariate(s) associated with the recruitment modeling. "Int" denotes an intercept-only RE recruitment model.

[b] Number of estimable parameters.

[c] ΔAIC$_c$ = difference between the model listed and best AIC$_c$ model.

populations, this does not suggest that other factors, such as habitat loss through logging and wildfire or climatic changes, were not important. We found little evidence that changes to NSO habitat components due to logging or fire disturbance had significant range-wide effects on trends in NSO populations. These may be important at smaller scales where they affect smaller segments of NSO populations, but they did not appear as major drivers across the entire range of the owl. Because this was a range-wide analysis, the covariates that were important in the analysis were those that were ubiquitous over all or most of the study areas. BOs increased substantially since 1993, are now common across the range of the owl, and occupy most of the landscape occupied by northern spotted owls (Fig. 9). In comparison, net range-wide changes in the amount of NSO nesting and roosting habitat from 1994 to 2013 have been relatively small (1.5% net decrease) (Davis et al., 2016).

4.1. *Demographic components of λ*

The demographic parameters we examined are related to the rate of population change (λ) either directly or indirectly (Fig. 11). For example, fecundity directly contributes to future recruitment of new individuals into NSO populations, whereas it is the additive effects of recruitment and apparent survival that directly define λ (Fig. 11). In NSOs, apparent survival determines the magnitude of λ while recruitment is largely responsible for the annual variation in λ (Franklin et al., 2000); if recruitment becomes zero, then $\lambda = \phi$. Thus, the linkages among fecundity, recruitment, and apparent survival, all negatively impacted by BO, are critically important for maintaining stationary populations of NSOs over time.

Of the extrinsic factors we hypothesized to contribute to NSO population declines, the presence of BOs was the dominant effect, with BO presence negatively affecting all the demographic components we examined. Although the negative effect of BOs on fecundity appeared weaker relative to an oscillating time trend, this was the first meta-analysis we have conducted where we detected a negative effect of BOs on NSO fecundity. In addition, the negative effect of BOs on apparent survival and recruitment was pronounced, which ultimately had strong negative effects on λ. The negative effects of BOs on the range-wide demographic parameters we reported here have been further corroborated by positive responses of NSO populations to experimental removal of BOs (Wiens et al., 2020).

Since 2014, the declines in both apparent survival and recruitment have accelerated, resulting in further losses to NSO populations beyond those reported by Dugger et al. (2016). In earlier years, permanent emigration from study areas was minimal for non-juvenile NSOs (Forsman et al., 2002; Zimmerman et al., 2007) so previous meta-analyses assumed that apparent survival was similar to true survival (Dugger et al., 2016). More recent evidence indicates that non-juvenile NSOs are dispersing at higher rates and moving farther distances when in competition with BOs (Jenkins et al., 2021; Jenkins et al., 2019). These changing dispersal dynamics could lead to higher permanent emigration, which could translate into larger differences between apparent and true survival rates. If true, we would expect to observe a reciprocal

Table 13

Coefficient estimates ($\widehat{\beta}$) and standard errors (SE) for covariates appearing in the top 5 ranked random effects models for recruitment rate in northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018.

Model	Akaike weight	Covariate				
		BO	HABp	EDGEp	Lag1R[a]	DISThi-p
		$\widehat{\beta}$ (SE)	$\widehat{\beta}$ (SE)	$\widehat{\beta}$ (SE)	$\widehat{\beta}$ (SE)	$\widehat{\beta}$ (SE)
RE *f*(BO+HABp)	0.35	−0.085 (0.012)	0.020 (0.025)	–	–	–
RE *f*(BO+EDGEp)	0.33	−0.084 (0.015)	–	0.088 (0.084)	–	–
RE *f*(BO+Lag1R)	0.23	−0.074 (0.015)	–	–	0.030 (0.010)	–
RE *f*(BO+DISThi-p)	0.07	−0.085 (0.015)	–	–	–	−0.168 (0.155)
RE *f*(BO)	0.01	−0.086 (0.015)	–	–	–	–

[a] Reproductive rate (R) lagged by 1 year.

Table 14

Model selection results for two species occupancy models from each stage (see Table 4) for northern spotted owls on 11 study areas in Washington, Oregon, and California from 1993–2018. Letters and symbols are defined as follows: B = BO; H = habitat components; T = linear time trend; N = northern spotted owl; S = SOI; E = ELEV; P = TPI; g = AREA; * = interaction; # = the probability of detection model for barred owl included many components that were held constant across all models. In stages where multiple models were competitive, bold is used to highlight the model components in which alternative structures were supported.

Stage	Spotted owl parameters			Barred owl parameters				K	−2LnL	AIC	ΔAIC	Akaike weight
	Ψ_1	γ	ε	Ψ_1	γ	ε	p					
1: Interspecific interactions	.	B	B	.	N	N	#	81	170935.5	171097.5	2223.8	>0.01
2: Habitat covariates	H	B, H	B, H	**.**	N, E	N	#	85	170783.4	170953.4	2079.7	>0.01
	H	B, H	B, H	**E**	N, E	N	#	86	170781.1	170953.1	2079.4	>0.01
	H	B, H	B, H	**P**	N, E	N	#	86	170779.2	170951.2	2077.5	>0.01
3: Trends	H	B, H, T	B, H, T	P	N, E, T	N, T	T, #	91	169589.7	169771.7	898.0	>0.01
4: Climate covariates	H	B, H, T	B, H, T, S	P	N, E, T	**N, T**	T, #	92	169584.0	169768.0	894.3	>0.01
	H	B, H, T	B, H, T, S	P	N, E, T	**N, T, S**	T, #	93	169580.8	169766.8	893.1	>0.01
5: Combine	H	B, H, T	B, H, T, S	**E**	N, E, T	**N, T**	T, #	92	169581.5	169765.5	891.8	>0.01
	H	B, H, T	B, H, T, S	**E**	N, E, T	**N, T, S**	T, #	93	169578.2	169764.2	890.5	>0.01
	H	B, H, T	B, H, T, S	**.**	N, E, T	**N, T**	T, #	91	169586.1	169768.1	894.4	>0.01
	H	B, H, T	B, H, T, S	**.**	N, E, T	**N, T, S**	T, #	92	169582.8	169766.8	893.1	>0.01
	H	B, H, T	B, H, T, S	**P**	N, E, T	**N, T**	T, #	92	169584.0	169768.0	894.3	>0.01
	H	B, H, T	B, H, T, S	**P**	N, E, T	**N, T, S**	T, #	93	169580.8	169766.8	893.1	>0.01
6: SAS[a] intercepts	g, H	g, B, H, T	g, B, H, T, S	g	g, N, E, T	**g, N, T, S**	T, #	152	168821.8	169125.8	252.1	>0.01
	g, H	g, B, H, T	g, B, H, T, S	g	g, N, E, T	**g, N, T**	T, #	151	168824.1	169126.1	252.4	>0.01
7: SAS climate	* no models tested in this stage led to improvements in AIC											
8: SAS trends	g, H	g, B, H, g*T	g, B, H, T, S	g	g, N, E, g*T	g, N, g*T, S	T, #	182	168630.8	168994.8	121.1	>0.01
9: SAS habitat	g, g*H	g, B, g*H, g*T	g, B, H, T, S	g	g, N, g*E, g*T	g, N, g*T, S	T, #	212	168458.7	168882.7	9.0	0.01
10: SAS Interspecific interactions	g, g*H	g, B, g*H, g*T	g, B, H, T, S	g	g, g*N, g*E, g*T	g, N, g*T	T, #	221	168431.7	168873.7	0.0	0.99

[a] Study area specific.

increase in recruitment rates of non-breeding NSOs from outside the study areas (assuming NSOs outside the study areas were moving farther and at higher rates as well). However, we observed steep declines in recruitment along with survival. Therefore, the trends in apparent survival still appear to be representative of true survival in the breeding population of NSOs rather than increased rates of permanent emigration. The high weight on models with individual heterogeneity on *p* also likely reflected the impact of BO affecting NSO responses

4.2. Rates of population change (λ)

Mean estimates of λ for NSOs were <1 for the period 1995–2017 for all 10 study areas, and from 1995–2012 for HUP, indicating declining populations. The 95% confidence intervals for mean λ for all 11 study areas failed to include 1 and, thus, differed from a stationary population (λ = 1; Fig. 7). In six of the study areas, mean λ was <0.95. The meta-analysis of λ provided strong evidence of population declines over the 1995–2017 period on all study areas, with greater declines documented in Washington than in Oregon and California. However, mean estimates of λ were <0.95 for two study areas in Oregon and one in California. The estimates of realized population change ($\widehat{\Delta}_t$) computed from the annual estimates of λ illustrated the magnitude of declines in population size (Fig. 8). By 2017, all the Washington and Oregon study areas had declined by >50% since 1995, with four of the study area populations declining by 75% or more. This left most study areas with only 20–30% of the original populations that occupied those areas in 1995.

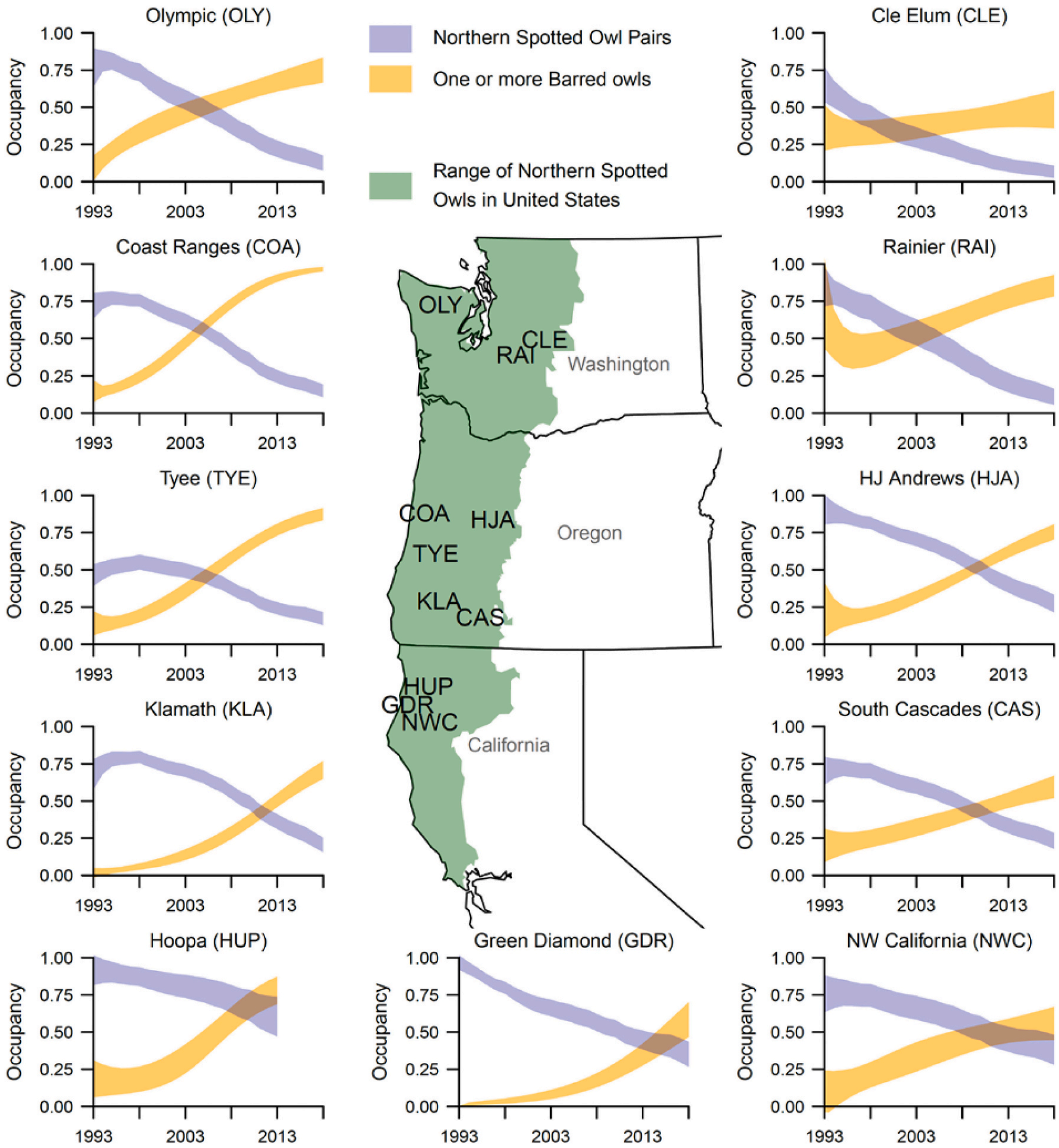

Fig. 9. Trends in territory occupancy for northern spotted owl pairs and barred owls on 11 study areas in Washington, Oregon, and California based on two-species occupancy models from 1993–2018.

The recruitment modeling that was conducted as a part of the analyses of λ was focused on covariates that might explain some of the variation in recruitment rate. Evidence was very strong for a negative association between NSO recruitment rate and proportion of NSO territories occupied by BO. Proportion of territories occupied by BO increased monotonically over the years of this analysis, raising the possibility that NSO population change was caused by some other variable with a similar time trend. However, territory-specific inferences about effects of BO on NSO occupancy dynamics (Diller et al., 2016; Dugger et al., 2016; Wiens et al., 2021; Yackulic et al., 2014; this paper) provided strong evidence of BO effects, lending more confidence to the assertion that increases in BO are contributing to lower recruitment rate of NSO populations. The negative effect of BO on both NSO fecundity and recruitment rate suggests that competition with BO not only lowers NSO reproductive potential but also the ability of younger NSO to acquire breeding territories.

We also found some evidence that average number of young per breeding pair of NSO in year $t-1$ (Lag1R) was positively associated with recruitment rates between year t and $t+1$ This effect was consistent with the prediction that greater reproductive output in one year would lead to more recruits in later years. Model selection results provided weak support for a positive relationship between recruitment rate and two habitat components, HABp and EDGEp, and a negative relationship between recruitment rate and proportion of territories with high-severity disturbance (DISTp-hi). All three of these weak relationships were in the predicted directions. There was no support for effects of any covariates describing climate or other habitat components.

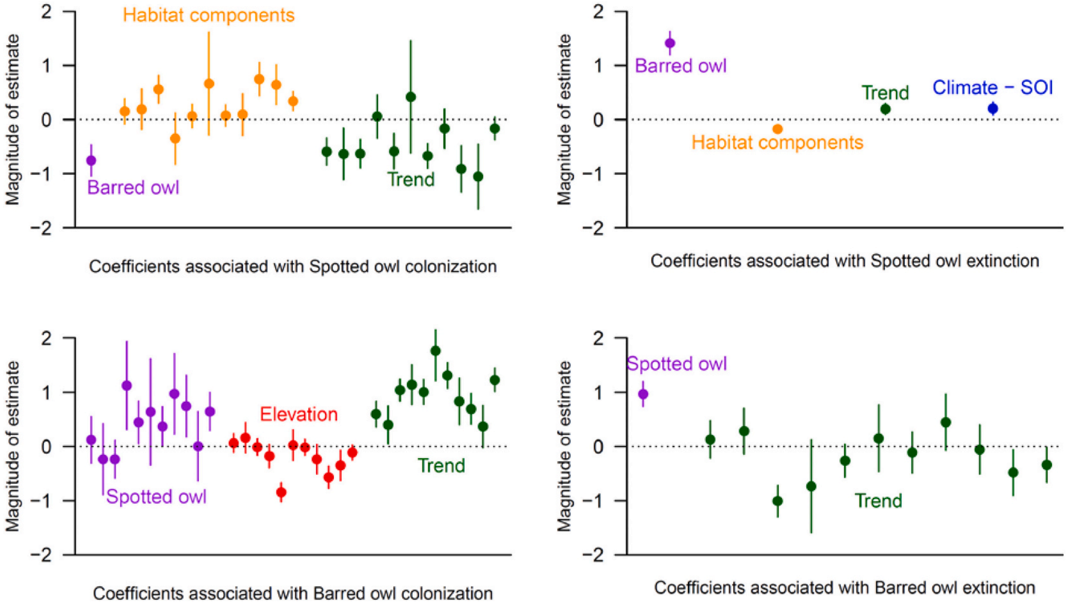

Fig. 10. Effects included in the top-ranked model used to estimate two-species occupancy dynamics for northern spotted and barred owls on 11 study areas in Washington, Oregon, and California from 1993–2018. Points signify means and whiskers span 95% confidence intervals. Single points in a given color signify effects that were shared across study areas, whereas eleven points signify study area specific effects arranged from left to right as follows: CAS, CLE, COA, GDR, HJA, HUP, KLA, NWC, OLY, RAI and TYE.

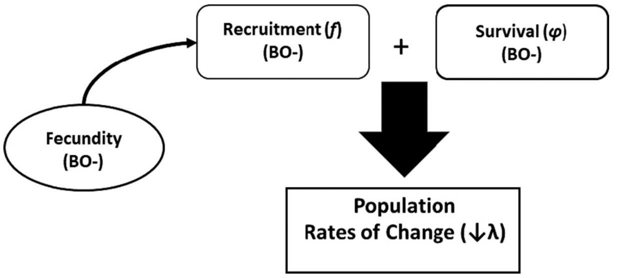

Fig. 11. Relationship of demographic traits to each other and ultimately to the rate of population change (λ). Direction of the effect of barred owl presence is indicated below each trait.

4.3. Trends in territory occupancy

The two-species occupancy analysis provided results consistent with the analysis of demographic parameters and rates of population change; NSO territory occupancy was declining substantially, coincident with increased BO occupancy of those territories. While BO occupancy was a dominant negative effect on colonization and positive effect on extinction of NSO territories, other factors, such as habitat components and climate, were also important in the dynamics of territory occupancy. These results were similar to previous findings (Dugger et al., 2016; Yackulic et al., 2019) and reinforced the importance of maintaining NSO habitat on the landscape, even if it is unoccupied by NSOs in the face of competitive exclusion by BOs (Dugger et al., 2011). Maintenance of such a landscape provides 1) areas available for re-colonization by NSOs should management actions allow for reduction of BO populations and 2) it facilitates connectivity by dispersing NSO among occupied areas (Sovern et al., 2014).

4.4. What will be the fate of NSO populations?

Based on our analysis, there are two alternative hypotheses concerning the future trajectory of NSO populations if no management actions are taken. The first is that these populations continue to decline to extinction. We observed this negative linear trajectory on several study areas (Fig. 8). Past projections based on range-wide vital rates and territory occupancy, and assuming no BO management, suggested a greater than 50% chance that NSOs would be extirpated within 50 years on 7 of the 11 study areas examined here (Yackulic et al., 2019) and eventual competitive exclusion of NSOs throughout their range (Yackulic, 2017). The second hypothesis is that current NSO populations will stabilize at smaller population sizes and continue to co-exist with larger BO populations for some time. This scenario is weakly indicated by study areas, such as RAI and NWC, where realized population declines appear to have slowed in recent years (Fig. 8). Based on our analyses here, it is highly unlikely that NSO populations will increase to their former levels if BOs continue to occupy the landscape at their current levels. Therefore, an expectation that NSO populations will return to levels above those currently reported is probably untenable unless there is large-scale management of BO populations.

Although the hypothesis for coexistence between BOs and NSOs is more optimistic, it needs to be tempered by the increased vulnerability of small populations to catastrophic events and genetic effects of inbreeding, already documented for NSOs in Washington (Miller et al., 2018). Real-world examples of these issues include the extinction of the middle-spotted woodpecker (*Dendrocopos medius*) in Sweden and the heath hen (*Tympanuchus cupido cupido*) on Martha's Vineyard island in the United States. The middle-spotted woodpecker exhibited a small but stationary population from 1967–1974 and then declined dramatically to extinction during 1975–1983 because of reduced fecundity due to inbreeding depression (Pettersson, 1985). The heath hen was extirpated from the eastern U. S. except for a small population of 300 birds on Martha's Vineyard island. However, a series of catastrophic events, including a severe wildfire followed by an unusually cold winter and an invasion of northern goshawks (*Accipiter gentilis*) reduced the population to a single pair of birds in 1928 and the subsequent extinction of the subspecies in 1932 (Simberloff, 1986). In this way, uncontrollable events can cause the extinction of small populations that were remnants of formerly larger populations.

Thus, without removal or reduction of BO populations, the more realistic scenario is probably that NSOs will become extirpated from portions of their range and possibly linger on as small populations in other areas until those populations are eliminated because of catastrophic events, resulting in the extinction of this subspecies. Increasing wildfire activity in the Pacific Northwest due to climate change coupled with past fire suppression (Davis et al., 2017; Reilly et al., 2017) is one avenue where catastrophic events may negatively affect NSO populations when large areas of older forest are degraded (Jones et al., 2016; Rockweit et al., 2017). For example, the recent large, severe wildfires of 2020 burned about 8900 km^2 of forest within the NSO range. Range-wide, these fires resulted in the loss of about 1510 km^2 of forest cover type used for nesting and roosting by NSOs (R. J. Davis, unpublished data). These large, severe wildfires usually occur under abnormal weather conditions; under normal conditions, intact stands of forests used by NSO for nesting and roosting may serve as fire refugia (Lesmeister et al., 2019).

Current trends and the predictability about future trends in NSO populations, based on this and previous meta-analyses, suggests that these populations will face extirpation if competition from BOs is not ameliorated in the short term.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109168.

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