2016

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THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 57–116
DOI: 10.1650/CONDOR-15-24.1

RESEARCH ARTICLE

The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls

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Submitted February 17, 2015; Accepted September 18, 2015; Published December 10, 2015

ABSTRACT

Estimates of species' vital rates and an understanding of the factors affecting those parameters over time and space can provide crucial information for management and conservation. We used mark–recapture, reproductive output, and territory occupancy data collected during 1985–2013 to evaluate population processes of Northern Spotted Owls (*Strix occidentalis caurina*) in 11 study areas in Washington, Oregon, and northern California, USA. We estimated apparent survival, fecundity, recruitment, rate of population change, and local extinction and colonization rates, and investigated relationships between these parameters and the amount of suitable habitat, local and regional variation in meteorological conditions, and competition with Barred Owls (*Strix varia*). Data were analyzed for each area separately and in a meta-analysis of all areas combined, following a strict protocol for data collection, preparation, and analysis. We used mixed effects linear models for analyses of fecundity, Cormack-Jolly-Seber open population models for analyses of apparent annual survival (ϕ), and a reparameterization of the Jolly-Seber capture–recapture model (i.e. reverse Jolly-Seber; RJS) to estimate annual rates of population change (λ_{RJS}) and recruitment. We also modeled territory occupancy dynamics of Northern Spotted Owls and Barred Owls in each study area using 2-species occupancy models. Estimated mean annual rates of population change (λ) suggested that Spotted Owl populations declined from 1.2% to 8.4% per year depending on the study area. The weighted mean estimate of λ for all study areas was 0.962 ($\pm$ 0.019 SE; 95% CI: 0.925–0.999), indicating an estimated range-wide decline of 3.8% per year from 1985 to 2013.

Variation in recruitment rates across the range of the Spotted Owl was best explained by an interaction between total winter precipitation and mean minimum winter temperature. Thus, recruitment rates were highest when both total precipitation (29 cm) and minimum winter temperature (−9.5°C) were lowest. Barred Owl presence was associated with increased local extinction rates of Spotted Owl pairs for all 11 study areas. Habitat covariates were related to extinction rates for Spotted Owl pairs in 8 of 11 study areas, and a greater amount of suitable owl habitat was generally associated with decreased extinction rates. We observed negative effects of Barred Owl presence on colonization rates of Spotted Owl pairs in 5 of 11 study areas. The total amount of suitable Spotted Owl habitat was positively associated with colonization rates in 5 areas, and more habitat disturbance was associated with lower colonization rates in 2 areas. We observed strong declines in derived estimates of occupancy in all study areas. Mean fecundity of females was highest for adults (0.309 ± 0.027 SE), intermediate for 2-yr-olds (0.179 ± 0.040 SE), and lowest for 1-yr-olds (0.065 ± 0.022 SE). The presence of Barred Owls and habitat covariates explained little of the temporal variation in fecundity in most study areas. Climate covariates occurred in competitive fecundity models in 8 of 11 study areas, but support for these relationships was generally weak. The fecundity meta-analysis resulted in 6 competitive models, all of which included the additive effects of geographic region and annual time variation. The 2 top-ranked models also weakly supported the additive negative effects of the amount of suitable core area habitat, Barred Owl presence, and the amount of edge habitat on fecundity. We found strong support for a negative effect of Barred Owl presence on apparent survival of Spotted Owls in 10 of 11 study areas, but found few strong effects of habitat on survival at the study area scale. Climate covariates occurred in top or competitive survival models for 10 of 11 study areas, and in most cases the relationships were as predicted; however, there was little consistency among areas regarding the relative importance of specific climate covariates. In contrast, meta-analysis results suggested that Spotted Owl survival was higher across all study areas when the Pacific Decadal Oscillation (PDO) was in a warming phase and the Southern Oscillation Index (SOI) was negative, with a strongly negative SOI indicative of El Niño events. The best model that included the Barred Owl covariate (BO) was ranked 4th and also included the PDO covariate, but the BO effect was strongly negative. Our results indicated that Northern Spotted Owl populations were declining throughout the range of the subspecies and that annual rates of decline were accelerating in many areas. We observed strong evidence that Barred Owls negatively affected Spotted Owl populations, primarily by decreasing apparent survival and increasing local territory extinction rates. However, the amount of suitable owl habitat, local weather, and regional climatic patterns also were related to survival, occupancy (via colonization rate), recruitment, and, to a lesser extent, fecundity, although there was inconsistency in regard to which covariates were important for particular demographic parameters or across study areas. In the study areas where habitat was an important source of variation for Spotted Owl demographics, vital rates were generally positively associated with a greater amount of suitable owl habitat. However, Barred Owl densities may now be high enough across the range of the Northern Spotted Owl that, despite the continued management and conservation of suitable owl habitat on federal lands, the long-term prognosis for the persistence of Northern Spotted Owls may be in question without additional management intervention. Based on our study, the removal of Barred Owls from the Green Diamond Resources (GDR) study area had rapid, positive effects on Northern Spotted Owl survival and the rate of population change, supporting the hypothesis that, along with habitat conservation and management, Barred Owl removal may be able to slow or reverse Northern Spotted Owl population declines on at least a localized scale.

Keywords: Barred Owl, fecundity, Northern Spotted Owl, occupancy, population change, *Strix occidentalis caurina*, *Strix varia*, survival

Efectos del hábitat, del clima y de *Strix varia* sobre la demografía a largo plazo de *Strix occidentalis caurina*

RESUMEN

Las estimaciones de las tasas vitales de las especies y el entendimiento de los factores que afectan estos patrones a lo largo del tiempo y del espacio pueden brindar información crucial para el manejo y la conservación. Usamos datos de marcado y recaptura, de rendimiento reproductivo y de ocupación del territorio colectados durante 1985–2013 para evaluar los procesos poblacionales de *Strix occidentalis caurina* en 11 áreas de estudio en Washington, Oregón y el norte de California. Estimamos la supervivencia aparente, la fecundidad, el reclutamiento, la tasa de cambio poblacional y las tasas de extinción local y de colonización, e investigamos las relaciones entre estos parámetros y la cantidad de hábitat adecuado, la variación en las condiciones meteorológicas local y regional y la competencia con *Strix varia*. Los datos fueron analizados para cada área por separado y mediante un meta-análisis con todas las áreas combinadas, siguiendo un estricto protocolo para la colecta, la preparación y el análisis de los datos. Usamos modelos lineales de efectos mixtos para los análisis de fecundidad, modelos poblacionales abiertos de Cormack-Jolly-Seber para los análisis de supervivencia anual aparente (ϕ) y una re-parametrización del modelo de captura-recaptura de Jolly-Seber (i.e. Jolly-Seber reverso: JSR) para estimar las tasas anuales de cambio poblacional (λ_{JSR}) y el reclutamiento. También modelamos la dinámica de ocupación del territorio de *S. o. caurina* y de *S. varia* en cada área de estudio usando modelos de ocupación de dos especies. Las tasas anuales medias estimadas de cambio poblacional (λ) sugirieron que las poblaciones de *S. o. caurina* disminuyeron de 1.2% a 8.4% por año dependiendo del área de estudio. La estimación media ponderada de λ para todas las áreas de estudio fue 0.962 (EE = 0.019; 95% IC = 0.925 a 0.999),

indicando una disminución en todo el rango estimada en 3.8% por año desde 1985 a 2013. La variación en las tasas de reclutamiento a lo largo del rango de *S. o. caurina* fue mejor explicada por una interacción entre la precipitación total de invierno y la temperatura media mínima de invierno. Por ende, las tasas de reclutamiento fueron máximas cuando la precipitación total (29 cm) y la temperatura mínima de invierno (–9.5°C) fueron las más bajas. La presencia de *S. varia* estuvo asociada con un incremento en las tasas locales de extinción de las parejas de *S. o. caurina* para todas las 11 áreas de estudio. Las covariables del hábitat estuvieron relacionadas con las tasas de extinción de las parejas de *S. o. caurina* en 8 de las 11 áreas de estudio y el hábitat más adecuado para los búhos estuvo generalmente asociado con una disminución en las tasas de extinción. La presencia de *S. varia* tuvo efectos negativos sobre las tasas de colonización de las parejas de *S. o. caurina* en 5 de las 11 áreas de estudio. La cantidad total de hábitat adecuado para *S. o. caurina* estuvo positivamente asociada con las tasas de colonización en 5 áreas, y un mayor disturbio del hábitat estuvo asociado con tasas de colonización más bajas en 2 áreas. Observamos fuertes disminuciones en las estimaciones derivadas de la ocupación en todas las áreas de estudio. La fecundidad media de las hembras fue alta para los adultos (0.309, EE = 0.027), intermedia para los individuos de dos años de edad (0.179, EE = 0.040) y baja para los individuos de un año de edad (0.065, EE = 0.022). La presencia de *S. varia* y las covariables del hábitat explicaron poco de la variación temporal en la fecundidad en la mayoría de las áreas de estudio. Las covariables climáticas aparecieron en los modelos de fecundidad competitivos en 8 de las 11 áreas de estudio, pero el apoyo para estas relaciones fue generalmente débil. El meta-análisis de fecundidad produjo 6 modelos de competencia, todos los cuales incluyeron los efectos aditivos de la región geográfica y de la variación temporal anual. Los dos modelos mejor clasificados también apoyaron débilmente los efectos aditivos negativos en la fecundidad de la cantidad de superficie de hábitat núcleo adecuado, de la presencia de *S. varia* y de la cantidad de hábitat de borde. Encontramos un fuerte apoyo para un efecto negativo de la presencia de *S. varia* en la supervivencia aparente de *S. o. caurina* en 10 de las 11 áreas de estudio, pero encontramos pocos efectos fuertes del hábitat en la supervivencia a la escala del área de estudio. Las covariables climáticas se encontraron en el tope de los modelos de supervivencia competitivos en 10 de las 11 áreas de estudio y en la mayoría de los casos las relaciones fueron como predichas; sin embargo, hubo poca consistencia entre las áreas con respecto a la importancia relativa de las covariables climáticas específicas. En contraste, los resultados de los meta-análisis sugirieron que la supervivencia de *S. o. caurina* fue más alta en todas las áreas de estudio cuando el PDO estaba en una fase cálida y cuando el SOI era negativo, siendo los SOI indicadores fuertemente negativos de los eventos de El Niño. El mejor modelo que incluyó la covariable de *S. o. caurina* (BO, por su nombre en inglés) estuvo clasificado en cuarto lugar y también incluyó PDO, pero el efecto de BO fue fuertemente negativo. Nuestros resultados indicaron que las poblaciones de *S. o. caurina* estaban disminuyendo a lo largo del rango de la subespecie y que las tasas anuales de disminución estaban acelerándose en muchas áreas. Encontramos fuerte evidencia de que *S. varia* afectó negativamente las poblaciones de *S. o. caurina*, principalmente a través de la disminución de la supervivencia aparente y del incremento de las tasas de extinción de los territorios locales. Sin embargo, la cantidad de hábitat adecuado para los búhos, el clima local y los patrones regionales del clima también se relacionaron con la supervivencia, la ocupación (vía la tasa de colonización), el reclutamiento y en menor grado, la fecundidad; aunque hubo inconsistencia sobre cuales covariables fueron importantes para determinados parámetros demográficos, o para las distintas áreas de estudio. En el área de estudio donde el hábitat fue una fuente importante de variación en la demografía de *S. o. caurina*, las tasas vitales estuvieron generalmente positivamente asociadas con el hábitat más adecuado para los búhos. Sin embargo, las densidades de *S. varia* pueden ser actualmente lo suficientemente altas a través del rango de *S. o. caurina* como para que a pesar del manejo continuo y la conservación de hábitat adecuado en tierras federales para los búhos (Davis et al. 2011, 2015), el pronóstico de largo plazo para la persistencia de *S. o. caurina* pueda verse cuestionado sin una intervención adicional de manejo. En base a nuestro estudio, la remoción de *S. varia* en el área de estudio de GDR tiene un efecto rápido y positivo sobre la supervivencia de *S. o. caurina* y sobre la tasa de cambio de la población, apoyando la hipótesis de que junto a la conservación y el manejo del hábitat, la remoción de *S. varia* puede ser capaz de ralentizar o revertir la disminución poblacional de *S. o. caurina* al menos a la escala local.

Palabras clave: cambio poblacional, fecundidad, ocupación, reclutamiento, *Strix occidentalis caurina*, *Strix varia*, supervivencia

INTRODUCTION

The development and application of statistical theory and procedures for estimating demographic parameters using data collected from marked individuals have increased rapidly in the last 50 yr (Williams et al. 2002). These advances have facilitated the use of long-term population monitoring, particularly longitudinal data on marked individuals, to investigate complex questions in avian evolutionary ecology and population dynamics (e.g., Tautin et al. 1999, Seber and Schwarz 2002, Nichols 2004, Cam 2009). In addition, estimates of species' vital rates and sources of biotic and abiotic variation in these parameters over time and space can provide crucial information for management and conservation (Jenouvrier 2013). However, while the temporal scale of many studies can be substantial, with long-term monitoring exceeding 40 or even 50 yr for some bird species (e.g., Lesser Snow Goose [*Chen caerulescens caerulescens*]; Koons et al.

2014, Wandering Albatross [*Diomedea exulans*]; Pardo et al. 2013, Neotropical migrants; Faaborg et al. 2013), the geographical scale of these studies is often limited because of funding and personnel constraints. Large-scale collaborative efforts among funding agencies and multiple researchers that focus on specific scientific, management, and conservation objectives can be the key to overcoming geographical research limitations, particularly for threatened or endangered species for which range-wide demographic data may be crucial (e.g., Blakesley et al. 2010, Forsman et al. 2011).

One species that has benefited from this sort of collaboration between land managers and researchers is the Northern Spotted Owl (*Strix occidentalis caurina*), which was listed as a threatened subspecies under the U.S. Endangered Species Act in 1990 (U.S. Fish and Wildlife Service 1990). The Northwest Forest Plan (NWFP) was adopted in 1994 and designed to protect habitat for all native species in the region, including the Northern Spotted Owl (USDA Forest Service and USDI Bureau of Land Management 1994). To understand whether this plan was benefiting the Northern Spotted Owl, collaboration among several federal resource agencies resulted in an Effectiveness Monitoring Program to estimate range-wide trends for Northern Spotted Owl populations on federal lands (Lint et al. 1999). An important condition of this monitoring program was the regular estimation of demographic characteristics and trends of Spotted Owl populations in 8 study areas on federal lands (Lint et al. 1999). In addition, researchers studying owl populations in several private and tribal study areas agreed to participate in these regular analytical efforts to examine range-wide population trends, regardless of land ownership (e.g., Anthony et al. 2006, Forsman et al. 2011). While trends in fecundity, apparent survival, and rate of population change were the focus of initial meta-analyses (Burnham et al. 1996, Franklin et al. 1999), demographic data have now been collected from study areas involved in this effort for $>$20 yr, making it possible to investigate additional biological and environmental factors that may influence Spotted Owl vital rates (e.g., Anthony et al. 2006, Forsman et al. 2011).

Of particular interest is the effect of the Barred Owl (*Strix varia*) on vital rates of Northern Spotted Owls. The Barred Owl is a medium-sized, congeneric owl species that was historically restricted to the forests of eastern North America, but has now invaded the entire range of the Northern Spotted Owl (Bent 1938, Livezy 2009). The cause of this range expansion is unclear, but there is mounting evidence that the species is having a negative effect on the Spotted Owl (e.g., Dugger et al. 2011, Forsman et al. 2011, Yackulic et al. 2014), most likely through competition for resources. Recent studies have confirmed high overlap in resource use between the 2 species (Hamer et al. 2001, 2007, Livezy 2007, Singleton et al. 2010, Wiens et al. 2014), with the larger Barred Owl usually dominating territorial interactions with the smaller Spotted Owl (Van Lanen et al. 2011) and occurring at much higher densities (Singleton et al. 2010, Wiens et al. 2014).

In addition to the effect of the Barred Owl on Spotted Owl demographics, the effects of habitat characteristics and weather and climatic patterns on Spotted Owl vital rates are also of fundamental interest (U.S. Fish and Wildlife Service 2011). The harvesting of old-growth forest habitat suitable for Spotted Owls and other dependent species (e.g., Marbled Murrelet [*Brachyramphus marmoratus*], red tree vole [*Arborimus longicaudus*]) on federal lands has declined since the adoption of the NWFP. However, low rates of loss continue on all lands within the NWFP area ($\sim$3% since 1993), although on federal lands this loss has been primarily attributed to large wildfires (Davis et al. 2011, 2015). Climate change is expected to increase the risk of large, high-intensity wildfire in the Pacific Northwest and throughout the western U.S. in general (Westerling et al. 2006, Davis et al. 2011, Stavros et al. 2014). In addition, climate change may cause changes in forest tree species composition (Peterson et al. 2014) and even potentially the growth rates of tree species in the Pacific Northwest (Littell et al. 2010, Albright and Peterson 2013). Thus, because of predicted changes in habitat availability and composition related to climate change and ongoing competitive pressures from an invasive species, it is essential for wildlife managers to understand the complex relationships between Spotted Owl demographics and the environmental and biotic factors that can affect Spotted Owls, such as long-term local weather patterns and regional climatic cycles, amount and configuration of suitable old-growth forest habitat, and the presence of Barred Owls in these habitats.

The objectives of our meta-analysis were to: (1) estimate the range-wide population status and trends in vital rates of Northern Spotted Owls, including apparent survival, fecundity, recruitment, rates of population change, and local extinction and colonization rates, and (2) investigate the potential effects of a suite of biotic and abiotic factors on Spotted Owl demographics, including Barred Owl presence, amount of suitable habitat, local weather, and regional climatic patterns. The following hypotheses reflect the relationships that we predicted between these factors and demographic rates of Spotted Owls.

(1) Barred Owls: We hypothesized that there would be negative relationships between the presence of Barred Owls and fecundity, apparent survival, rates of population change, and local colonization rates of Spotted Owls. We also predicted a positive relationship between Barred Owl presence and local extinction rates of Spotted Owls (Kelly et al. 2003, Olson et al. 2005, Anthony et al. 2006, Bailey et al. 2009, Dugger et

TABLE 1. Hypothesized relationships between climate and weather variables and apparent survival (ϕ), number of young fledged per female (NYF), and recruitment (f) of Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA.

Climate covariate	ϕ	NYF	f	Sources
Palmer Drought Severity Index (PDSI) [a]	+	+	None	Glenn et al. (2010, 2011a)
Southern Oscillation Index (SOI) [b]	+	+	None	Glenn et al. (2011a)
Pacific Decadal Oscillation Index (PDO) [c]	+	+	+ with lags	Glenn et al. (2010, 2011a)
Winter temperature (WT) [d]	+	+	+	Dugger et al. (2005), Glenn et al. (2010, 2011a, 2011b)
Winter precipitation (WP) [d]	−	−	−	Dugger et al. (2005), Glenn et al. (2010, 2011a, 2011b)
Nesting season temperature [e]	+	+	None	Howell (1964), Franklin et al. (2000), Olson et al. (2004), Glenn et al. (2011a, 2011b)
Nesting season precipitation [f]	−	−	None	Howell (1964), Franklin et al. (2000), Olson et al. (2004), Glenn et al. (2011a, 2011b)

[a] Standardized mean growing season values (Washington and Oregon: May–September; California: April–November) that ranged from −6 to 6, with negative values denoting drier conditions.
[b] Annual mean monthly values (July–June) that ranged from −1.21 to 1.81. Negative values denote warmer, drier winters (El Niño conditions), and positive values denote cold, wet, snowy winters (La Niña conditions).
[c] Annual mean monthly values (July–June) that ranged from −1.38 to 1.49. Positive values denote the warm phase, with less rain and higher temperatures, and negative values denote the cool phase, with more rain and lower temperatures.
[d] Mean monthly minimum temperature (WT; °C) and total precipitation (WP; cm) during winter (November–February).
[e] Mean monthly minimum temperature (°C) during the early (ENT; March–April) or late (LNT; May–June) nesting season.
[f] Total precipitation (cm) during the early (ENP; March–April) or late (LNP; May–June) nesting season.

al. 2011, Forsman et al. 2011, Sovern et al. 2014, Yackulic et al. 2014).

(2) Habitat: We hypothesized that increasing amounts of Spotted Owl nesting and roosting habitat would positively affect survival, fecundity, recruitment, and rates of population change, and would also increase colonization rates while decreasing extinction rates in individual territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, 2011, Seamans and Gutiérrez 2007, Forsman et al. 2011). We expected that these effects could vary at different spatial scales (i.e. territory vs. study area scale) and might be independent of, or interact with, Barred Owl presence. Additionally, we predicted that the spatial arrangement of habitat that resulted in concentrated areas of nesting and roosting habitat or increased amounts of edge habitat could have positive effects on the vital rates of Spotted Owls (Franklin et al. 2000, Olson et al. 2004).

(3) Weather and climate: At the local climate scale, previous research has documented negative relationships between cold, wet weather in winter or early spring and fecundity and survival of Spotted Owls (Franklin et al. 2000, Dugger et al. 2005, Forsman et al. 2011). On a regional scale, large-scale climate indices, such as the Palmer Drought Severity Index (PDSI), Southern Oscillation Index (SOI), and Pacific Decadal Oscillation (PDO), also have been correlated with Spotted Owl demographic rates (Glenn et al. 2010, 2011a, 2011b, Forsman et al. 2011). With a few exceptions at the northern end of the Spotted Owl's distribution, these large-scale relationships have suggested the positive effect of wetter growing seasons (PDSI) or cooler, wetter winters (SOI, PDO) on demographic rates, probably as an index to overall productivity and prey population cycles in the system (Glenn et al. 2010, 2011a, 2011b, Forsman et al. 2011). We predicted similar relationships in our analyses (Table 1).

METHODS

Study Areas

The 11 study areas in our analysis included 3 in Washington, 5 in Oregon, and 3 in California, USA (Figure 1). The duration of studies in these areas ranged from 22 to 29 yr (Table 2). Eight of the 11 study areas (codes from Table 2: OLY, CLE, COA, HJA, TYE, KLA, CAS, and NWC) were part of the Northwest Forest Plan Effectiveness Monitoring Program; of these 8 areas, 4 were primarily on federal lands (OLY, HJA, CAS, and NWC), and 4 included a mixture of federal and private lands (CLE, COA, TYE, and KLA). The 3 study areas that were not part of the Northwest Forest Plan Monitoring Program included 1 on lands owned by the Green Diamond Resource Company (GDR), 1 on the Hoopa Tribe Reservation (HUP), and 1 on private and federal lands in

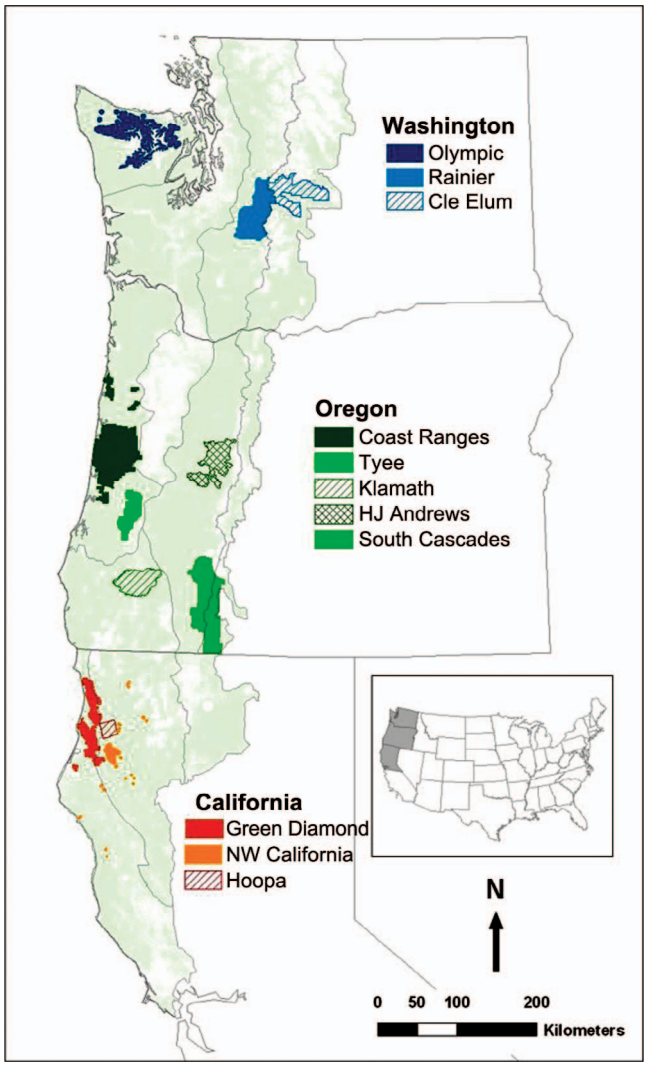

FIGURE 1. Locations of 11 study areas used in the analysis of vital rates and population trends of Northern Spotted Owls, 1985–2013.

Washington (RAI). The RAI study area was monitored by Raedeke Associates in cooperation with Plum Creek Timber Company, the National Park Service, the USDA Forest Service, and Hancock Forest Management. The 11 study areas ranged in size from 356 to 3,922 km^2 and were distributed across a broad geographical region in which climate, topography, vegetation, and elevation varied widely (Figure 1, Table 3). Although they were not selected randomly, the study areas represented most of the physiographical provinces within the range of the Northern Spotted Owl. For details regarding study area characteristics see Appendix A.

Survey Methods and Workshop Protocols

We monitored Spotted Owls by surveying each study area each year to locate and resight previously banded owls, band unmarked owls, and document the number of young produced by each territorial female. Specific protocols used in these surveys have been extensively described in previous reports (Franklin et al. 1996, Lint et al. 1999, Reid et al. 1999; see summary in Appendix B). Our analysis was the sixth time that data from these study areas were used to assess the range-wide population status and trends of the Northern Spotted Owl (Anderson and Burnham 1992, Burnham et al. 1994, Forsman et al. 1996a, Franklin et al. 1999, Anthony et al. 2006, Forsman et al. 2011). In keeping with previous analyses, we adhered to strict protocols for data preparation and model development, and all participants agreed to follow these protocols (Anderson et al. 1999; see Appendix B for details).

Delineation of Territory Boundaries

Spatially delineated Spotted Owl territories were important to the development of detection vs. nondetection datasets for our analyses of site occupancy and for estimation of habitat and Barred Owl covariates within study areas. We defined an owl territory as a landscape patch that represented the cumulative area of use by an owl, or pair of owls, during the study period. To delineate territories we first documented the center of every owl use area for every year of study. Territory centers were the UTM coordinates of the most biologically important location in each year, which we determined based on the following hierarchical ranking: (1) active nest, (2) fledged young, (3) primary roost location, (4) diurnal location, and (5) nocturnal detection (Forsman et al. 2011). We then used the Euclidean Allocation Distance tool in ArcGIS 10 (ESRI, Redlands, California, USA) to delineate a Thiessen polygon around all the annual center locations for each territory. Thiessen polygons are based on a set of predefined sample points, such that the boundaries of each polygon define the area that is closest to each point relative to all other points. The Thiessen polygon for each owl territory was static (did not vary by year), encompassed all the annual territory center locations, and extended outward to a maximum of half of the median nearest-neighbor distance or midway between the annual territory center locations of owls occupying adjacent territories, whichever distance was shorter. Median nearest-neighbor distances varied among study areas, and were longer in the northern portions of the Spotted Owl range (1.75 km) than in the southern portions of the range (0.6 km; Table 3). The predefined Thiessen polygons were then used to represent individual owl territories (Figure 2A). For analyses of survival and fecundity, the Thiessen polygons in each study area were merged to delineate the study area (Figure 2B). This area was then buffered by 23 km to delineate an "outer zone" to represent an area that might influence recruitment into

TABLE 2. Years of study and sample sizes of banded owls used to estimate vital rates of Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013.

Study area	Study area code	Start year [a]	λ start year [b]	Expansion year [c]	Number of owls banded by age class [d]				Total encounters [e]
					S1	S2	Adult	Total	
Washington									
Cle Elum	CLE	1989	1992	none	35	34	159	228	1,219
Rainier	RAI	1992	1993	1998	11	12	168	191	742
Olympic	OLY	1990	1990	1994	21	39	349	409	1,715
Oregon									
Coast Ranges	COA	1990	1992	none	63	100	496	659	3,616
H. J. Andrews	HJA	1987	1990	2000	52	130	594	776	3,981
Tyee	TYE	1990	1990	none	156	128	246	530	2,897
Klamath	KLA	1990	1990	1998	179	152	394	725	3,609
South Cascades	CAS	1991	1992	2001	31	88	557	676	2,856
California									
NW California	NWC	1985	1988	none	146	109	315	570	2,935
Hoopa	HUP	1992	1992	none	46	57	143	246	1,217
Green Diamond Resources	GDR	1990	1990	1998	162	228	592	982	4,733
All areas combined					902	1,077	4,013	5,992	29,520

[a] Year banding study was begun.
[b] First year of data used in the analysis of λ. Start year for occupancy analysis was 1999 for GDR and 1995 for all other study areas.
[c] Indicates year in which study area was expanded in the λ analysis.
[d] Indicates age when owls were first captured and banded on territories: S1 = 1 yr old, S2 = 2 yr old, Adult = ≥3 yr old.
[e] Excluding multiple encounters of individuals in the same year.

the study area (Figure 2B). Thus, individual territories, study areas, and buffered study areas (Figure 2) were the 3 spatial scales used to estimate the amount of suitable habitat and Barred Owl presence vs. absence, and to develop detection histories for the occupancy analysis, as described below.

Development of Covariates

Temporal trends. We modeled temporal variation in Spotted Owl vital rates in a variety of ways, including annual time effects (*t*), linear effects (T), log-linear effects (lnT), and spline models (SPLINE). We used spline models rather than quadratic time effect models because spline

TABLE 3. Size, ownership, location, and precipitation (precip) in the 11 study areas included in the January 2014 analysis of demographic status and trends of Northern Spotted Owls in Washington, Oregon, and California, USA, 1985–2013.

Study area [a]	Area (km^2)	Landowner	Region	Mean annual precip (cm)	Latitude	½ median NND (km) [b]
Washington						
CLE	1,784	Mixed	Washington mixed conifer	136	46.996	1.75
RAI	2,167	Mixed	Washington Douglas-fir	215	47.195	1.50
OLY	2,230	Federal	Washington Douglas-fir	282	47.800	1.75
Oregon						
COA	3,922	Mixed	Oregon coastal Douglas-fir	212	44.381	1.25
HJA	1,604	Federal	Oregon Cascades Douglas-fir	201	44.213	1.00
TYE	1,026	Mixed	Oregon coastal Douglas-fir	126	43.468	1.00
KLA	1,422	Mixed	Oregon–California mixed conifer	116	42.736	1.25
CAS	3,377	Federal	Oregon Cascades Douglas-fir	119	42.695	1.75
California						
NWC	460	Federal	Oregon–California mixed conifer	154	40.848	0.75
HUP	356	Tribal	Oregon–California mixed conifer	176	41.051	1.00
GDR	1,465	Private	California Coast	187	41.122	0.60
Total	19,813					

[a] See Table 2 for study area codes.
[b] Nearest neighbor distances, representing the maximum distances used in the delineation of Northern Spotted Owl territories, using Thiessen polygons placed around all annual owl activity centers associated with each territory over the course of this study.

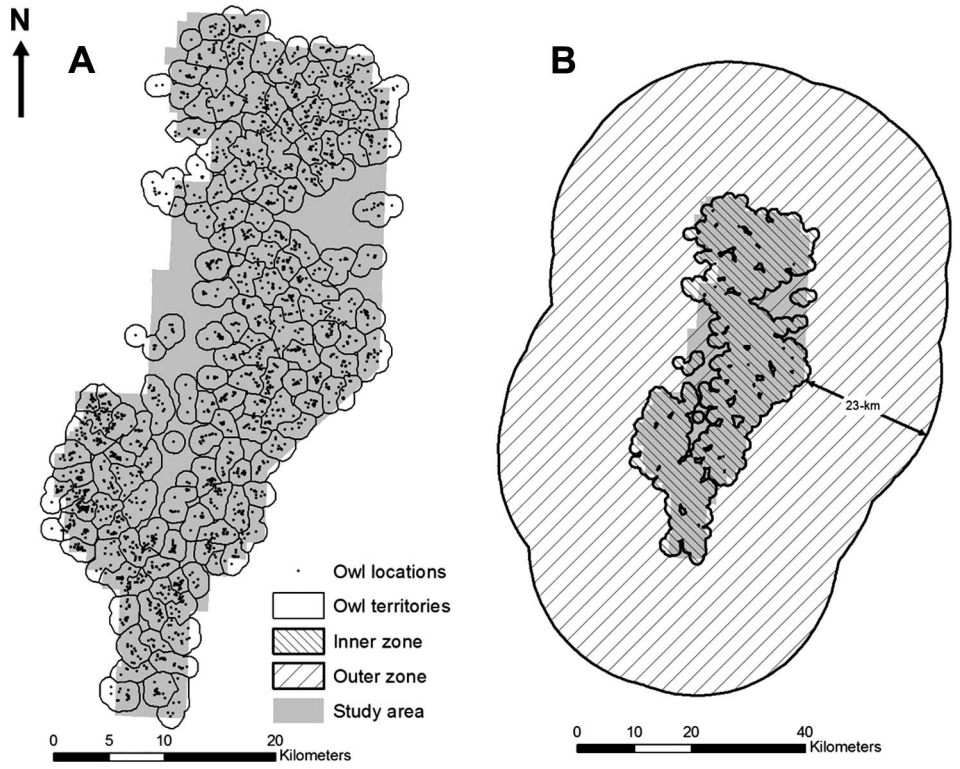

FIGURE 2. An example, using the Tyee study area (TYE), of (**A**) individual Northern Spotted Owl territories based on Thiessen polygons placed around annual Spotted Owl activity centers from 1990 to 2013. In each study area, Northern Spotted Owl territories (i.e. Thiessen polygons) were (**B**) combined to represent the study area scale (inner zone) used to generate habitat covariates for the fecundity and apparent survival analyses. Habitat covariates for the recruitment analysis were generated from a 23-km buffer added around the outside of each study area (outer zone).

models could capture the quadratic effect were it to be present, but also allowed more overall flexibility for complex temporal patterns over long time periods (Bonner et al. 2009). In particular, spline models could accommodate a slowly varying external influence (e.g., regional climatic pattern) or a single "blip" in the middle of the time series. If we observed strong support for a spline model across multiple study areas, this might indicate that we were omitting some fundamental covariate. We used a penalized cubic spline model with knots every 5 yr going backward from the year with the last estimable parameter and with the first interval $\geq$5 years. For the fecundity analyses only, we also investigated a temporal even–odd year effect (EO), in which years of high reproductive output alternated with years of low reproductive output.

Barred Owl covariate. We did not specifically survey Barred Owls along with Spotted Owls. However, Barred Owls frequently responded when we used playback calls or vocal imitations to locate Spotted Owls, and we recorded all such detections. Based on a calling experiment conducted by Wiens et al. (2011), we estimated that cumulative annual detection probabilities of Barred Owls were $>$85% at territories in which we conducted $\geq$3 nocturnal surveys for Spotted Owls. Based on these detection data, we created a Barred Owl covariate that was specific to year and study area and reflected the proportion of Northern Spotted Owl territories (i.e. Thiessen polygons) in which Barred Owls were detected $\geq$1 time per year in each study area (Anthony et al. 2006, Forsman et al. 2011; Appendix C Figure 13). We used this covariate to model the Barred Owl effect on fecundity and apparent survival in individual study areas and in the meta-analysis. For the occupancy analysis, we used detections of Barred Owls from the multiple Spotted Owl surveys conducted each year to estimate the effects of each species on the other, including probability of detection and rates of colonization and extinction (Bailey et al. 2009, Yackulic et al. 2014).

Habitat covariates. Habitat covariates were year-specific covariates applied at the study area scale for survival and fecundity analyses (Figure 2B). For occupancy analyses in individual study areas, habitat covariates were developed as year- and territory-specific covariates for individual owl territories (i.e. Thiessen polygons; Figure 2A). Covariates developed to represent the amount and spatial distribution of Northern Spotted Owl habitat within study areas included: (1) the proportion of Northern Spotted Owl nesting and roosting habitat in

each study area each year (HAB), (2) habitat disturbance, or the mean percentage of nesting and roosting habitat lost during 3-yr intervals prior to and including each survey year (HD), (3) a neighborhood focal statistic defined as the proportion of 30 × 30 m pixels in each study area with ≥50% nesting and roosting habitat within 800 m of each pixel (CORE), and (4) the proportion of edge habitat within each study area (EDGE), with edge as the amount of nesting and roosting habitat within 100 m of all other cover types (Appendix D Figure 14). We hypothesized that higher proportions of HAB and CORE would have positive effects on Spotted Owl vital rates, and that EDGE would have a variable effect, depending on the amount of nesting and roosting habitat remaining (EDGE and HAB interaction) and differences in the dominant types of prey available in each study area (Franklin et al. 2000). We predicted that study areas with more habitat disturbance (i.e. more habitat loss) would have lower survival rates than areas experiencing less habitat disturbance. These covariates were developed for all analyses as follows:

Amount of suitable nesting and roosting habitat (HAB). We used the range-wide map of Northern Spotted Owl nesting and roosting habitat developed by Davis et al. (2011) as our baseline measure of the amount of Spotted Owl nesting and roosting habitat in 1994 for Oregon and Washington and in 1996 for California. This map was developed using MaxEnt, a species distribution model that correlated species presence data with relevant environmental data to generate a geographical representation of the realized niche of the Northern Spotted Owl (Phillips et al. 2006, Phillips and Dudík 2008). The environmental data underlying this habitat map included stand age, canopy cover, average tree height, mean conifer diameter, conifer density, and forest type, and was derived from vegetation maps developed through a "gradient nearest neighbor" (GNN) analysis conducted for the entire Pacific Northwest (Ohmann and Gregory 2002). We used yearly maps of forest disturbance (LandTrendr; Kennedy et al. 2010) to adjust the base map of Davis et al. (2011) for annual loss of nesting and roosting habitat, thereby producing a time series of binary maps that reflected the year-specific amount of nesting and roosting habitat across the entire range of the Northern Spotted Owl from 1985 to 2013. The covariate developed from these maps (HAB) was the annual proportion of 30 × 30 m pixels that was labeled as nesting and roosting owl habitat within or adjacent to each study area or each individual owl territory (Appendix D Figure 14). Therefore, in contrast to the previous meta-analysis of Northern Spotted Owl population data that omitted California (Forsman et al. 2011), we had a standardized map of suitable nesting and roosting habitat that encompassed the entire range of the Northern Spotted Owl.

As with all maps derived from models, there is some uncertainty and error associated with the accuracy of the final product, but the baseline habitat map developed by Davis et al. (2011) and used in this analysis included only environmental variables from the GNN data that were highly correlated with the ground plot information ($r \geq 0.7$). In addition, the resulting Northern Spotted Owl habitat map performed reasonably well in map accuracy tests (Area Under the Curve (AUC) values of 0.78 to 0.88, and Spearman rank correlations >0.9; Davis et al. 2011). Thus, while caution is advised when using modeled habitat maps of this sort because it is difficult to derive precise representations of all of the habitat characteristics that are important to a species (Yackulic et al. 2012, Loehle et al. 2015), we believe that the map that we used in this analysis represented the best available range-wide map of Northern Spotted Owl nesting and roosting habitat.

For analyses of apparent survival, fecundity, recruitment, and rates of population change, we created boundaries for habitat delineation within each study area by merging all owl territories (Thiessen polygons) for a specific study area into one large polygon (Figure 2B). The amount of habitat was then estimated each year as the percent cover of nesting and roosting habitat within each study area. Because the occupancy analysis was spatially explicit, we calculated the habitat covariates used to model occupancy dynamics as the percent cover (HABp) and absolute amount (HABa) of nesting and roosting habitat within each owl territory in each study area.

To evaluate the hypothesis that the amount of suitable habitat surrounding the study area might influence immigration and recruitment into the study area, we developed a habitat covariate (HAB2) that was the estimated proportion of nesting and roosting habitat within a 23-km buffer of each study area boundary as described above, similar to methods used by Forsman et al. (2011; Figure 2B, Appendix D Figure 14).

Habitat disturbance (HD). The habitat disturbance covariate (HD) was based on LandTrendr remotely sensed change detection data (Kennedy et al. 2010), and was calculated as the percentage of nesting and roosting habitat that was disturbed (≥30% reduction in vegetation cover) in each study area or owl territory within 3 yr prior to each year of study (e.g., HD for 1990 = the percent cover of nesting and roosting habitat that was disturbed in 1987–1989; Appendix D Figure 14). We used the proportion of disturbance relative to the amount of habitat present at the start of each interval because we reasoned that the same absolute amount of habitat loss would have different impacts depending on the amount of habitat that was present at the outset (i.e. small amounts of habitat loss would have greater impacts in areas that had less habitat to start with).

Amount of core-area habitat (CORE). The CORE habitat covariate was calculated using the Neighborhood Statistic Tool in ArcGIS 10 (ESRI, Redlands, California, USA) to estimate the annual proportion of 30 × 30 m pixels in each study area that was surrounded by ≥50% nesting and roosting habitat within an 800-m radius (Appendix D Figure 14). The 800-m radius (500 ha) was selected based on previous analyses that examined the average size of high-use areas ("core areas") of Northern Spotted Owls (Bingham and Noon 1997, Glenn et al. 2004, Schilling et al. 2013). Pixels were categorized as "0" if they were surrounded by <50% nesting and roosting habitat, or "1" if they were surrounded by ≥50% nesting and roosting habitat. This covariate characterized the amount and distribution of habitat in the landscape, not habitat in a particular map pixel.

Amount of edge habitat (EDGE). We used the amount of edge between nesting and roosting habitat and other cover types to evaluate the hypothesis that the amount of edge was associated with vital rates of Northern Spotted Owls (Franklin et al. 2000, Olson et al. 2004, Forsman et al. 2011). We defined the EDGE covariate as the percentage of nesting and roosting habitat in the study area or owl site that was within 100 m of a boundary with another cover type (Appendix D Figure 14), including younger forest seral stages, unforested areas, and pine-dominated or high-elevation forest types that did not meet our definition of nesting and roosting habitat. We estimated EDGE using the same annual binary habitat maps used to estimate the HAB covariate, but resampled with spatial pattern analysis software (GUIDOS 1.3; Soille and Vogt 2009) at 100 m (1 ha) pixel resolution.

Weather and climate. We used a variety of covariates to investigate any possible effects of weather and climate on vital rates of Northern Spotted Owls (Table 1). All weather and climate covariates were time-specific, linear effects applied at the scale of individual study areas. These variables included measures of seasonal and annual weather, as well as long-term climatic conditions. Specific covariates included total precipitation and mean minimum temperature during various life-history stages, the Palmer Drought Severity Index (PDSI), the Southern Oscillation Index (SOI), and the Pacific Decadal Oscillation (PDO; Franklin et al. 2000, Seamans et al. 2002, LaHaye et al. 2004, Olson et al. 2004, Dugger et al. 2005, Glenn 2010, 2011a, 2011b, Forsman et al. 2011). Mean temperature and precipitation data were obtained from PRISM (Parameter Elevated Regression on Independent Slope Models) maps of each study area (PRISM Climate Group, http://prism.oregonstate.edu). PRISM maps were raster-based digital maps with 4-km^2 resolution for mean monthly temperature (minimum and maximum; °C) and precipitation (cm), developed from weather station data and a digital elevation model (Daly 2006). From the mean monthly PRISM maps we calculated total precipitation and mean minimum monthly temperature for seasons that corresponded with important life-history stages of Spotted Owls as follows: winter (W; November 1–February 28), early nesting season (EN; March 1–April 30), late nesting season (LN; May 1–June 30), and the entire annual cycle (A; July 1–June 30). Temperature and precipitation values for each study area and time period were obtained by computing the average values of PRISM raster cells that fell within the study area boundaries.

The PDSI is a measurement of moisture conditions standardized for comparison across regions (http://www.ncdc.noaa.gov/temp-and-precip/climatological-rankings/). The PDSI is calculated using precipitation, temperature, and soil moisture data, which allows the derivation of the basic components of the water balance, including evapotranspiration, soil recharge, runoff, and moisture loss from the surface layer (Alley 1984). We considered the PDSI an index of primary productivity that had the potential to influence the abundance of Spotted Owl prey. Values ranged from –6 (extremely dry) to +6 (extremely wet), with 0 representing normal water balance conditions. The PDSI was calculated separately for each climatic region in Washington, Oregon, and California. Most study areas fell within a single climatic region. When study areas included multiple climatic regions, we used a weighted average PDSI based on the proportion of the study area that fell within each region. We also averaged monthly values of the SOI (http://www.cpc.ncep.noaa.gov/data/indices/soi), and the PDO (http://jisao.washington.edu/pdo/PDO.latest) to generate annual measures (July 1 to June 30) that reflected region-wide climatic patterns that affected all study areas.

Land ownership, region, latitude, and prey species richness. In our meta-analyses, we evaluated whether Spotted Owl vital rates or rates of population change varied in relation to land ownership, region, latitude, and prey species richness. Land ownership (OWN) was a categorical variable that divided the 11 study areas into 3 ownership categories depending on whether primary ownership was federal, private, or a relatively equal mix of federal and private (Table 3). The region (REG) covariate classified each study area into 1 of 6 geographic regions based on state boundaries and major vegetation types (Table 3). Latitude (LAT) was a continuous variable measured at the center of each study area. The prey diversity index (PREY) was a discrete variable that characterized the maximum number of potential mammalian prey species (range: 6–17) that were available to Spotted Owls in each study area. We estimated the PREY covariate by using extensive data on the diets of Spotted Owls (Cutler and Hays 1991, Carey et al. 1992, Zabel et al. 1995, Ward et al. 1998, Forsman et al. 2001, 2004, Rosenberg et al. 2003) and species distribution maps in NatureServe (http://www.natureserve.org/conservation-

tools/data-maps-tools/digital-distribution-maps-mammals-western-hemisphere), summarized across the range of the Northern Spotted Owl in 50-km hexagons. Long-term data on prey abundance were not available for any of the Spotted Owl study areas, so the PREY covariate was a simple attempt to address variation in prey species richness among study areas.

Reproduction covariate. We used a covariate that was specific to year and study area, mean number of young fledged per female (NYF) in the current year *t*, to test whether reproductive effort affected adult survival in the interval between year *t* and year $t+1$ (Franklin et al. 1996, Anthony et al. 2006, Forsman et al. 2011; Appendix E Figure 15). We also investigated the effect of reproduction on detection probability in year *t*, because breeding birds are generally easier to detect than nonbreeders (Anthony et al. 2006, Forsman et al. 2011, Stoelting et al. 2015).

Barred Owl removal study. Beginning in 2009, a paired before–after control–impact (BACI) study design was implemented in the GDR study area, where lethal removal of Barred Owls was the treatment effect on Northern Spotted Owl vital rates (Diller et al. 2014). The GDR demographic study area was partitioned into treatment (Barred Owls lethally removed) and control (Barred Owls undisturbed) areas to estimate the response of Spotted Owl fecundity, survival, and rate of population change to the removal activities. To account for geographical differences in the history of timber harvesting, physiographical patterns, and density of Barred Owl and Spotted Owl territories, the GDR study area was divided into 3 paired treatment and control areas totaling 84,205 and 72,711 ha, respectively. Within these treatment areas, investigators attempted to remove all Barred Owls detected (Diller et al. 2014). For analyses involving individual study areas, a BACI (e.g., Stewart-Oaten et al. 1986) design was incorporated for the GDR study area, with parameters estimated separately for treatment and control areas both before and after removals began, unless otherwise noted. For the meta-analyses conducted with data from all study areas combined, only data from control and treatment areas prior to the Barred Owl removals (up to 2008) and control areas after removals began (2009–2013) were included, so that the GDR data were comparable with data from the other study areas.

Analytical Methods

We primarily used a random effects approach (Burnham and White 2002, Franklin et al. 2002, Forsman et al. 2011, Burnham 2013; see Appendix F) to examine trends in fecundity, survival, recruitment, and rates of population change of Northern Spotted Owls, and associations between these vital rates and other environmental covariates (i.e. Barred Owl presence, habitat, and climate). We calculated estimates and evaluated the effects of covariates on fecundity, survival, and rates of population change for both individual study areas and in meta-analyses with data from all study areas combined. We estimated annual recruitment rates within a meta-analysis using a random effects approach, but because of the complicated nature of the 2-species occupancy analysis, we modeled Northern Spotted Owl occupancy dynamics for individual study areas using fixed effects models. Logit-link functions were used for apparent survival and log-link functions were used for recruitment and lambda in fixed effects models, while the identity link function was used in all random effects models.

Because vital rates and population trajectories of Northern Spotted Owls differed only slightly between federal and nonfederal study areas (Anthony et al. 2006, Forsman et al. 2011), we did a single analysis and calculated mean estimates for the entire range of the owl, rather than performing separate analyses for federal and nonfederal study areas. However, we evaluated the validity of the assumption that demographic rates were similar on federal and nonfederal lands by including a land ownership covariate in the meta-analyses of fecundity, survival, and recruitment. For the meta-analysis of survival we also used a categorical covariate (NWFP) to explicitly evaluate the null hypothesis that survival rates did not differ between the 8 areas under primarily federal ownership (OLY, CLE, COA, HJA, TYE, KLA, CAS, and NWC) and the 3 other areas (RAI, HUP, and GDR).

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_c value and highest Akaike weight (w_i) as our best model, but models within 2 AIC_c units ($\Delta AIC_c \leq 2.0$) were considered competitive (Burnham and Anderson 2002). When evaluating models with $\Delta AIC_c \leq 2.0$, we also examined the maximized log-likelihood ($-2\ln L$) or deviance values to ensure that ΔAIC_c values were not solely a result of adding an additional, uninformative covariate (Arnold 2010). We also evaluated the strength of evidence for specific effects in competing models based on the degree to which 95% confidence intervals (95% CI) for slope coefficients (β) overlapped 0 (Anthony et al. 2006, Forsman et al. 2011). Covariates in competitive models with 95% CI that did not overlap 0 were considered to have the strongest evidence of an effect. Covariates in competitive models with <10% of the 95% CI overlapping 0 ("slightly" overlapping) were considered to have less evidence of an effect compared with covariates with 95% CI that did not overlap 0. Covariates with confidence limits with >10% of the interval above or below 0 ("widely" overlapping) were considered to have no support for the importance of the effect. Values reported in the results are

means ± SE unless otherwise noted (see Appendix G for a consideration of possible sources of bias associated with estimates of Northern Spotted Owl demographic parameters).

Annual rate of population change (λ). We estimated annual rates of population change (λ) in individual study areas using the λ- and recruitment- (f) parameterizations of the temporal symmetry models (Pradel 1996) implemented in program MARK. For this analysis we used all banded, territorial birds (S1, S2, adults) combined into a single age class. We ran 5 random effects models on λ_t, including the intercept-only (no effect), general time (t), linear time trend (T), log-linear time trend (lnT), and spline models (SPLINE; with knots every 5 yr backward from 2013, such that the first interval was ≥5 yr; Bonner et al. 2009). We dealt with expansions or contractions in areas surveyed (Table 2) using the design matrix in program MARK, such that all estimates of λ reflected changes in owl numbers and were not confounded with sampling changes (Anthony et al. 2006, Forsman et al. 2011; see Appendix H for further details). Start years varied by study area, but estimates were generated from the start date through 2012 in all cases (Table 2). However, for general models with time-specific capture and survival probabilities, the first and last estimates (λ_1, λ_{k-1}) were confounded with other parameters, and the second estimate was frequently biased (λ_2; Hines and Nichols 2002). Thus, we only present estimates from 2 yr after the start date through 2011, and used these estimates in random effects models.

Estimates of realized population change. We estimated realized population change ($\hat{\Delta}_t$), which portrays the population trajectory ($\Delta_t = N_t/N_x$) in each year of the study (N_t) relative to population size in the first year (N_x) that λ_t was estimated (Franklin et al. 2004).

Annual estimates of $\hat{\lambda}_t$ were based on the full fixed effects model [$\phi(t)\ p(t)\ f(t)$; i.e. time-dependent (t) survival (φ), capture probability (p), and recruitment (f)], and annual estimates of realized population change ($\hat{\Delta}_t$) were computed as:

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

We estimated 95% confidence limits (CL) for $\hat{\Delta}_t$ using a parametric bootstrap algorithm (Franklin et al. 2004). Estimates of annual survival ($\hat{\phi}_t$), recruitment ($\hat{f}_t$), and recapture probabilities ($\hat{p}_t$) from the full fixed effects model [$\phi(t)\ p(t)\ f(t)$], and an estimate of initial abundance ($\hat{N}_x$), were used to stochastically generate 1,000 sets of individual capture histories. These simulated capture history datasets were analyzed to obtain 1,000 estimates of λ_t and Δ_t, and these estimates were used to generate empirical confidence intervals based on the i^{th} and j^{th} values of Δ_t arranged in ascending order, where $i = 25$ (0.025*1,000) and $j = 975$ (0.975*1,000).

Meta-analysis of annual rate of population change. We conducted the meta-analysis of the annual finite rate of population change using the same data that we used to estimate λ_t for individual study areas. However, we only used data for 1992–2013 so that we could make inferences based on the same years for all study areas. As in the analysis of individual areas, we used $\hat{c} = 1$ for modeling all rates of population change (Anthony et al. 2006, Forsman et al. 2011; see Appendix H). We used the global model [$\phi(g*t)\ p(g*t)\ f(g*t)$] as the basis for random effects modeling of covariate effects on recruitment, where g indicated individual study areas. We only included climate and habitat covariates that we predicted would have effects on recruitment. In some cases we modeled 1- or 2-yr lag effects of climate covariates, because we hypothesized that this was likely the most appropriate relationship if climate was associated with annual reproductive output (NYF) and it took fledged young at least 1 or 2 yr to be recruited into the territorial population.

Territory occupancy modeling. We investigated the co-occurrence dynamics of Northern Spotted Owls and Barred Owls based on 19 yr of detection data for both species (1995–2013) in 10 study areas, and 15 yr of detection data (1999–2013) in the GDR study area. We excluded data from the Barred Owl removal treatment areas in the GDR study area after 2008. We created detection histories that consisted of a sequence of detections (1) and nondetections (0) for both species within and among years on all study areas. We applied these data to the multiseason (robust design) extension of the conditional, 2-species occupancy model (MacKenzie et al. 2004, 2006) following Miller et al. (2012) and Yackulic et al. (2014), and used program MARK to estimate occupancy parameters and model selection results. 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) because it is more stable than the parameterization of the original 2-species models developed by MacKenzie et al. (2004, 2006), which can fail to converge when covariates are included. Based on prior research (Van Lanen et al. 2011, Wiens et al. 2014), we assumed that the Barred Owl was the dominant species (coded as "A") and that the Northern Spotted Owl was the subordinate species (coded as "B"). Although occupancy dynamics parameters for both Spotted Owls and Barred Owls were generated in this analysis, here we focus on the patterns of occupancy and occupancy dynamics (extinction and colonization rates) for Spotted Owls only, in relation to the presence or absence of Barred Owls. The specific parameters of interest were: (1) initial probability

of occupancy of Northern Spotted Owls when Barred Owls were absent (Ψ_1^B) and when Barred Owls were present (Ψ_1^{BA}), (2) the probability that a territory unoccupied by a Spotted Owl in year i was occupied by a Spotted Owl in year $i + 1$ (i.e. colonization) when Barred Owls were present (γ_i^{BA}) and when Barred Owls were absent (γ_i^B), (3) the probability that a territory occupied by a Spotted Owl in year i was unoccupied in year $i + 1$ (i.e. local extinction) when Barred Owls were present (ε_i^{BA}) and when Barred Owls were absent (ε_i^B), and (4) annual probability of territory occupancy by Northern Spotted Owls when Barred Owls were present (Ψ_i^{BA}) and when Barred Owls were absent (Ψ_i^B), which was derived using the best model structure for detection, extinction, and colonization rates.

We analyzed each study area separately using fixed effects models and an iterative model selection process identified a priori (see Appendix H for details). We modeled colonization and extinction rates for both species with linear time trends (T), year-specific effects (t), no temporal effects (intercept-only), the presence vs. absence of the other species, and the effects of habitat covariates. Finally, the effects of 2- and 3-yr lags in Spotted Owl annual reproductive output were also modeled for Spotted Owl colonization probabilities (see Yackulic et al. 2014 for details on this general approach).

Fecundity. Analyses for individual study areas were conducted on the number of young produced per territorial female (NYF), but our results are presented as fecundity, defined as the number of female young produced per territorial female per year. This was calculated as NYF/2, because the sex ratio of juvenile owls at hatching is approximately 1:1 (Fleming et al. 1996). Spotted Owls 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 sampling over the course of an entire breeding season was not biased toward birds that reproduced, and that the sample of owls used in our analyses was representative of the territorial population. Owls that were recruited into the banded population were assigned to 1 of 3 discrete age classes based on their age at first capture as a territorial bird (S1 = 1 yr old, S2 = 2 yr old, Adult = ≥3 yr old; Table 2). We determined age classes based on known age of birds first banded as juveniles, or plumage attributes of birds first banded as nonjuveniles (Forsman 1981, Moen et al. 1991, Franklin et al. 1996).

Mean annual NYF was computed by age class and then averaged across years for estimates of age-specific reproductive output. Standard errors were calculated as the standard errors of the averages among years, which gave equal weight to all years regardless of the number of owls sampled (Anthony et al. 2006, Forsman et al. 2011). This approach essentially treated year as a random effect, with year effects being large relative to within-year sampling variation.

We developed an a priori model set and used a linear mixed model approach implemented with PROC MIXED in SAS (SAS Institute 2008) to investigate patterns of variation and hypothesized relationships between covariates and NYF (see Appendix H for details). Models included the effects of age (S1, S2, Adult), annual time variation (t), linear or quadratic time trends (T, TT), an autoregressive time effect (AR1), the Barred Owl (BO) covariate, a temporal even–odd year effect (EO) in which years of high reproductive output alternated with years of low reproductive output, and the weather, climate, and habitat covariates described previously.

Meta-analysis of fecundity. We restricted the meta-analysis of fecundity to adult females because the sample size of younger age classes was small (<10%), particularly in the most recent years of study. We used the same covariates as in the individual study area analyses to generate an a priori model set, with the addition of models investigating the effects of latitude (LAT), region (REG), land ownership (OWN), and prey species richness (PREY) as fixed random variables. We used mixed models to analyze mean NYF per year, and treated sampling units (study areas within years) as random effects (Anthony et al. 2006, Forsman et al. 2011).

Apparent survival. We used capture–recapture (resighting) data and Cormack-Jolly-Seber open population models (Lebreton et al. 1992) to estimate recapture probabilities (p) and annual apparent survival probabilities (ϕ) of nonjuvenile, territorial owls (Table 2). Annual estimates of survival corresponded roughly to the interval from June 15 in year t to June 14 in year $t + 1$, which reflected the approximate midpoint of the annual field season during which demographic (mark–resighting) data were collected (March–August). Estimates and model selection results to investigate the effects of Barred Owls, reproduction, habitat, weather, climate, and time effects on apparent survival of Spotted Owls were generated using the Method of Moments random effects module in program MARK (White and Burnham 1999; Appendix F, H).

Meta-analysis of apparent survival. We used the same general protocol for the meta-analysis of apparent survival as for the analysis of apparent survival in individual study areas (for details see Appendix H). We ran random effects models in program MARK (White et al. 2001) to investigate the effect of covariates (i.e. time, Barred Owls, cost of reproduction, weather, climate, habitat, latitude, region, and prey species richness), always excluding the last confounded estimate of survival (ϕ_K; Burnham and White 2002, Burnham 2013; Appendix F).

RESULTS

Annual Rate of Population Change

Individual study areas. We estimated annual rates of population change (λ) using capture histories for 5,992

TABLE 4. Estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits of mean annual rate of population change based on a reverse Jolly-Seber model ($\hat{\lambda}_{RJS}$) and temporal process variance ($\hat{\sigma}_{temporal}$) for Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Estimates of $\hat{\lambda}_{RJS}$ were generated using the intercept-only random effects model [RE(.)]. Estimates of temporal process variance were based on the best random effects models using time-specific estimates of survival (ϕ), capture probability (p), and rate of population change (λ) or recruitment (f).

Study area [a]	Model [b]	$\hat{\lambda}_{RJS}$	SE	LCL	UCL	$\hat{\sigma}_{temporal}$	LCL	UCL	Annual change
Washington									
CLE	$\phi(t)$ p(sex + t) $\lambda(t)$: RE λ(T)	0.916	0.011	0.894	0.938	0.000	0.000	0.139	−8.4%
RAI	$\phi(t)$ $p(t)$ $\lambda(t)$: RE λ(.)	0.953	0.017	0.919	0.987	0.000	0.000	0.017	−4.7%
OLY	$\phi(t)$ p(sex*t) $\lambda(t)$: RE λ(T)	0.961	0.015	0.931	0.990	0.051	0.000	0.136	−3.9%
Oregon									
COA	$\phi(t)$ $p(t)$ $\lambda(t)$: RE λ(T)	0.949	0.019	0.911	0.987	0.078	0.047	0.134	−5.1%
HJA	$\phi(t)$ p(sex + t) $\lambda(t)$: RE λ(SPLINE)	0.965	0.008	0.949	0.980	0.026	0.000	0.062	−3.5%
TYE	$\phi(t)$ p(sex + t) $\lambda(t)$: RE λ(T)	0.976	0.017	0.944	1.008	0.068	0.041	0.113	−2.4%
KLA	$\phi(t)$ p(sex + t) $\lambda(t)$: RE λ(T)	0.972	0.017	0.940	1.005	0.068	0.033	0.127	−2.8%
CAS	$\phi(t)$ $p(t)$ $\lambda(t)$: RE λ(.)	0.963	0.024	0.916	1.010	0.096	0.056	0.168	−3.7%
California									
NWC	$\phi(t)$ p(sex + t) $\lambda(t)$: RE λ(SPLINE)	0.970	0.009	0.951	0.989	0.032	0.000	0.075	−3.0%
HUP	$\phi(t)$ $p(t)$ $\lambda(t)$: RE λ(T)	0.977	0.010	0.958	0.996	0.000	0.000	0.068	−2.3%
GDR-CB [c]	$\phi(t)$ p(sex + t) $f(t)$: RE λ(BACI: Trt + T, Trt)	0.988	0.009	0.970	1.006	0.032	0.000	0.081	−1.2%
GDR-TB [c]	$\phi(t)$ p(sex + t) $f(t)$: RE λ(BACI: Trt + T, Trt)	0.961	0.018	0.926	0.996	0.068	0.026	0.130	−3.9%
GDR-CA [c]	$\phi(t)$ p(sex + t) $f(t)$: RE λ(BACI: Trt + T, Trt)	0.878	0.070	0.741	1.015	0.119	0.000	0.559	−12.2%
GDR-TA [c]	$\phi(t)$ p(sex + t) $f(t)$: RE λ(BACI: Trt + T, Trt)	1.030	0.040	0.952	1.108	0.063	0.000	0.321	3.0%
Weighted mean for all study areas [d]		0.962	0.019	0.925	0.999				−3.8%

[a] See Table 2 for study area codes.
[b] Best Random Effects (RE) model structure with time or sex effects from analyses of the a priori model set based on the best base model. Model notation indicates structure for effects of time (t), sex (sex), linear time trend (T), a spline (SPLINE, with knots every 5 yr backward from 2013), or constant (.) models. The best model for the GDR study area included a treatment effect (Trt) to distinguish areas where Barred Owl removal occurred, both before (1992–2008) and after (2009–2013) removals began (BACI).
[c] GDR-TB = treatment areas before Barred Owls were removed; GDR-CB = control areas before Barred Owls were removed in treatment areas; GDR-TA = treatment areas after Barred Owls were removed (2009–2013); GDR-CA = control areas after Barred Owls removed in treatment areas (2009–2013).
[d] Included GDR-CB and GDR-CA areas only.

territorial owls from all age classes (S1, S2, Adult; Table 2). We used a base model for random effects modeling that included general time effects on survival [$\phi(t)$] and lambda ($\lambda(t)$; Table 4) in all study areas except GDR, where the recruitment [$f(t)$] and lambda [$\lambda(t)$] parameterization was used to facilitate convergence. The best fixed effects structure for capture rates included annual time effects [$p(t)$] in 4 study areas (RAI, COA, CAS, and HUP), additive effects of sex and annual time [p(sex + t)] in 6 areas (CLE, HJA, TYE, KLA, NWC, and GDR; capture rates higher for males), and an interaction between sex and time [p(sex*t)] in 1 area (OLY).

The best random effects model for 7 of the 11 study areas included a negative linear time trend on λ (RE(T); Table 4), with 95% CIs of covariate coefficients widely overlapping 0 only for CLE and OLY (Figure 3), suggesting that annual rates of decline were increasing over time in many areas. The spline model [RE(SPLINE)] performed best for HJA and NWC, although the linear time trend model was also competitive for NWC, and the coefficient was negative with a 95% CI that did not overlap zero. The intercept-only model [RE(.)] received the most support for RAI and CAS.

Mean estimates of λ from the RE(.) models suggested declining population trends (i.e. $\hat{\lambda} < 1.0$) in almost all study areas, with strong evidence of declines in CLE, RAI, OLY, COA, HJA, NWC, HUP, GDR-CB, GDR-TB, and GDR-CA, and less evidence of declines in TYE, KLA, and CAS (Figure 4). The only estimate of λ that suggested an increasing population was observed in GDR treatment areas after Barred Owl removals began in 2009 (GDR-TA; $\hat{\lambda} = 1.03$), although the 95% CI widely overlapped 1.0. Estimated annual rates of decline were variable (Table 4), but were lowest in the GDR control areas before Barred Owl removals began in treatment areas in 2009 (1.2% annual decline), and highest in the CLE study area in Washington (8.4% annual decline) and in GDR control areas after 2009 (12.0% annual decline). The weighted mean estimate of λ for all study areas (excluding GDR-TB and GDR-TA) was 0.962 ± 0.019 (95% CI: 0.925 to 0.999), indicating an estimated decline of 3.8% per year across the range of the Northern Spotted Owl.

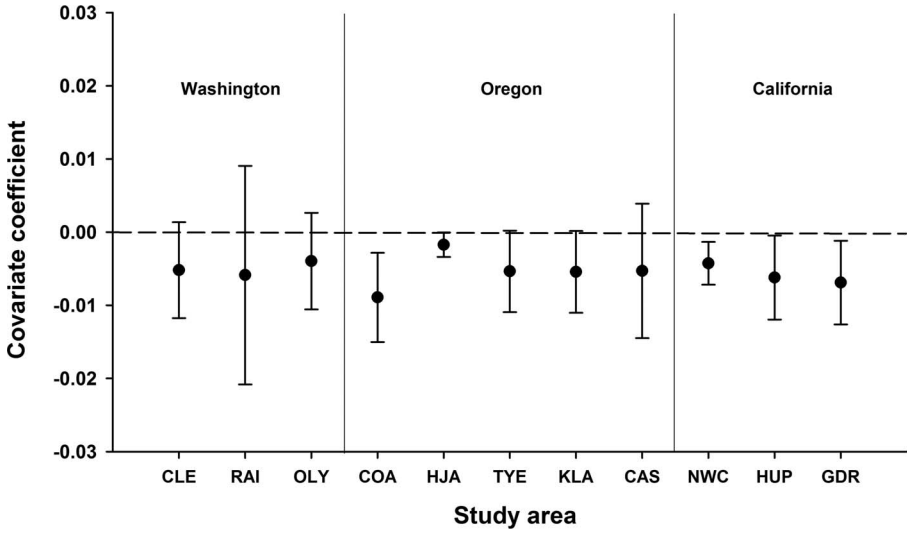

FIGURE 3. Estimates of covariate coefficients and 95% confidence intervals for the linear time trend (T) on λ from the best random effects model containing a linear time trend, for Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA. The estimate for the GDR study area represents the parallel (additive) trend on control and treatment areas before Barred Owl removals began (1990–2008). See Table 2 for study area abbreviations.

Realized population change. Our estimates of realized population change indicated that populations in Washington declined by 55–77% (Figure 5A). Declines in Oregon were more variable, ranging from 31% in TYE to 68% in COA (Figure 5B), and in 2 cases (KLA and TYE) the 95% CIs for realized population change widely overlapped 1.0 for most or all of the last several years, indicating uncertainty about annual rates of population change for these areas. In California, declines ranged from 32% to 55%, except in the treatment areas of GDR (GDR-T), where the estimated overall population decline was only 9% (Figure 5C). Realized population change estimates

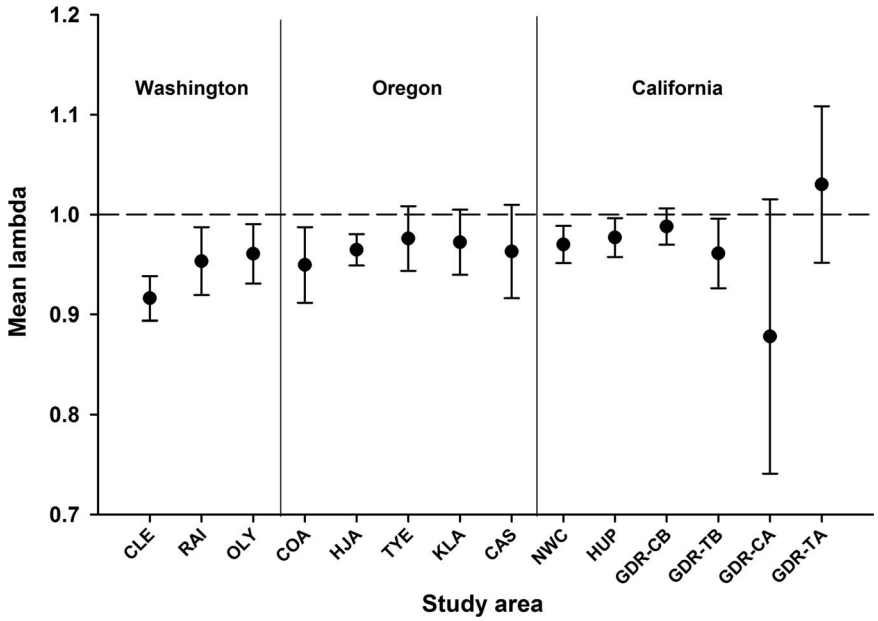

FIGURE 4. Estimated mean rates of population change ($\hat{\lambda}$) and 95% confidence intervals for Northern Spotted Owls from the random effects (RE) intercept-only model [RE λ(.)] in each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Estimates for the GDR study area are presented separately for control and treatment areas before (1990–2008) and after (2009–2013) Barred Owls were removed (GDR-CB = control before removal, GDR-TB = treatment before removal, GDR-CA = control after removal, GDR-TA = treatment after removal). See Table 2 for study area abbreviations.

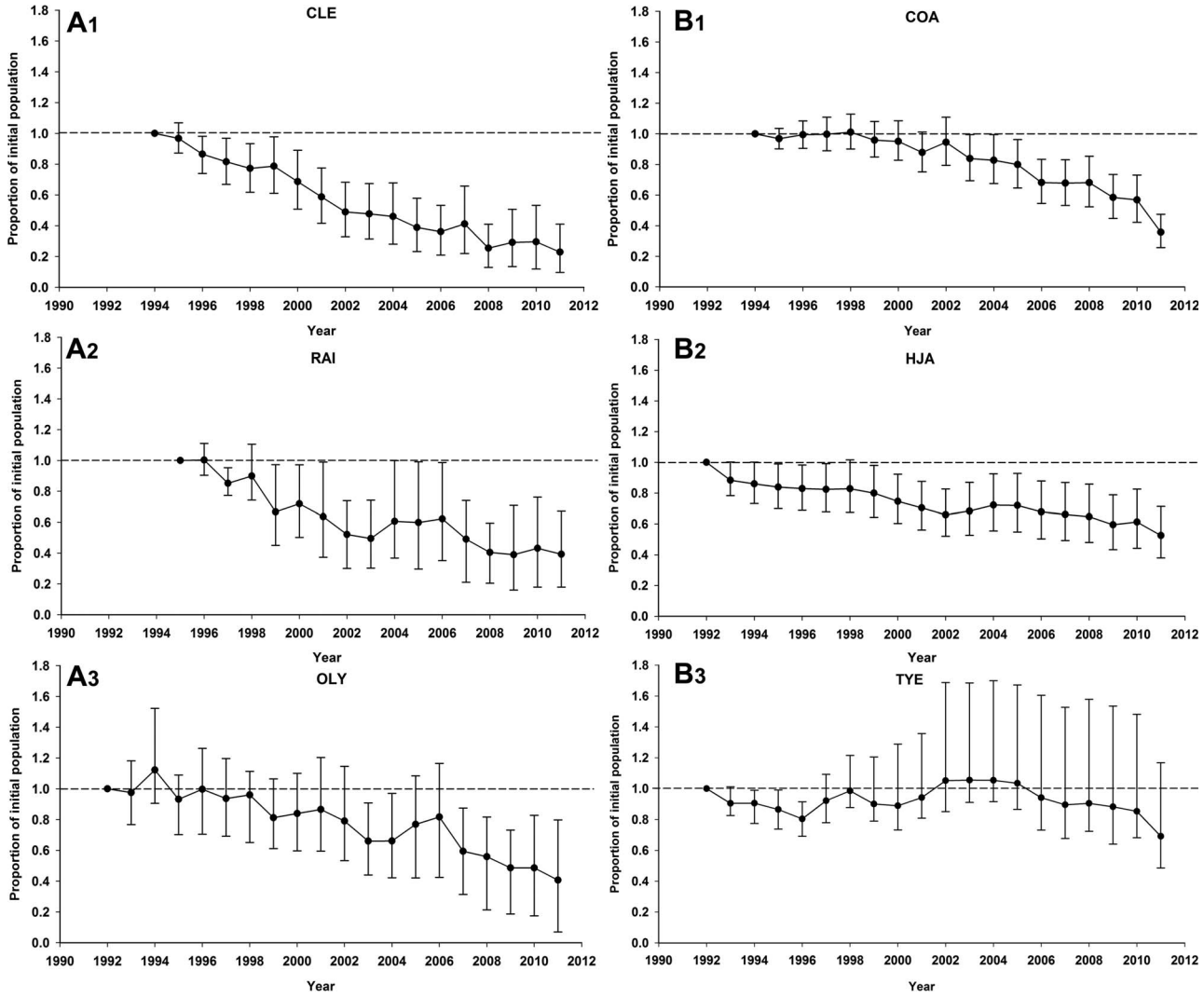

FIGURE 5. Annual estimates of realized population change (Δ_t) with 95% confidence intervals for Northern Spotted Owls at (**A**) 3 study areas in Washington, (**B**) 5 study areas in Oregon, and (**C**) 3 study areas in California, USA. Estimates for the GDR study area are presented separately for control and treatment areas in relation to Barred Owl removals beginning in 2009. See Table 2 for study area abbreviations.

for HUP and GDR-T included confidence limits that overlapped 1.0 in many years, indicating uncertainty about annual rates of population change in these areas.

Meta-analysis of annual rate of population change: recruitment. As described above, we focused the meta-analysis of population change on recruitment parameterization, in which λ was written as the sum of apparent survival and recruitment rate. The fixed effects model on which all random effects models for recruitment were based included area by year interactions on survival, capture probabilities, and recruitment [ϕ(Area*t) p(Area*t) f(Area*t)]. The best random effects model had nearly all of the model weight and included interactions between total winter precipitation (WP) and mean winter minimum temperature (WMT; Table 5). As predicted, recruitment was negatively affected by WP as a main effect ($\hat{\beta}$ = –0.0003 ± 0.0001 SE, 95% CI: –0.0005 to –0.0001). However, contrary to our prediction, the main effect of WMT was also negatively related to recruitment rates ($\hat{\beta}$ = –0.0066 ± 0.0037 SE, 95% CI: –0.0140 to 0.0006), although the interaction between precipitation and temperature was positive ($\hat{\beta}$ = 0.0001 ± 0.0000 SE, 95% CI: –0.0000 to 0.0001). Thus, recruitment was highest when both total precipitation (29 cm) and mean minimum winter temperature (–9.5°C) were lowest, and higher WP resulted in lower recruitment rates when WMT was low (<4°C; Figure 6). When the total precipitation level was near its average for all years and study areas (112 cm), recruitment rates were nearly constant across the range of mean minimum temperatures.

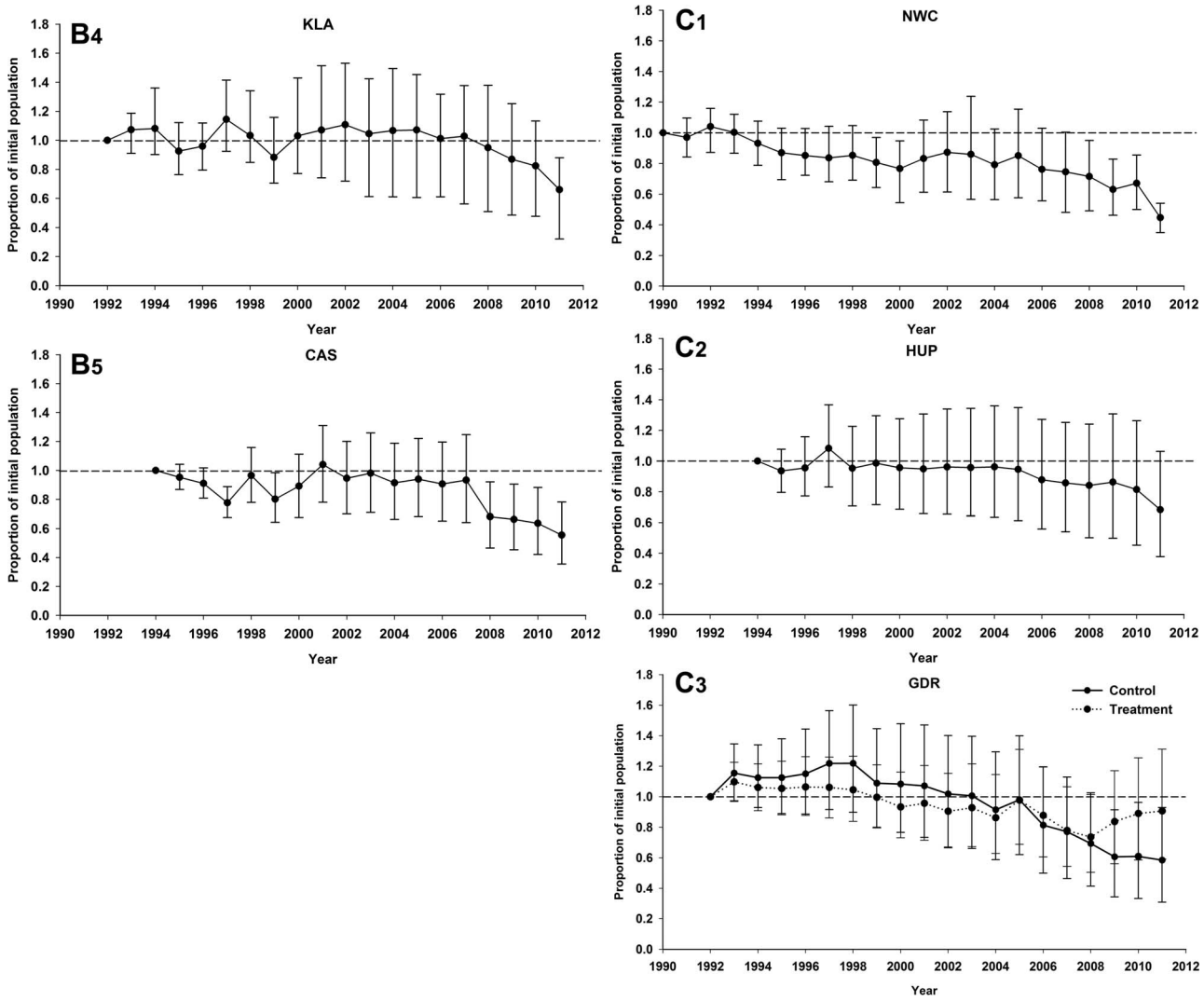

FIGURE 5. Continued.

Occupancy

Initial territory occupancy by Northern Spotted Owls was best modeled by territory-specific habitat covariates for 7 of the 11 study areas (OLY, COA, TYE, CAS, NWC, HUP, and GDR), and, in most cases, relationships were as predicted (Table 6). However, support for a relationship between initial occupancy and habitat was weak as the 95% CIs of habitat covariates widely overlapped 0 for all areas except NWC and TYE. For NWC, initial territory occupancy was negatively related to increasing amounts of edge habitat, whereas in TYE, more nesting and roosting habitat at the core scale resulted in higher rates of initial territory occupancy.

Colonization rates of Spotted Owl territories did not vary temporally or spatially in the RAI and HUP study areas, but strong evidence for negative trends in colonization rates was observed in CLE, HJA, and KLA, with less evidence for a negative trend observed in COA, where the 95% CI slightly overlapped 0 (Table 7A). In 5 of 11 areas (OLY, COA, TYE, KLA, and CAS) there was strong evidence that the presence of Barred Owls was negatively associated with Spotted Owl colonization rates, as 95% CIs did not overlap 0 in all 5 areas (Table 7A). Habitat characteristics were related to colonization rates of Spotted Owls in 9 of 11 areas (Table 6). Consistent with predictions, the total amount of suitable owl habitat was positively associated with Spotted Owl colonization rates in OLY, COA, TYE, CAS, and NWC, and the 95% CIs for these covariate coefficients did not overlap 0 in all cases, suggesting strong support for these relationships (Table 7A). Habitat disturbance (HD) was negatively associated with colonization rates in CLE and HJA, but the 95% CIs of the covariate coefficients slightly overlapped 0 in both cases, suggesting that these relationships were only weakly supported. EDGE was positively related to

TABLE 5. Model selection results from the meta-analysis of the finite rate of population change (λ) of adult Northern Spotted Owls in 11 demographic study areas in Washington, Oregon, and California, USA, 1994–2013. Random effects models (RE) of recruitment were run using a general fixed effects base model [ϕ(Area*t) p(Area*t) f(Area*t)] that included the interaction between study area (Area) and general time effects (t) on apparent survival (ϕ), capture probability (p), and recruitment (f). Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c). The model deviance (Deviance), number of parameters (K), difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), and Akaike model weights (w_i) are given for all models.

Random effects model [a]	ΔAIC_c	K	w_i	Deviance
RE f(WP*WMT)	0.00 [b]	657.94	0.997	14035.84
RE f(LAG1R + HD)	11.33	691.40	0.003	13975.98
RE f(.)	40.49	738.00	0.000	13905.61
RE f(WP + WMT)	55.37	685.30	0.000	14033.01
RE f(BO)	68.39	681.85	0.000	14053.37
RE f(BO + LAG1R)	82.60	697.80	0.000	14033.60
RE f(WP*WMT*L1WP)	86.28	702.00	0.000	14028.33
RE f(LAG2R)	86.57	699.47	0.000	14034.01
RE f(BO + LAG2R)	87.23	699.14	0.000	14035.37
RE f(HD)	88.66	694.48	0.000	14046.73
RE f(LAG1R)	89.48	702.14	0.000	14031.22
RE f(WP)	89.49	701.10	0.000	14033.45
RE f(LAG2R + HD)	90.51	701.70	0.000	14033.18
RE f(L1WMT + WP)	92.60	697.98	0.000	14043.21
RE f(EDGE)	95.06	700.60	0.000	14040.08
RE f(WMT)	95.40	699.23	0.000	14043.34
RE f(BO + HD)	96.58	698.96	0.000	14045.09
RE f(L1WP*L1WMT)	101.30	699.96	0.000	14047.69
RE f(CORE)	103.57	702.35	0.000	14044.86
RE f(L1WP)	105.07	701.80	0.000	14047.54
RE f(WP + WMT + L1WP)	112.09	700.47	0.000	14057.40
RE f(L1WMT)	117.06	701.74	0.000	14059.66
RE f(L1WP + L1WMT)	126.01	700.70	0.000	14070.82
RE f(PDO)	129.87	701.80	0.000	14072.33
RE f(HAB2)	148.06	699.87	0.000	14094.65

[a] Model notation indicates structure for the following: reproductive rate with 1 yr (LAG1R) and 2 yr (LAG2R) lags, proportion of territories with Barred Owl detections (BO), Pacific Decadal Oscillation (PDO), mean monthly minimum temperature during winter (WMT), 1-yr lag in mean monthly minimum temperature during winter (L1WMT), total precipitation during winter (WP), 1-yr lag in total precipitation during winter (L1WP), a neighborhood focal statistic that defines the number of 30 m^2 pixels with ≥50% suitable habitat within 800 m of each pixel in each owl site (CORE), the amount of interface between suitable habitat and other cover types within each owl site (EDGE), the percentage of suitable habitat that was disturbed (HD), and the estimated proportion of suitable owl habitat within a 23-km buffer distance of the study area boundaries (HAB2).

[b] The AIC_c of the top model = 59829.22.

Spotted Owl territory colonization rates in KLA and GDR, but the 95% CI for this covariate coefficient slightly overlapped 0 for GDR, suggesting weaker support for a relationship in this area (Table 7A).

The most consistent pattern in Northern Spotted Owl territory occupancy dynamics was the strong positive association between the presence of Barred Owls and territory extinction rates of Spotted Owls in all 11 study areas (Table 6, Figure 7), with 95% CIs of covariate coefficients not overlapping 0 in 10 cases (CLE, OLY, COA, HJA, TYE, KLA, CAS, NWC, HUP, and GDR), and only slightly overlapping 0 for RAI (Table 7B). As predicted, extinction rates were higher in all areas when Barred Owls were present (Figure 7). Habitat covariates also were associated with territory extinction rates of Spotted Owls in 8 of 11 study areas. Lower territory extinction rates of Spotted Owls were associated with higher amounts (HABa; RAI, OLY, HJA, and CAS) and greater proportions (HABp; COA) of nesting and roosting habitat in each territory, or higher amounts of nesting and roosting habitat at the core scale (CORE; KLA and NWC). However, the 95% CIs of habitat covariate coefficients slightly overlapped 0 for OLY, COA, and CAS, suggesting weaker support for habitat effects in these areas. In the GDR study area, more core habitat was associated with increased Spotted Owl extinction rates (95% CI of covariate coefficient did not overlap 0), which was contrary to general predictions. However, this was possibly consistent with the best structure for initial occupancy and colonization rates, which suggested that habitat heterogeneity was important in the GDR area. Strong evidence for positive time trends in Spotted Owl territory extinction rates was observed in 4 study areas (RAI, OLY, NWC, and HUP), as the 95% CIs on the trend coefficients for these areas did not overlap 0.

Based on models incorporating the best structure for initial occupancy, extinction, and colonization rates (Table 8), our derived estimates showed that time-specific territory occupancy rates for Spotted Owls were declining in all study areas (Figure 8). In Washington, occupancy rates for Northern Spotted Owls declined from 56–100% in 1995 to 11–26% in 2013. During this same time period, Northern Spotted Owl territory occupancy rates in Oregon declined from 61–88% in 1995 to 28–48% in 2013. In California, Spotted Owl occupancy rates declined from 75% to 38% in NWC and from 79% to 47% in HUP between 1995 and 2013. In the control areas in the GDR study area, occupancy rates declined from 92% in 1999 to 55% in 2013.

Fecundity

Individual study areas. We estimated fecundity using 12,969 records in which we determined the number of young produced by territorial females of known age, 91% of which were females ≥3 years old (i.e. adults; Table 9). Female age was an important factor affecting fecundity in all study areas, with mean fecundity generally lowest for 1-yr-olds, intermediate for 2-yr-olds, and highest for adults. In most study areas, the mean annual fecundity of

TABLE 6. Model selection results, including the difference from the top model in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c), number of parameters (K), model deviance (Deviance), and AIC_c weights (w_i), for competitive models (≤ 2 AIC_c) from the analysis of occupancy dynamics of Northern Spotted Owls and Barred Owls in 11 demographic study areas in Washington, Oregon, and California, USA, during 1994–2013. Model parameter structure and direction of effect are presented for initial occupancy ($\hat{\psi}_1$), colonization ($\hat{\gamma}_i$), extinction ($\hat{\varepsilon}_i$), and detection ($\hat{p}_{ij}$) probabilities, with matching model numbers within a study area reflecting (**A**) Northern Spotted Owl, and (**B**) Barred Owl components for specific models. See Table 2 for study area codes.

Study area	Model [a]	$\hat{\psi}_1$	$\hat{\gamma}$	$\hat{\varepsilon}$	$\hat{p}$	ΔAIC_c [b]	K	Deviance	w_i
(**A**) Northern Spotted Owl									
Washington									
CLE	1	.	T(−), HD(−)	bo(+)	*j*, TR(+), bo(−)	0.0	27	4861.84	0.64
	2	.	T(−), HD(−)	bo(+)	*j*, TR(+), bo(−)	1.2	27	4863.02	0.36
RAI	1	.	.	T(+), HABa(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.0	46	4889.11	0.81
OLY	1	EDGE(−)	HABa(+), bo(−)	T(+), HABa(−), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.0	50	8892.09	0.45
	2	EDGE(−)	HABa(+), bo(−)	T(+), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	1.1	49	8895.33	0.25
	3	.	HABa(+), bo(−)	T(+), HABa(−), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	1.5	49	8895.67	0.22
Oregon									
COA	1	HABa(+)	T(−), HABa(+), bo(−)	*t*, HABp(−), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.0	82	20357.77	0.24
	2	HABa(+)	T(−), HABa(+), bo(−)	*t*, HABp(−), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.5	81	20360.37	0.18
	3	HABa(+)	HABa(+), bo(−)	*t*, HABp(−), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.8	81	20360.68	0.16
	4	.	T(−), HABa(+), bo(−)	*t*, HABp(−), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	1.0	81	20360.85	0.15
	5	HABa(+)	T(−), HABa(+), bo(−)	*t*, HABp(−), bo(+)	*t*, *j*, TR(+), bo(−)	1.2	81	20361.10	0.13
	6	HABa(+)	T(−), HABa(+), bo(−)	*t*, bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	1.3	81	20361.22	0.12
HJA	1	.	T(−), HD(−)	HABa(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.0	78	18691.36	0.44
TYE	1	CORE(+)	*t*, HABa(+), bo(−)	T(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.0	96	17164.61	0.86
KLA	1	.	T(−), EDGE(+), bo(−)	CORE(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.0	63	14101.30	0.31
	2	.	T(−), EDGE(+), bo(−)	CORE(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.7	62	14104.09	0.22
	3	.	T(−), EDGE(+), bo(−)	EDGE(−), bo(+)	*t*, *j*, TR(+), bo(−)	1.5	63	14102.77	0.15
CAS	1	EDGE(−)	HABa(+), bo(−)	HABa(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.0	52	13906.31	0.28
	2	EDGE(−)	HABa(+), bo(−)	HABa(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.7	51	13909.05	0.20
	3	EDGE(−)	HABa(+), bo(−)	HABa(−), bo(+)	*t*, *j*, TR(+), bo(−)	0.8	51	13909.14	0.19
	4	EDGE(−)	HABa(+), bo(−)	bo(+)	*t*, *j*, TR(+), bo(−)	1.2	51	13909.55	0.16
	5	.	HABa(+), bo(−)	HABa(−), bo(+)	*t*, *j*, TR(+), bo(−)	1.7	51	13910.06	0.12
California									
NWC	1	EDGE(−), bo(+)	HABa(+)	T(+), CORE(−), bo(+)	*j*, TR(+), bo(−), BO(+)	0.0	35	6455.63	0.23
	2	EDGE(−), bo(+)	HABa(+)	T(+), CORE(−), bo(+)	*j*, TR(+), bo(−), BO(+)	0.6	34	6458.36	0.17
	3	EDGE(−), bo(+)	HABa(+)	T(+), CORE(−), bo(+)	*j*, TR(+), bo(−), BO(+)	0.9	34	6458.67	0.14
	4	EDGE(−), bo(+)	HABa(+)	T(+), CORE(−), bo(+)	*j*, TR(+), bo(−), BO(+)	2.0	34	6459.71	0.09
HUP	1	EDGE(−)	.	T(+), bo(+)	*j*, TR(+), bo(−)	0.0	40	7072.20	0.18
	2	EDGE(−)	.	T(+), bo(+)	*j*, TR(+), bo(−)	0.1	39	7074.44	0.18
	3	EDGE(−)	.	T(+), bo(+)	*j*, TR(+), bo(−)	0.6	40	7072.77	0.14
	4	EDGE(−)	.	T(+), bo(+)	*j*, TR(+), bo(−)	0.6	39	7074.96	0.14
	5	CORE(−)	.	T(+), bo(+)	*j*, TR(+), bo(−)	1.4	40	7073.57	0.09
	6	EDGE(−)	.	T(+), bo(+)	*j*, TR(+), bo(−)	1.7	39	7076.04	0.08
	7	EDGE(−)	.	bo(+)	*j*, TR(+), bo(−)	1.7	39	7076.09	0.08

TABLE 6. Continued.

Study area	Model [a]	$\hat{\psi}_1$	$\hat{\gamma}$	$\hat{\varepsilon}$	$\hat{p}$	ΔAIC_c [b]	K	Deviance	w_i
GDR	1	HD(+)	EDGE(+)	CORE(+), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.0	46	9762.76	0.27
	2	HD(+)	EDGE(+)	CORE(+), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.6	45	9765.44	0.20
	3	HD(+)	EDGE(+)	CORE(+), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	0.9	46	9763.71	0.17
	4	HD(+)	EDGE(+)	CORE(+), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	1.3	45	9766.12	0.15
	5	HD(+)	EDGE(+)	HABa(+), bo(+)	*t*, *j*, TR(+), bo(−), BO(−)	1.5	46	9764.22	0.13
(**B**) Barred Owl									
Washington									
CLE	1	.	HD(−)	HABa(−), nso(+)	TR(−)				
	2	.	HD(−)	HD(+), nso(+)	TR(−)				
RAI	1	.	.	HABa(−), nso(+)	T(+), nso(−)				
OLY	1	.	HABa(+)	nso(+)	T(+), nso(−)				
	2	.	HABa(+)	nso(+)	T(+), nso(−)				
	3	.	HABa(+)	nso(+)	T(+), nso(−)				
Oregon									
COA	1	.	T(+), HD(−)	T(−), EDGE(−), nso(+)	T(+), *j*, TR(−), NSO(−)				
	2	.	T(+)	T(−), EDGE(−), nso(+)	T(+), *j*, TR(−), NSO(−)				
	3	.	T(+), HD(−)	T(−), EDGE(−), nso(+)	T(+), *j*, TR(−), NSO(−)				
	4	.	T(+), HD(−)	T(−), EDGE(−), nso(+)	T(+), *j*, TR(−), NSO(−)				
	5	.	T(+), HD(−)	T(−), EDGE(−), nso(+)	T(+), *j*, TR(−), NSO(−)				
	6	.	T(+), HD(−)	T(−), EDGE(−), nso(+)	T(+), *j*, TR(−), NSO(−)				
HJA	1	.	T(+), nso(+)	HABp(−), nso(+)	*t*, *j*, TR(−), nso(−)				
TYE	1	.	T(+), HABa(+)	T(−), HABa(−), nso(+)	*t*, *j*, TR(−)				
KLA	1	.	T(+), HABp(+), nso(−)	T(−), nso(+)	T(−), *j*, TR(−), nso(−)				
	2	.	T(+), HABp(+)	T(−), nso(+)	T(−), *j*, TR(−), nso(−)				
	3	.	T(+), HABp(+), nso(−)	T(−), nso(+)	T(−), *j*, TR(−), nso(−)				
CAS	1	.	T(+), EDGE(−), nso(+)	T(−), HABa(−), nso(+)	T, TR(−)				
	2	.	T(+), EDGE(−), nso(+)	HABa(−), nso(+)	T, TR(−)				
	3	.	T(+), EDGE(−)	T(−), HABa(−), nso(+)	T, TR(−)				
	4	.	T(+), EDGE(−), nso(+)	T(−), HABa(−), nso(+)	T, TR(−)				
	5	.	T(+), EDGE(−), nso(+)	T(−), HABa(−), nso(+)	T, TR(−)				
California									
NWC	1	.	T(+), nso(+)	HD(+), nso(+)	T(+), TR(+), nso(−)				
	2	.	T(+), nso(+)	HD(+), nso(+)	TR(+), nso(−)				
	3	.	T(+), nso(+)	HD(+)	T(+), TR(+), nso(−)				
	4	.	T(+), nso(+)	nso(+)	T(+), TR(+), nso(−)				
HUP	1	.	T(+), EDGE(+)	T(+), HABa(−), nso(+)	*j*				
	2	.	T(+), EDGE(+)	HABa(−), nso(+)	*j*				

TABLE 6. Continued.

Study area	Model [a]	$\hat{\psi}_1$	$\hat{\gamma}$	$\hat{\varepsilon}$	$\hat{p}$	ΔAIC_c [b]	K	Deviance	w_i
	3	.	T(+), HD(−)	T(+), HABa(−), nso(+)	*j*				
	4	.	T(+), EDGE(+)	T(+), nso(+)	*j*				
	5	.	T(+), EDGE(+)	T(+), HABa(−), nso(+)	*j*				
	6	.	T(+), EDGE(+)	T(+), HABa(−)	*j*				
	7	.	T(+), EDGE(+)	T(+), HABa(−), nso(+)	*j*				
GDR	1	.	T(+), EDGE(−)	HABa(+), nso(+)	T(+)				
	2	.	T(+), EDGE(−)	nso(+)	T(+)				
	3	.	T(+), HD(−)	HABa(+), nso(+)	T(+)				
	4	.	T(+)	HABa(+), nso(+)	T(+)				
	5	.	T(+), EDGE(−)	HABa(+), nso(+)	T(+)				

[a] Model notation indicates the following parameter structures and the direction of the effect if appropriate: linear time trend (T), independent annual variation (*t*), the effect of Barred Owl presence on a territory (bo), the effect of Northern Spotted Owl presence on a territory (nso), the effect of Barred Owl detections during a survey (BO), the effect of Northern Spotted Owl detections during a survey (NSO), a detection response related to previous detection history within seasons (i.e. "trap response"; TR), differences in detection rates within seasons (*j*), the total area of suitable habitat within each owl site (HABa), the proportion of each owl site that contained suitable habitat (HABp), a neighborhood focal statistic that defined the number of 30 m^2 pixels with $\geq$50% suitable habitat within 800 m of each pixel in each owl site (CORE), the amount of interface between suitable habitat and other cover types within each owl site (EDGE), and the percentage of suitable habitat that was disturbed (HD).

[b] Lowest AIC_c value from top-ranking model for each study area: CLE = 4916.83; RAI = 4985.27; OLY = 8995.01; COA = 20526.07; HJA = 18851.46; TYE = 17362.77; KLA = 14230.38; CAS = 14012.13; NWC = 6527.87; HUP = 7155.04; and GDR = 9856.94.

adult females was between 0.18 and 0.34. The one notable exception was the CLE study area in Washington, where mean annual fecundity for adult females ($\bar{x}$ = 0.570 ± 0.045) was nearly twice as high as in any other area.

Female age was strongly associated with NYF and occurred in top or competitive models for all study areas (Table 10). However, there was considerable model uncertainty for other effects. Of the 11 study areas, 5 had top models or competitive models that included negative

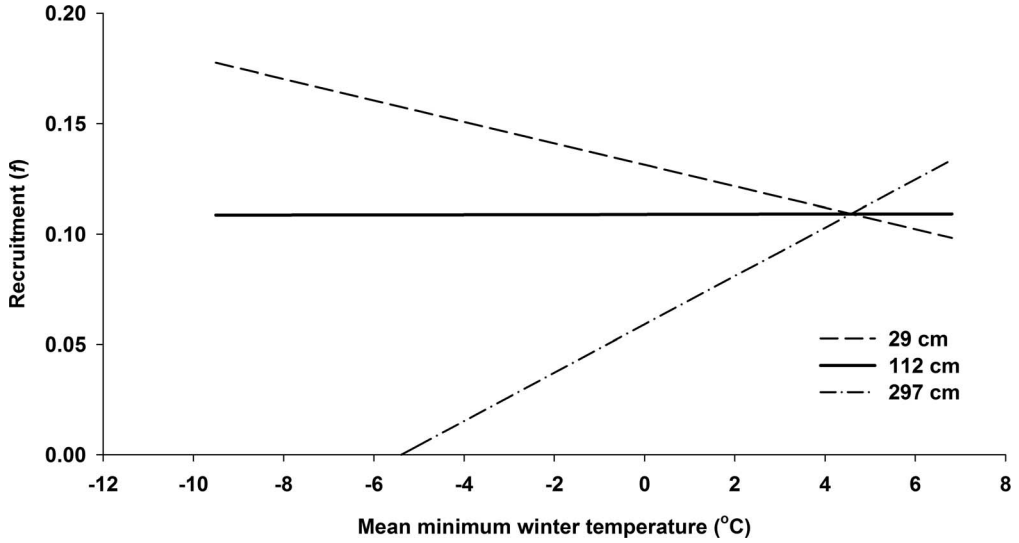

FIGURE 6. Predicted estimates of recruitment of Northern Spotted Owls from the best random-effects (RE) model from the meta-analysis of lambda, using the survival (ϕ), recruitment (*f*), and capture probability (*p*) parameterization with study area (Area) and general time (*t*) fixed effects [ϕ(Area*t*) *p*(Area*t*) *f*(Area*t*) RE *f*(WP*WMT)]. Estimates of recruitment are plotted across the range of mean minimum winter temperatures (WMT) from the data, for the minimum (29 cm), mean (112 cm), and maximum (297 cm) levels of total winter precipitation (WP) across all study areas and years.

TABLE 7. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) for best time trend, habitat, or Barred Owl model structure on (**A**) colonization ($\hat{\gamma}_i$), and (**B**) extinction ($\hat{\varepsilon}_i$) probabilities for Northern Spotted Owls from the analysis of occupancy dynamics of Northern Spotted Owls and Barred Owls in 11 demographic study areas in Washington, Oregon, and California, USA, during 1994–2013.

(**A**) Colonization ($\hat{\gamma}_i$)

Study area [a]	Best model [b]	$\hat{\gamma}_i$ effect	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	γ(T + HD), ε(bo)	T	−0.146	0.051	−0.245	−0.047
		HD	−1.156	0.852	−2.826	0.515
RAI	γ(.), ε(T + HABa + bo)	.				
OLY	γ(HABa + bo), ε(T + HABa + bo)	HABa	0.767	0.158	0.457	1.076
		bo	−1.256	0.543	−2.321	−0.191
Oregon						
COA	γ (T + HABa + bo), ε(*t* + HABp + bo)	T	−0.053	0.031	−0.114	0.008
		HABa	0.532	0.121	0.295	0.769
		bo	−0.882	0.343	−1.554	−0.211
HJA	γ(T + HD), ε(HABa + bo)	T	−0.068	0.033	−0.133	−0.004
		HD	−3.802	2.798	−9.285	1.681
TYE	γ(*t* + HABa + bo), ε(T + bo)	HABa	0.761	0.148	0.471	1.052
		bo	−1.352	0.447	−2.228	−0.476
KLA	γ(T + EDGE + bo), ε(CORE + bo)	T	−0.053	0.023	−0.099	−0.008
		EDGE	0.309	0.115	0.084	0.535
		bo	−1.215	0.506	−2.208	−0.223
CAS	γ(HABa + bo), ε(HABa + bo)	HABa	0.433	0.149	0.142	0.725
		bo	−0.942	0.391	−1.708	−0.176
California						
NWC	γ(HABa), ε(T + CORE + bo)	HABa	0.562	0.246	0.081	1.043
HUP	γ(.), ε(T + bo)	.				
GDR	γ(EDGE), ε(CORE + bo)	EDGE	0.339	0.196	−0.044	0.722

(**B**) Extinction ($\hat{\varepsilon}_i$)

Study area [a]	Best model [b]	$\hat{\varepsilon}_i$ effect	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	γ(T + HD), ε(bo)	bo	1.022	0.449	0.142	1.902
RAI	γ(.), ε(T + HABa + bo)	T	0.093	0.043	0.009	0.176
		HABa	−0.732	0.254	−1.229	−0.235
		bo	2.556	1.488	−0.360	5.472
OLY	γ(HABa + bo), ε(T + HABa + bo)	T	0.106	0.033	0.040	0.171
		HABa	−0.337	0.199	−0.726	0.052
		bo	1.526	0.450	0.644	2.409
Oregon						
COA	γ(T + HABa + bo), ε(*t* + HABp + bo)	HABp	−0.185	0.101	−0.382	0.013
		bo	1.919	0.353	1.226	2.611
HJA	γ(T + HD), ε(HABa + bo)	HABa	−0.538	0.136	−0.804	−0.272
		bo	2.174	0.407	1.376	2.971
TYE	γ(*t* + HABa + bo), ε(T + bo)	T	−0.065	0.028	−0.121	−0.010
		bo	1.426	0.297	0.844	2.008
KLA	(T + EDGE + bo), ε(CORE + bo)	CORE	−0.270	0.105	−0.477	−0.063
		bo	1.102	0.380	0.357	1.846
CAS	γ(HABa + bo), ε(HABa + bo)	HABa	−0.283	0.164	−0.604	0.038
		bo	2.601	0.417	1.783	3.412
California						
NWC	γ(HABa), ε(T + CORE + bo)	T	0.099	0.039	0.022	0.175
		CORE	−0.398	0.149	−0.690	−0.106
		bo	0.914	0.422	0.086	1.742
HUP	γ(.), ε(T + bo)	T	0.071	0.037	−0.002	0.143
		bo	1.318	0.392	0.550	2.085
GDR	(EDGE), ε(CORE + bo)	CORE	0.279	0.140	0.004	0.553
		bo	1.959	0.450	1.076	2.842

[a] See Table 2 for study area codes.
[b] See Table 6 for model covariate notation.

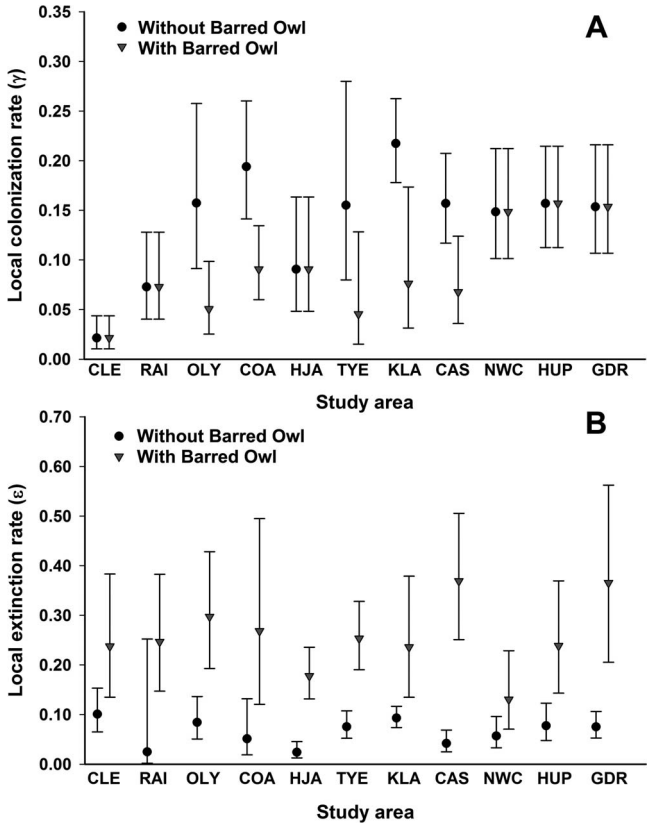

FIGURE 7. Mean (**A**) local colonization ($\hat{\gamma}$) and (**B**) extinction ($\hat{\varepsilon}$) rates with 95% confidence intervals for Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013, relative to when a territory was also occupied by Barred Owls (gray triangles) and when Barred Owls were not present (black circles). Estimates reflect mean values for other factors in the best model for each study area. Data from the Barred Owl removal treatment areas in the GDR study area were excluded after 2008, so that all study areas were comparable. See Table 2 for study area abbreviations.

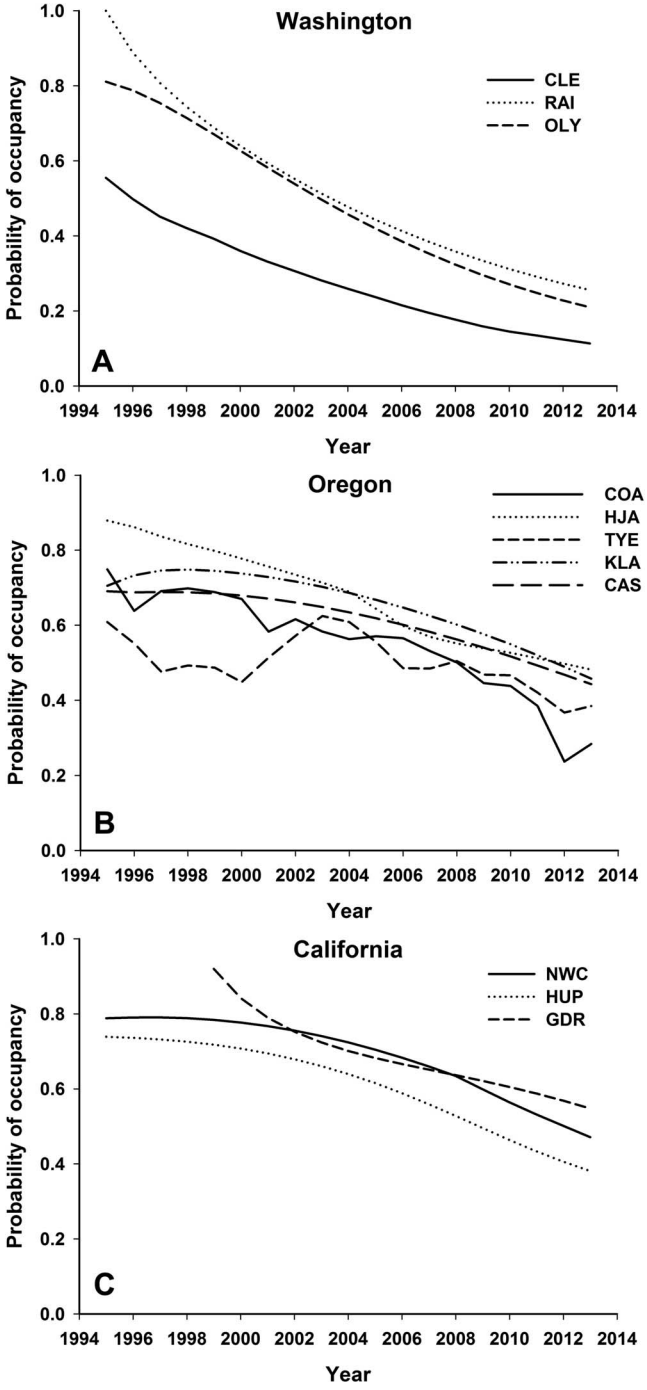

FIGURE 8. Estimates of the probability of territory occupancy for Northern Spotted Owls in 11 study areas in (**A**) Washington, (**B**) Oregon, and (**C**) California, USA. See Table 2 for study area abbreviations.

linear (T) or quadratic (TT) time trends on fecundity, including 1 area in Washington (CLE), 3 areas in Oregon (COA, HJA, and TYE), and 1 area in California (NWC; Table 10, 11). The 95% CIs for the covariate coefficients ($\hat{\beta}$) from these models excluded 0 for TYE and NWC, suggesting strong support for a declining trend in fecundity in these areas (Table 11). There was less support for declining trends in CLE, COA, and HJA, as 95% CIs slightly overlapped 0 for these study areas. Annual variation in fecundity was particularly high in study areas in Washington, which may have made it more difficult to detect trends in that region (Figure 9). For example, it was common for there to be years of no reproduction in the RAI and OLY study areas in Washington, whereas years with no reproduction were rare in study areas in Oregon, and were never observed in any of the California study areas.

Barred Owl presence (BO) was included in a top or competing fecundity model in only 2 of the 11 study areas (COA and KLA; Table 10, 12) and the relationship was negative, with 95% CIs for the covariate coefficients not

TABLE 8. Estimates of annual territory occupancy (Ψ_i), with standard errors (SE) and lower (LCL) and upper (UCL) confidence limits, for Northern Spotted Owls during the first year of the study (1999 for the GDR study area; 1995 for all other areas), and also the last year (2013), based on the best model parameter structure for initial occupancy ($\hat{\psi}_1$), colonization ($\hat{\gamma}_i$), extinction ($\hat{\varepsilon}_i$), and detection ($\hat{p}_{ij}$) probabilities in each of 11 study areas in Washington, Oregon and California, USA.

Study Area [a]	$\hat{\Psi}_{start}$	SE	LCL	UCL	$\hat{\Psi}_{2013}$	SE	LCL	UCL
Washington								
CLE	0.555	0.060	0.436	0.668	0.113	0.031	0.065	0.190
RAI	1.000	1.000	1.000	1.000	0.256	0.057	0.161	0.381
OLY	0.811	0.066	0.648	0.909	0.209	0.041	0.141	0.300
Oregon								
COA	0.749	0.050	0.640	0.834	0.284	0.039	0.214	0.366
HJA	0.879	0.043	0.769	0.941	0.482	0.049	0.388	0.577
TYE	0.609	0.065	0.477	0.726	0.384	0.054	0.285	0.495
KLA	0.705	0.061	0.574	0.810	0.457	0.037	0.386	0.530
CAS	0.691	0.056	0.572	0.788	0.443	0.035	0.377	0.511
California								
NWC	0.788	0.082	0.586	0.908	0.471	0.069	0.342	0.605
HUP	0.739	0.082	0.553	0.867	0.381	0.051	0.287	0.484
GDR [b]	0.920	0.065	0.669	0.985	0.548	0.042	0.466	0.628

[a] See Table 2 for study area codes.
[b] Data from the GDR study area excluded the Barred Owl removal treatment areas after 2008 so that results were comparable with other study areas.

overlapping 0 in both cases. It is important to note that the proportion of each study area occupied by Barred Owls gradually increased over time (Appendix C Figure 13), so the temporal effect and BO effect were highly correlated and not easily separated. This may explain the lack of effect (or counterintuitive effect) of Barred Owls on fecundity in some areas.

Habitat covariates (HAB and CORE) were included in the top or competitive models for fecundity in 7 study areas (CLE, COA, HJA, TYE, CAS, NWC, GDR, GDR-C, and GDR-T; Table 10, 13). More nesting and roosting habitat (HAB or CORE) was associated with higher NYF in these areas; however, only in TYE, NWC, GDR, and GDR-C did the 95% CIs for covariate coefficients not

TABLE 9. Estimates of means ($\bar{x}$) with standard errors (SE) of age-specific fecundity (number of female young produced per female per year) of Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013.

		1-yr-old (S1)			2-yr-old (S2)			≥3-yr-old (Adult)		
Study area [a]	Years	n [b]	$\bar{x}$	SE	n [b]	$\bar{x}$	SE	n [b]	$\bar{x}$	SE
Washington										
CLE	1989–2013	26	0.107	0.077	37	0.506	0.100	519	0.570	0.045
RAI	1992–2013	7	0.083	0.083	12	0.100	0.100	316	0.264	0.055
OLY	1990–2013	4	0.250	0.250	16	0.292	0.126	726	0.294	0.056
Oregon										
COA	1990–2013	24	0.000	0.000	60	0.060	0.026	1,611	0.223	0.036
HJA	1990–2013	13	0.000	0.000	45	0.103	0.040	1,388	0.288	0.037
TYE	1990–2013	65	0.016	0.011	92	0.229	0.061	1,112	0.263	0.032
KLA	1990–2013	93	0.048	0.021	139	0.257	0.044	1,427	0.335	0.032
CAS	1991–2013	37	0.042	0.032	56	0.132	0.044	1,235	0.323	0.046
California										
NWC	1985–2013	76	0.080	0.049	100	0.140	0.036	1,240	0.315	0.024
HUP	1992–2013	21	0.000	0.000	28	0.067	0.045	446	0.223	0.032
GDR-CB [a]	1990–2008	39	0.109	0.043	72	0.088	0.032	870	0.302	0.034
GDR-TB [a]	1990-2008	30	0.039	0.026	54	0.126	0.064	595	0.308	0.030
GDR-CA [a]	2009–2013	1	0.000	0.000	2	0.000	0.000	94	0.182	0.080
GDR-TA [a]	2009–2013	6	0.000	0.000	23	0.063	0.063	212	0.212	0.050
Mean fecundity [c]			0.065	0.022		0.175	0.039		0.309	0.027

[a] See Table 2 for general study area codes and Table 4 for GDR study area notation.
[b] Total number of cases sampled in each age class.
[c] Mean fecundity by age class excludes means for GDR-CA and GDR-TA in 2009–2013.

TABLE 10. Model selection results for models with $\Delta AIC_c < 2$ from the analysis of mean age-specific number of young fledged per year per female (NYF) for Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c), and the difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), the number of parameters (K), Akaike weight (w_i), and model deviance ($-2\log L$) are included for each candidate model.

Study area [a]	Model [b]	ΔAIC_c [c]	K	w_i	$-2\log L$
Washington					
CLE	A + AR(1)	0.00	5	0.09	100.00
	A + ENT	1.44	5	0.04	101.44
	A + T + AR(1)	1.72	6	0.04	99.22
	A + AR(1) + HAB	1.78	6	0.04	99.28
RAI	A + EO + ENT*ENP	0.00	8	0.28	27.51
	A + ENT*ENP	0.55	7	0.21	31.29
OLY	EO	0.00	3	0.16	65.10
	A + EO + SOI	1.86	6	0.06	59.08
	A + EO	1.89	5	0.06	61.90
Oregon					
COA	A + TT + EO + AR(1)	0.00	8	0.09	−17.36
	A + EO + BO	0.71	6	0.06	−11.20
	A + EO + HAB + Y09S	1.33	7	0.05	−13.24
	A + EO + T	1.44	6	0.04	−10.47
	A + EO + HAB + Y09P	1.47	7	0.04	−13.11
	A + EO + T + Y09S	1.70	7	0.04	−12.87
	A + EO + T + Y09P	1.99	7	0.03	−12.59
HJA	A*EO	0.00	7	0.09	−1.48
	A*EO + HAB	0.88	8	0.06	−3.40
	A + EO + ENT	1.19	6	0.05	2.39
	A + EO + LNP	1.43	6	0.04	2.64
	A*EO + T	1.50	8	0.04	−2.78
	A + EO	1.58	5	0.04	5.35
TYE	A + AR(1) + HAB	0.00	6	0.25	35.51
	A + T + AR(1)	0.09	6	0.24	35.60
	A + TT + AR(1)	1.21	7	0.14	34.21
KLA	A + LNP*BO	0.00	7	0.13	11.89
	A + APL1*BO	1.32	7	0.07	13.20
	A + EO + BO	1.35	6	0.07	15.73
CAS	A + EO + ENT	0.00	6	0.15	22.31
	A + EO + ENT + CORE	0.04	7	0.14	19.76
	A + EO + ENT + HAB	0.11	7	0.14	19.83
	A + EO + ENT + ENP	1.78	7	0.06	21.50
California					
NWC	A + HAB + WMT + WP	0.00	7	0.06	35.62
	A + HAB + WMT*WP	0.61	8	0.04	33.73
	A + HAB	0.99	5	0.04	41.40
	A + HAB + ENP	1.06	6	0.04	39.11
	A + HAB + SOI	1.32	6	0.03	39.38
	A*EO + HAB	1.68	8	0.03	34.80
	A + T	1.80	5	0.02	42.21
HUP	A + ENT*ENP	0.00	7	0.15	−4.37
	A + ENT + ENP	0.78	6	0.10	−0.91
GDR [d]	A + EO + WP + CORE	0.00	7	0.12	−23.60
	A + EO + CORE + WMT + WP	0.17	8	0.11	−26.00
	A + EO + WP + HAB	0.23	7	0.11	−23.37
	A + EO + HAB + WMT + WP	0.50	8	0.10	−25.67
GDR-C [e]	A + EO + WP + CORE	0.00	7	0.25	−8.46
	A + EO + WP + HAB	0.36	7	0.21	−8.11
GDR-T [f]	A + EO + WMT + WP	0.00	7	0.10	16.50
	A + EO + WP	0.15	6	0.09	19.21
	A + EO + HAB + WMT + WP	1.13	8	0.06	14.98
	A + EO + CORE + WMT + WP	1.13	8	0.06	14.98
	A + EO + EDGE + WMT + WP	1.58	8	0.04	15.42
	A + EO + WP + HAB	1.69	7	0.04	18.19

TABLE 10. Continued.

Study area [a]	Model [b]	ΔAIC_c [c]	K	w_i	$-2\log L$
	A + EO + WP + CORE	1.71	7	0.04	18.22

[a] See Table 2 for general study area codes.
[b] Model notation indicates structure for the effects of owl age (A), even–odd year variation (EO), linear time trend (T), quadratic time trend (TT), autoregressive time trend (AR(1)), a time step in which fecundity experienced a sudden change in 2009 (Y09S), a "broken stick" time effect in which fecundity experienced a gradual change beginning in 2009 (Y09P), total annual precipitation from the previous year (APL1), proportion of territories with Barred Owl detections (BO), southern oscillation index (SOI), mean monthly minimum temperature during the early nesting season (ENT), total precipitation during the early nesting season (ENP), total precipitation during the late nesting season (LNP), mean monthly minimum temperature during winter (WMT), total precipitation during winter (WP), percent cover of suitable owl habitat (HAB), a neighborhood focal statistic that defined the number of 30 m^2 pixels with $\geq$50% suitable habitat within 800 m of each pixel in each owl site (CORE), and the amount of interface between suitable habitat and other cover types within each owl site (EDGE).
[c] The AIC_c values for the top models were: CLE = 111.18, RAI = 48.47, OLY = 71.77, COA = 1.91, HJA = 15.07, TYE = 48.96, KLA = 27.78, CAS = 35.96, NWC = 51.27, HUP = 12.18, GDR = −7.73, GDR-C = 7.65, and GDR-T = 32.62.
[d] Estimates based on all Spotted Owl territories.
[e] Estimates based only on Spotted Owl territories within control areas where Barred Owls were not removed.
[f] Estimates based only on Spotted Owl territories within treatment areas where Barred Owls were removed.

overlap 0, suggesting that there was little support for strong associations between habitat and NYF in most study areas (Table 13).

Climate covariates occurred in competitive models for 8 of 11 study areas (Table 10, 14), but the best covariate and the direction of the effect varied among areas (Table 14). For example, the effect of mean monthly minimum temperature during the early nesting season (ENT) occurred in the best model or a competitive model for 5 areas (CLE, RAI, HJA, CAS, and HUP), but the effect was positive in 3 areas (CLE, HJA, and CAS) and negative in 2 others (RAI and HUP; Table 14), with 95% CIs that did not overlap 0 for CLE, CAS, and HUP. Precipitation during the early nesting season (ENP) occurred in competitive models

TABLE 11. Best model containing a linear (T), quadratic (TT), or autoregressive (AR(1)) time effect on the mean annual number of young fledged per adult female Northern Spotted Owl (NYF) in each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors, and 95% confidence limits (lower: LCL; upper: UCL) are presented for the linear and/or quadratic term in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	A + T + AR(1)	1.72	−0.004	0.004	−0.013	0.005
RAI	A + EO + T	8.37	−0.002	0.006	−0.015	0.011
OLY	A + EO + T	4.57	−0.005	0.006	−0.017	0.006
Oregon						
COA	A + TT [d] + EO + AR(1)	0.00	−0.002	0.004	−0.010	0.007
			−0.000	0.000	−0.001	0.000
HJA	A*EO + T	1.50	−0.003	0.002	−0.008	0.002
TYE	A + T + AR(1)	0.09	−0.009	0.002	−0.013	−0.004
KLA	A + EO + TT [d] + HAB	2.06	0.028	0.014	−0.001	0.057
			−0.001	0.000	−0.002	−0.001
CAS	A + TT [d] + EO + AR(1) + HAB	2.86	0.009	0.007	−0.006	0.024
			0.001	0.000	0.000	0.001
California						
NWC	A + T	1.80	−0.009	0.002	−0.013	−0.004
HUP	A + EO + HAB + T09P	5.52	–0.068	0.026	–0.120	–0.015
GDR	A + EO + T	2.60	−0.006	0.002	−0.010	−0.002
GDR-C	A + EO + T	6.10	−0.012	0.002	−0.016	−0.007
GDR-T	A + EO + T + HAB	3.60	−0.048	0.027	−0.102	0.005

[a] See Table 2 for general study area codes and Table 10 for GDR study area notation.
[b] See Table 10 for model covariate notation.
[c] See Table 10 for model AIC_c values.
[d] The first estimate is the linear term, and the second is the quadratic term.

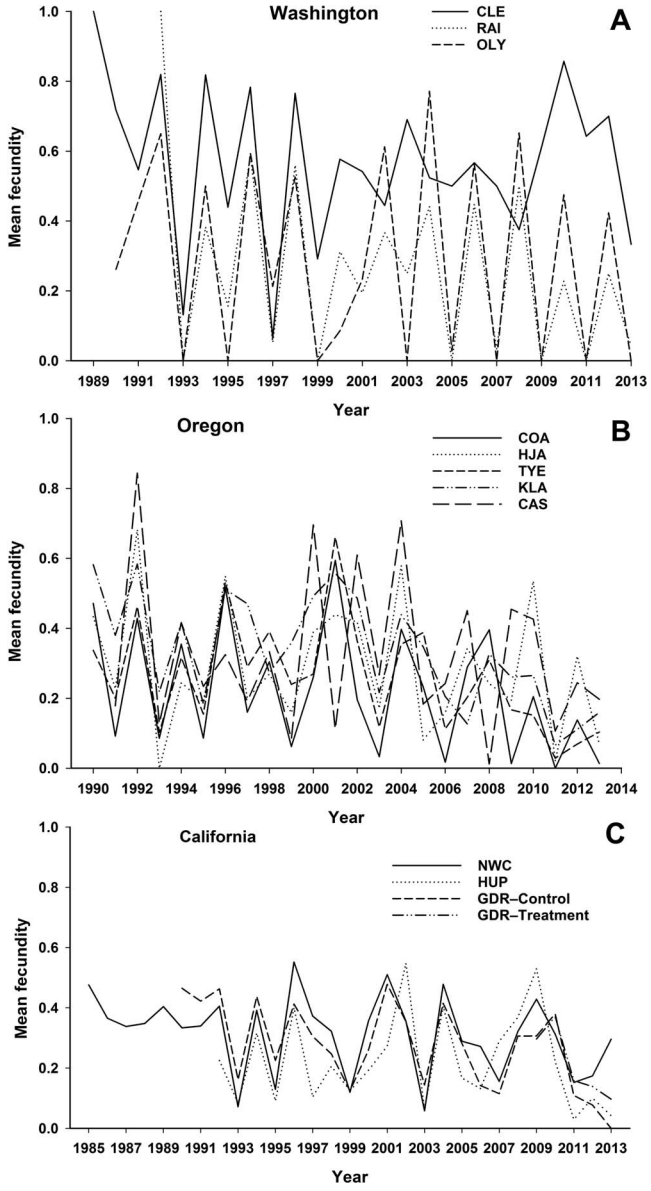

FIGURE 9. Annual fluctuations in mean fecundity (number of female young fledged per female) of Northern Spotted Owls in (**A**) 3 study areas in Washington, (**B**) 5 study areas in Oregon, and (**C**) 3 study areas in California, USA. Mean fecundity was graphed separately for the areas within the Green Diamond (GDR) study area where Barred Owls were removed (2009–2013; GDR–Treatment) and where Barred Owls were not removed (1990–2013; GDR–Control). See Table 2 for study area abbreviations.

for only 2 study areas (RAI and HUP), and in both areas ENP interacted with ENT. The 95% CIs around the ENP covariate coefficients excluded or slightly overlapped 0 in both cases, and the association was negative (as predicted) in 1 area (HUP), but positive in the other (RAI). Precipitation during the late nesting season (LNP) was included in a best or competitive model for only 1 study area (KLA), where it occurred as an interaction with the presence of Barred Owls, and where the 95% CI for the effect of LNP did not overlap 0. Mean minimum winter temperature (WMT) and total winter precipitation (WP) were included in top or competitive models for only 2 study areas (NWC and GDR). In both cases, higher minimum temperatures during winter were associated with higher fecundity, and more winter precipitation was associated with lower fecundity, but all 95% CIs for the WMT and WP covariate coefficients overlapped 0, except for the effects of WMT in the Barred Owl treatment areas in the GDR study area. The Southern Oscillation Index (SOI) occurred in a competitive model for only 1 study area (OLY), where the 95% CI around the covariate coefficient slightly overlapped 0, suggesting weak support for this effect (Table 10, 14).

Estimation of spatial (site-to-site), temporal (year-to-year), and residual variance in the territory-specific data indicated that the proportion of variance in NYF attributable to territories (spatial variance) was generally low (<6%; Table 15). The proportion of variance attributable to fluctuations over time (temporal variance) ranged from 5% to 20%, while the proportion of unexplained variation (residual variance) was generally high (>77%). As a consequence, the variation in NYF that was able to be explained by time and territory was overwhelmed by unexplained residual variation (i.e. other factors not considered).

Meta-analysis of fecundity. The meta-analysis of fecundity produced 6 competitive models, all of which included the additive effects of region and time (Table 16). These models all suggested that fecundity varied by time, and was parallel across regions (Figure 10). A linear time trend (T) in fecundity was not supported because of the complex pattern in fecundity over time that resulted due to the dissipation of the even–odd year effect in most study areas after about 1999. Model weights were fairly evenly distributed among the 6 competitive models, but the 2 models with the highest model weights were a model that included the negative effect of core habitat (CORE; $\hat{\beta} = -0.14$, 95% CI: –0.25 to –0.02), and a model that included the additive negative effects of Barred Owls (BO; $\hat{\beta} = -0.14$, 95% CI: –0.30 to 0.01) and the amount of edge habitat (EDGE; $\hat{\beta} = -0.60$, 95% CI: –1.20 to 0.00; Table 16). Three other competitive models included 1 or more of these 3 covariates (CORE, BO, EDGE), and the amount of nesting and roosting habitat (HAB; $\hat{\beta} = -0.23$, 95% CI: –0.46 to 0.01) was also included in a competitive model. However, only for core habitat did the 95% CI for the covariate coefficient not overlap 0, although this relationship suggested that more core habitat was associated with decreased fecundity, contrary to predictions. None of the models that included the effects of land ownership, latitude, prey species richness, habitat

TABLE 12. Best model including the effect of Barred Owls (BO) on the mean annual number of young fledged per adult female Northern Spotted Owl (NYF) for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors, and 95% confidence limits (lower: LCL; upper: UCL) are included for the Barred Owl effect in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	A + ENT + BO	3.94	−0.038	0.791	−1.626	1.550
RAI	A + EO + BO	7.54	−0.325	0.240	−0.812	0.163
OLY	A + EO + BO	4.35	−0.139	0.243	−0.631	0.354
Oregon						
COA	A + EO + BO	0.71	−0.186	0.059	−0.305	−0.068
HJA	A + EO + BO	3.70	−0.081	0.122	−0.327	0.164
TYE	A + TT + BO + AR(1)	2.78	0.294	0.290	−0.289	0.876
KLA	A + LNP*BO [d]	0.00	−1.734	0.415	−2.564	−0.905
			0.095	0.038	0.020	0.170
CAS	A + TT + BO + AR(1) + HAB	7.22	0.482	0.573	−0.675	1.639
California						
NWC	A + BO + HAB	3.27	0.126	0.452	−0.775	1.027
HUP	A + ENT + BO	5.93	−0.083	0.102	−0.288	0.121
GDR	A + EO + BO + T	5.08	0.054	0.537	−1.019	1.128
GDR-C	A + WP + BO	7.85	−1.336	0.381	−2.100	−0.571
GDR-T	A + EO + BO	4.15	−0.668	0.401	−1.471	0.135

[a] See Table 2 for general study area codes and Table 10 for GDR study area notation.
[b] See Table 10 for model covariate notation.
[c] See Table 10 for model AIC_c values.
[d] First estimate is the main BO effect, second is the interactive effect of BO and LNP.

disturbance, or climate were competitive, indicating that these covariates did not explain variation in fecundity across the range of the Northern Spotted Owl. The region effect on fecundity (Figure 10) appeared to be largely related to the pattern previously described in the individual study area analysis (Table 9, Figure 9), in which the east slope of the Cascades in Washington (region: Washington mixed conifer; 1 study area: CLE) had much higher fecundity than all other areas (Figure 9, 10).

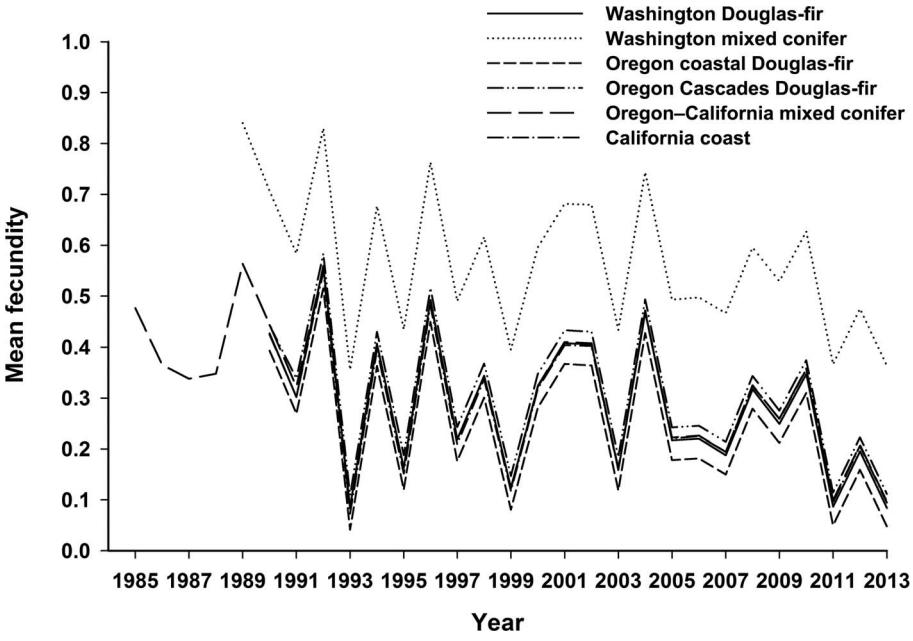

FIGURE 10. Annual fluctuations in mean fecundity (number of female young fledged per female) of Northern Spotted Owls in 6 geographic regions from the meta-analysis of 11 study areas in Washington, Oregon, and California, USA, 1985–2013.

TABLE 13. Best model containing the effect of habitat on the mean annual number of young fledged per adult female Northern Spotted Owl (NYF) for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients (β), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the habitat effect in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	A + AR(1) + HAB	1.78	1.183	1.411	−1.684	4.050
RAI	A + CORE + ENT*ENP	3.27	−2.484	3.460	−9.541	4.574
OLY	EO + HAB	2.47	−0.566	8.682	−18.160	17.024
Oregon						
COA	A + EO + HAB + Y09S	1.33	2.056	1.299	–0.558	4.669
HJA	A*EO + HAB	0.88	3.571	2.549	−1.564	8.705
TYE	A + AR(1) + HAB	0.00	2.048	0.528	0.981	3.115
KLA	A + EO + TT + HAB	2.06	6.115	3.405	−0.696	12.925
CAS	A + EO + ENT + CORE	0.04	2.448	1.516	−0.595	5.490
California						
NWC	A + HAB + WMT + WP	0.00	5.273	1.195	2.889	7.657
HUP	A + CORE + ENT*ENP	2.77	0.125	0.644	−1.172	1.423
GDR	A + EO + WP + CORE	0.00	0.494	0.187	0.121	0.867
GDR-C	A + EO + WP + CORE	0.00	0.951	0.237	0.476	1.426
GDR-T	A + EO + WP + WMT + HAB	1.13	0.557	0.447	−0.340	1.454

[a] See Table 2 for general study area codes and Table 10 for GDR study area notation.
[b] See Table 10 for model covariate notation.
[c] See Table 10 for model AIC_c values.

TABLE 14. Best model containing the effect(s) of climate or weather on the mean annual number of young fledged per adult female Northern Spotted Owl (NYF) for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the climate or weather effect(s) in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	A + ENT	1.44	0.105	0.041	0.023	0.188
RAI	A + ENT*ENP [d]	0.00	−0.036	0.008	−0.053	−0.020
			0.437	0.101	0.231	0.642
			−0.010	0.003	−0.016	−0.005
OLY	A + EO + SOI	1.86	−0.101	0.059	−0.220	0.019
Oregon						
COA	A + EO + ENT + HAB	3.26	0.023	0.018	−0.013	0.058
HJA	A + EO + ENT	1.19	0.039	0.022	−0.006	0.084
TYE	A + LNT*BO [e]	5.59	−0.136	0.044	−0.223	−0.049
			0.324	0.130	0.065	0.584
KLA	A + LNP*BO [e]	0.00	−0.015	0.005	−0.025	−0.005
			0.095	0.038	0.020	0.170
CAS	A + EO + ENT	0.00	0.078	0.019	0.040	0.116
California						
NWC	A + HAB + WP + WMT [f]	0.00	−0.002	0.001	−0.003	–0.000
			0.047	0.021	0.005	0.089
HUP	A + ENT*ENP [d]	0.00	−0.008	0.003	−0.014	−0.001
			−0.137	0.048	−0.233	−0.040
			0.003	0.001	0.000	0.005
GDR	A + EO + WP + CORE	0.00	–0.001	0.000	−0.002	–0.000
GDR-C	A + EO + WP + CORE	0.00	−0.001	0.000	−0.003	–0.001
GDR-T	A + EO + WP + WMT	0.00	−0.002	0.001	−0.003	–0.001
			0.039	0.023	–0.008	0.085

[a] See Table 2 for general study area codes and Table 10 for GDR study area notation.
[b] PDO indicates the Pacific Decadal Oscillation. See Table 10 for additional model covariate notation.
[c] See Table 10 for model AIC_c values.
[d] The first and second estimates are the main effects of ENT and ENP, respectively, and the third is the interactive effect.
[e] The first estimate is the main effect of LNT or LNP, the second estimate is the interactive effect with BO.
[f] The first estimate is the main effect of WP and the second estimate is the main effect of WMT.

TABLE 15. Variance components of the mean annual number of young fledged per adult female Northern Spotted Owl (NYF) from the mixed-model analysis of year- and territory-specific effects in 11 study areas in Washington, Oregon, and California, USA, 1985–2013.

	Spatial [b]		Temporal [c]		Residual		
Study area [a]	Estimate	% total	Estimate	% total	Estimate	% total	Total
Washington							
CLE	0.058	6%	0.132	15%	0.708	79%	0.898
RAI	0.000	0%	0.016	4%	0.404	96%	0.420
OLY	0.010	2%	0.102	21%	0.385	77%	0.497
Oregon							
COA	0.007	1%	0.087	16%	0.451	83%	0.545
HJA	0.007	1%	0.073	11%	0.572	88%	0.652
TYE	0.022	4%	0.073	11%	0.540	85%	0.635
KLA	0.012	1%	0.045	7%	0.626	92%	0.683
CAS	0.024	3%	0.137	18%	0.588	79%	0.749
California							
NWC	0.010	1%	0.045	7%	0.654	92%	0.708
HUP	0.033	6%	0.057	10%	0.480	84%	0.570
GDR	0.015	2%	0.038	6%	0.584	92%	0.636
GDR-C	0.010	1%	0.043	7%	0.574	92%	0.626
GDR-T	0.020	3%	0.037	6%	0.592	91%	0.649

[a] See Table 2 for general study area codes and Table 10 for GDR study area notation.
[b] Spatial process variance is the random effects estimate of territory variability.
[c] Temporal process variance is the random effects estimate of annual variability.

Apparent Survival

Individual study areas. We used the encounter histories of 5,090 owls (excluding 1-yr-olds [S1]; see Appendix H) to estimate apparent survival in individual study areas (Table 2, 17). The best fixed effects model that we used as the basis for random effects modeling included time effects on apparent survival and capture rates for 6 areas ($\phi(t)$ $p(t)$; RAI, OLY, COA, TYE, CAS, and HUP), and a time effect on survival and an additive time and sex effect (males higher than females) on capture rates for 5 areas ($\phi(t)$ $p(\text{sex} + t)$; CLE, HJA, KLA, NWC, and GDR). For the GDR study area the fixed effects model structure also included an interactive effect of the Barred Owl treatment effect and time on survival, and additive effects of Barred Owl treatment, sex, and time on recapture rates [$\phi(\text{Trt}^*t)$ $p(\text{sex} + t + \text{Trt})$]. Survival and captures rates in the GDR study area were higher in treatment areas after Barred Owl removals began in 2009, and males had higher recapture rates than females. The best random effects model varied widely by study area, with temporal variation best modeled by a trend or explained by a variety of factors, including Barred Owls, climate, and habitat (Appendix I Figure 16). Mean estimates of apparent survival ranged from a low of 0.804 ± 0.032 in GDR control areas after Barred Owl removals began in 2009, to a high of 0.870 ± 0.009 in the HJA study area and 0.870 ± 0.021 in the GDR treatment areas after Barred Owl removals began.

Five of the 11 study areas included either a negative linear (T) or log-linear (lnT) time trend on survival in the best model (GDR) or competitive models (CLE, RAI, CAS, and HUP), but the effect was strong in only 1 area (RAI) as evidenced by a 95% CI for the covariate coefficient that did

TABLE 16. Model selection results for models with $\Delta\text{AIC}_c < 5$ from the meta-analysis of the mean annual number of young fledged per adult female Northern Spotted Owl (NYF) in 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c) and the difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c). The number of parameters (K), Akaike weight (w_i), and model deviance ($-2\log L$) are included for each candidate model.

Model [a]	ΔAIC_c	K	w_i	$-2\log L$
REG + t + CORE	0.00 [b]	36	0.18	12.95
REG + t + BO + EDGE	0.03	37	0.18	10.40
REG + t + EDGE	0.64	36	0.13	13.59
REG + t + BO + CORE	1.01	37	0.11	11.39
REG + t + BO	1.30	36	0.10	14.25
REG + t + HAB	1.90	36	0.07	14.84
REG + t + BO + HAB	2.29	37	0.06	12.67
REG + t	2.77	35	0.05	18.27
REG + t + BO + PR	3.02	37	0.04	13.39
REG + t + BO + HD	3.36	37	0.03	13.73
REG + t + PR	3.42	36	0.03	16.37

[a] Model notation indicates structure for effects of geographic region (REG), prey species richness index (PR), and percentage of suitable habitat that was disturbed (HD). See Table 10 for additional model covariate notation.
[b] The AIC_c value of the top model = 94.60.

TABLE 17. Estimates of mean apparent survival ($\hat{\bar{\phi}}$) and temporal process variance ($\hat{\sigma}_{temporal}$), with associated standard errors and 95% lower (LCL) and upper (UCL) confidence limits, for adult female Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Estimates of mean apparent survival were generated using the intercept-only random effects model [RE(.)]. Estimates of temporal process variance were based on the best random effects model (Mean, T, lnT, TT, or SPLINE) for each study area using time-specific estimates of apparent survival (ϕ) and capture probability (p).

Study area [a]	Model [b]	$\hat{\bar{\phi}}$	SE	LCL	UCL	$\hat{\sigma}_{temporal}$	LCL	UCL
Washington								
CLE	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(T)	0.836	0.013	0.811	0.862	0.033	0.000	0.079
RAI	$\phi(t)\ p(t)$ RE ϕ(T)	0.835	0.020	0.758	0.874	0.065	0.029	0.121
OLY	$\phi(t)\ p(t)$ RE ϕ(TT)	0.852	0.010	0.832	0.872	0.033	0.000	0.079
Oregon								
COA	$\phi(t)\ p(t)$ RE ϕ(T)	0.861	0.014	0.834	0.888	0.058	0.034	0.099
HJA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(SPLINE)	0.870	0.009	0.852	0.888	0.029	0.000	0.059
TYE	$\phi(t)\ p(t)$ RE ϕ(T)	0.858	0.010	0.838	0.878	0.034	0.015	0.060
KLA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(T)	0.848	0.009	0.830	0.866	0.033	0.015	0.059
CAS	$\phi(t)\ p(t)$ RE ϕ(T)	0.851	0.011	0.829	0.873	0.043	0.022	0.075
California								
NWC	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(lnT)	0.844	0.010	0.824	0.834	0.036	0.010	0.065
HUP	$\phi(t)\ p(t)$ RE ϕ(lnT)	0.858	0.011	0.836	0.879	0.023	0.000	0.063
GDR-CB	$\phi(\text{Trt}*t)\ p(\text{sex} + t + \text{Trt})$ RE ϕ[B(T), A(Trt*T)]	0.858	0.008	0.840	0.875	0.008 [c]	0.000	0.036
GDR-TB	$\phi(\text{Trt}*t)\ p(\text{sex} + t + \text{Trt})$ RE ϕ[B(T), A(Trt*T)]	0.857	0.009	0.841	0.872			
GDR-CA	$\phi(\text{Trt}*t)\ p(\text{sex} + t + \text{Trt})$ RE ϕ[B(T), A(Trt*T)]	0.804	0.032	0.741	0.867			
GDR-TA	$\phi(\text{Trt}*t)\ p(\text{sex} + t + \text{Trt})$ RE ϕ[B(T), A(Trt*T)]	0.870	0.021	0.828	0.911			

[a] See Table 2 for general study area codes, and Table 4 for GDR study area notation.
[b] Best Random Effects (RE) model structure from analyses of the a priori model set based on the best time or sex fixed effects base model for each area. Model notation indicates structure for effects of time (t), sex (sex), linear time trend (T), log-linear time trend (lnT), quadratic time trend (TT), spline (SPLINE, with knots every 5 yr backward from 2013), or constant (.) models. The best fixed effects model for the GDR study area included a treatment effect (Trt) to distinguish areas in which Barred Owl removal occurred both before (1992–2008) and after (2009–2013) removals began.
[c] Survival estimates for all 4 treatment and control groups in the GDR study area were generated from the single best model, so a single estimate of temporal process variance applies.

not overlap 0 (Table 18). However, in 9 of the 10 study areas where it was investigated, the Barred Owl covariate (BO), which exhibited increasing positive trends over time in all areas (Appendix C Figure 13), was included in the random effects structure in the best model or a competitive model (Table 19). The 95% CIs around the covariate coefficients for the Barred Owl effect did not overlap 0 for 4 areas (RAI, COA, HJA, and NWC) and barely overlapped 0 for 3 others (CLE, CAS, and HUP), and in all cases coefficients (or interactions) were negative, suggesting that the presence of Barred Owls was negatively associated with apparent survival in many study areas. Although the Barred Owl covariate was not modeled for GDR (because it was confounded with treatment effects), the best random effects survival model for GDR included higher apparent survival in treatment areas where Barred Owls were removed, although the 95% CI around the covariate coefficient for the treatment effect included 0 (After*Trt*T interaction; Table 19). Based on the best survival models that included either time trends or the negative effect of Barred Owl detections, we concluded that there was strong support for declining apparent survival in at least 8 of 11 study areas (CLE, RAI, HJA, TYE, CAS, NWC, HUP, and GDR).

The effect of population-level reproductive rates (R) occurred in top models of apparent survival for 2 areas (RAI and OLY), and in competitive models for 3 areas (CLE, CAS, and HUP; Table 20). However, 95% CIs around the covariate coefficients for R overlapped 0 in all but 1 study area (RAI), suggesting that there was no support for an effect of R on survival in most study areas.

The amount of nesting and roosting habitat (HAB) did not occur in top or competitive models of apparent survival for any of the 10 areas for which it was investigated (Table 21). The amount of core habitat was the best habitat covariate overall for 1 area (KLA) and occurred in competitive models for 2 other areas (RAI and HUP); however, 95% CIs for all CORE covariate coefficients widely overlapped 0, suggesting little support for this effect. Where investigated, the amount of interface between nesting and roosting habitat and other cover types (EDGE) occurred in a top or competitive model for only 2 of 9 areas (CLE and COA). In both cases the 95% CIs around the EDGE covariate coefficients slightly overlapped 0, but, similarly to the fecundity analysis, the coefficients were positive, which was contrary to what we predicted. The annual amount of nesting and roosting habitat disturbance (HD) occurred in a top or competitive model

TABLE 18. Best model containing a time effect on apparent survival of nonjuvenile Northern Spotted Owls for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the specified effect in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	Effect	$\hat{\beta}$	SE	LCL	UCL
Washington							
CLE	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(T)	1.64	T	−0.0023	0.0021	−0.0064	0.0019
RAI	$\phi(t)\ p(t)$ RE ϕ(T)	1.08	T	−0.0068	0.0033	−0.0133	−0.0003
OLY	$\phi(t)\ p(t)$ RE ϕ(TT)	3.12	T	−0.0066	0.0079	−0.0221	0.0089
			TT	0.0002	0.0004	−0.0005	0.0009
Oregon							
COA	$\phi(t)\ p(t)$ RE ϕ(T)	4.05	T	−0.0034	0.0022	−0.0077	0.0010
HJA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(SPLINE)	4.67	T	−0.0052	0.0169	−0.0384	0.0280
			TT	0.0008	0.0015	−0.0022	0.0038
			TTT	−0.0004	0.0001	−0.0006	−0.0001
			Knot1	0.0003	0.0001	0.0000	0.0006
			Knot2	0.0000	0.0000	0.0000	0.0000
			Knot3	0.0000	0.0000	0.0000	0.0000
TYE	$\phi(t)\ p(t)$ RE ϕ(T)	6.11	T	−0.0007	0.0016	−0.0038	0.0025
KLA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(T)	2.13	T	−0.0011	0.0015	−0.0041	0.0018
CAS	$\phi(t)\ p(t)$ RE ϕ(T)	1.74	T	−0.0013	0.0020	−0.0052	0.0026
California							
NWC	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(lnT)	16.97	lnT	−0.0243	0.0118	−0.0474	−0.0013
HUP	ϕ(t) $p(t)$ RE ϕ(lnT)	1.46	lnT	−0.0160	0.0141	−0.0435	0.0116
GDR	ϕ(Trt*t) $p(\text{sex} + t$ +Trt) RE ϕ[B(T), A(Trt*T)]	0.00	T	−0.0019	0.0011	−0.0041	0.0002
			After	1.7947	0.9742	−0.1148	3.7041
			After*T	−0.0869	0.0463	−0.1777	0.0040
			After*Trt	−1.0606	1.0984	−3.2135	1.0923
			After*Trt*T	0.0535	0.0523	−0.0491	0.1560

[a] See Table 2 for study area codes.
[b] See Table 17 for model covariate notation.
[c] Lowest AIC_c value from the top-ranking model for each study area: CLE = 1880.93; RAI = 2111.78; OLY = 3621.57; COA = 5766.12; HJA = 6399.33; TYE = 3315.49; KLA = 4571.47; CAS = 5112.13; NWC = 3802.80; HUP = 1728.54; and GDR = 7256.91.

for 2 of 10 areas (TYE and CAS), and was the best habitat covariate overall for the GDR study area. In both cases, higher estimates of the amount of reduction in nesting and roosting habitat were associated with lower survival, and in the TYE area this effect was included as part of a complex interaction with the proportion of territories in which Barred Owls were detected.

Climate covariates included in the analysis of survival (PDSI, SOI, PDO, ENP, ENT, LNP, LNT, WP, and WMT) occurred in top or competitive models for all study areas except GDR, but there was little consistency among areas as to which covariate was important (Table 22). In the CLE study area, the Palmer Drought Severity Index (PDSI) was positively related to apparent survival, and 95% CI for the covariate coefficient slightly overlapped 0. The Southern Oscillation Index (SOI) occurred in the top model for COA and as an additive effect with PDSI for CLE. In both cases the covariate coefficients were negative and the 95% CIs either did not overlap 0 (COA) or only slightly overlapped 0 (CLE). The Pacific Decadal Oscillation (PDO) covariate occurred in competitive models for 2 areas and in both areas the relationship with apparent survival was positive, with 95% CI around covariate coefficients that either did not overlap 0 (RAI), or slightly overlapped 0 (OLY). Precipitation during the early nesting period (ENP) occurred as a main effect in a competitive model for OLY, with the 95% CI slightly overlapping 0. In addition, ENP occurred in the best model for NWC as part of an interaction with temperature during the early nesting period (ENT). In both cases, increased precipitation during the early nesting period (ENP) was associated with decreased survival rates, but for NWC there was an ameliorating effect of temperature (ENT) associated with the interaction. Mean minimum temperature during the early nesting season (ENT) was negatively associated with survival for NWC, where it occurred in an interaction with ENP, and although the 95% CI for the ENT coefficient overlapped 0, the 95% CIs for the ENP and the ENT*ENP interaction term coefficients did not. In contrast, the effect of ENT was positive for GDR, with higher temperatures during the early nesting season associated with higher survival. Total precipitation during the late nesting season (LNP) was in a top or competitive model only for the KLA area, where it occurred in an interaction with late nesting season temperature (LNT). The main effects of LNT and LNP were

TABLE 19. Best model containing a Barred Owl (BO) effect on apparent survival of nonjuvenile Northern Spotted Owls for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL), are included for the specified Barred Owl effect in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	Effect	$\hat{\beta}$	SE	LCL	UCL
Washington							
CLE	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(BO)	0.14	BO	−0.40	0.23	−0.86	0.05
RAI	$\phi(t)\ p(t)$ RE ϕ(R + BO)	0.00	BO	−0.31	0.14	−0.58	−0.04
OLY	$\phi(t)\ p(t)$ RE ϕ(BO)	2.42	BO	−0.05	0.08	−0.20	0.09
Oregon							
COA	$\phi(t)\ p(t)$ RE ϕ(BO*SOI)	1.09	BO	−0.01	0.05	−0.11	0.09
			BO*SOI	−0.20	0.06	−0.32	−0.08
HJA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(BO + WMT)	0.00	BO	−0.16	0.01	−0.17	−0.14
TYE	$\phi(t)\ p(t)$ RE ϕ(BO*HD)	0.00	BO	−0.49	0.15	−0.79	−0.19
			BO*HD	15.58	5.68	4.45	26.71
KLA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(LNT + BO)	1.63	BO	−0.05	0.10	−0.25	0.16
CAS	$\phi(t)\ p(t)$ RE ϕ(WMT + BO)	0.09	BO	−0.19	0.13	−0.44	0.06
California							
NWC	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(BO + ENT*ENP)	0.00	BO	−0.26	0.11	−0.47	−0.05
HUP	$\phi(t)\ p(t)$ RE ϕ(BO)	0.00	BO	−0.14	0.08	−0.30	0.02
GDR [d]	ϕ(Trt*t) p(sex + t + Trt:2009) RE ϕ[B(T), A(Trt*T)]	0.00	T	–0.00	0.00	0.00	–0.00
			After	1.80	0.97	–0.12	3.70
			After*T	–0.09	0.05	–0.18	0.00
			After*Trt	−1.06	1.11	−3.24	1.12
			After*Trt*T	0.05	0.05	–0.05	0.16

[a] See Table 2 for study area codes.
[b] Model notation indicates structure for effects of owl sex (sex), time variation (t), the annual percentage of suitable habitat that was disturbed (HD), reproduction (R), mean monthly minimum temperature during the early nesting season (ENT), total precipitation during the early nesting season (ENP), mean monthly minimum temperature during the late nesting season (LNT), mean monthly minimum temperature during winter (WMT), the southern oscillation index (SOI), proportion of territories with Barred Owl detections (BO), and a treatment effect to distinguish areas where Barred Owl removals occurred (Trt) starting in 2009 in the GDR study area.
[c] See Table 18 for AIC_c value from top-ranked model for each study area.
[d] Barred Owl effects were not modeled directly in this study area due to the Barred Owl removal experiment that was conducted from 2009 to 2013; however, the best model included a BACI design and a positive treatment effect (After*Trt*T) after Barred Owl removals began.

positively related to survival, with 95% CIs around the covariate coefficients not overlapping 0, but the interaction was negative, suggesting that both high precipitation and high temperature in combination had a negative effect on survival. Mean minimum temperature during the late nesting season (LNT) was also in a competitive model for TYE; the effect was positive, with a 95% CI for the covariate coefficient that did not overlap 0. Mean minimum winter temperature (WMT) was in the top or competitive model for 3 study areas (HJA, CAS, and HUP), and the fact that 95% CI for the WMT coefficient did not overlap 0 suggested strong support for a positive relationship with apparent survival in the Oregon Cascades (HJA and CAS), but less support for an association with survival in the HUP area in northern California, where the 95% CI around the WMT covariate coefficient slightly overlapped 0. Total winter precipitation (WP) did not occur in a top or competitive model for any study area.

Meta-analysis of apparent survival. We based the meta-analysis of apparent survival on the same encounter histories that we used for birds in the individual study areas (5,090 nonjuvenile owls [≥2 yr of age]; Table 2). There was no indication that survival rates of owls in the 8 study areas associated with the monitoring program (NWFP in Table 23) differed from survival rates of owls in the 3 nonfederal study areas ($\hat{\beta} = 0.007 \pm 0.092$ SE, 95% CI: –0.012 to 0.024; Table 23, 24). Therefore, we proceeded with the meta-analysis of all 11 study areas combined. The best random effects model included a common intercept across all study areas, positive effects of PDO, and negative effects of SOI (Table 23, 24). The 95% CI around PDO and SOI slightly overlapped 0 (Table 24), suggesting some support for higher survival when the PDO was in a warming phase (warmer, drier winters in the Pacific Northwest) and when the SOI was negative, with a strongly negative SOI indicative of El Niño events (warmer, drier winters in the Pacific Northwest; Figure 11). Compared with the random effects model with no covariates [RE(.)], the best model with PDO and SOI explained ~12% of the variation in apparent survival. The

TABLE 20. Best model containing a reproductive (R) effect on apparent survival of nonjuvenile Northern Spotted Owls for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the reproductive effect in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	$\hat{\beta}$	SE	LCL	UCL
Washington						
CLE	$\phi(t)$ p(sex + t) RE ϕ(R + BO)	1.69	−0.02	0.03	−0.09	0.04
RAI	$\phi(t)$ $p(t)$ RE ϕ(R + BO)	0.00	−0.12	0.05	−0.22	−0.01
OLY	$\phi(t)$ $p(t)$ RE ϕ(R)	0.00	−0.05	0.03	−0.10	0.01
Oregon						
COA	$\phi(t)$ $p(t)$ RE ϕ(R)	4.34	0.01	0.05	−0.09	0.10
HJA [d]						
TYE	$\phi(t)$ $p(t)$ RE ϕ(R + HD)	5.67	0.02	0.04	−0.05	0.09
KLA	$\phi(t)$ p(sex + t) RE ϕ(R)	2.39	0.00	0.04	−0.08	0.07
CAS	$\phi(t)$ $p(t)$ RE ϕ(R)	1.61	−0.02	0.03	−0.09	0.04
California						
NWC	$\phi(t)$ p(sex + t) RE ϕ(R + HD)	16.57	0.03	0.04	−0.06	0.12
HUP	$\phi(t)$ $p(t)$ RE ϕ(R + BO)	0.76	0.05	0.05	−0.04	0.15
GDR [e]						

[a] See Table 2 for study area codes.
[b] See Table 19 for model covariate notation.
[c] See Table 18 for AIC_c value from top-ranked model for each study area.
[d] Reproductive covariates were not available during the first 3 yr of the study. Consequently, models that included a reproduction covariate were not considered for this study area.
[e] Reproductive effects were not modeled for the GDR study area due to the confounding effects of Barred Owl removal.

best model that included the Barred Owl covariate was ranked 4th and also included PDO (Table 23). Compared with the model that included only the random effect of area [RE(Area)], the model that included Area, PDO, and BO explained ~13% of the variation in survival (Figure 12). The Barred Owl covariate was negatively associated with apparent survival across all study areas as predicted ($\hat{\beta} = -0.057 \pm 0.030$ SE, 95% CI: −0.117 to −0.001; Table 24).

TABLE 21. Best model containing a habitat effect on apparent survival of nonjuvenile Northern Spotted Owls for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the specified habitat effect(s) in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	Effect	$\hat{\beta}$	SE	LCL	UCL
Washington							
CLE	$\phi(t)$ p(sex + t) RE ϕ(EDGE)	0.00	EDGE	2.23	1.29	−0.30	4.76
RAI	$\phi(t)$ $p(t)$ RE ϕ(R + CORE)	0.86	CORE	3.79	2.21	−0.54	8.11
OLY [d]							
Oregon							
COA	$\phi(t)$ $p(t)$ RE ϕ(SOI*EDGE)	0.00	EDGE	1.76	1.15	−0.50	4.01
			SOI*EDGE	6.68	1.74	3.27	10.10
HJA	$\phi(t)$ p(sex + t) RE ϕ(HAB)	4.82	HAB	1.14	0.86	−0.55	2.83
TYE	$\phi(t)$ $p(t)$ RE ϕ(BO*HD)	0.00	HD	−3.34	0.84	−4.99	−1.69
			BO*HD	15.58	5.68	4.45	26.71
KLA	$\phi(t)$ p(sex + t) RE ϕ(CORE)	2.04	CORE	0.15	0.16	−0.17	0.46
CAS	$\phi(t)$ $p(t)$ RE ϕ(WMT + HD)	0.32	HD	−1.03	1.11	−3.20	1.15
California							
NWC	$\phi(t)$ p(sex + t) RE ϕ(HD + BO)	15.09	HD	−1.51	0.88	−3.23	0.21
HUP	$\phi(t)$ $p(t)$ RE ϕ(CORE + BO)	1.01	CORE	−0.88	1.01	−2.87	1.10
GDR	ϕ(Trt*t) p(sex + t + Trt) RE ϕ(HD + Trt)	5.50	HD	−0.06	0.73	−1.50	1.37

[a] See Table 2 for study area codes.
[b] Model notation indicates structure for effects of annual percent cover of suitable owl habitat (HAB), a neighborhood focal statistic that defines the annual number of 30 m^2 pixels with ≥50% suitable habitat within 800 m of each pixel in each owl site (CORE), and the annual amount of interface between suitable habitat and other cover types within each owl site (EDGE). See Table 19 for other model covariate notation.
[c] See Table 18 for AIC_c value from top-ranked model for each study area.
[d] Habitat covariates at this study area varied little over the course of the study, which resulted in habitat covariates being confounded with the intercept. Consequently, models that included effects of habitat were not considered for this study area.

The best annual time trend model included the additive effects of study area and a cubic spline with 4 knots (Table 23). Negative trends in survival were evident from all trend models (Table 24). However, the trend models were all ranked relatively low, indicating that other covariates (e.g., PDO, SOI, and BO) better captured the overall temporal variation in survival across study areas (Table 23).

DISCUSSION

Estimates of annual rates of population change and occupancy rates from our study indicated that Northern Spotted Owls were continuing to decline in all parts of their range (Figure 5), and that the rate of decline was increasing in many areas, including southern Oregon and northern California. The only exception was the treatment area within GDR, where populations started increasing after Barred Owl removals were initiated in 2009. Our analysis was the first range-wide assessment of Northern Spotted Owl population status to include estimates of occupancy dynamics, which revealed that territory occupancy of Northern Spotted Owls was declining in all 11 study areas. The lowest occupancy rates were observed in 2013 in the COA study area in Oregon (28%) and the 3 study areas in Washington (11–26%; Figure 8).

With the exception of the Barred Owl treatment area within the GDR study area after the removal of Barred Owls (GDR-TA), estimates of mean λ for Northern Spotted Owls were <1.0 in all our study areas (range: 0.878–0.988; Figure 4). Annual rates of population decline were highest in study areas in Washington, the COA study area in northwestern Oregon, and control areas in the GDR study area in northwestern California (Table 25). Estimates of realized population change (Figure 5) clearly illustrated these declines in the numbers of territorial owls in all study areas over the study period, with an indication of accelerated rates of decline in some areas since the last meta-analysis (Forsman et al. 2011). In all study areas except RAI and the GDR treatment areas, estimates of population decline were higher than, and in some cases more than twice as high as, estimates of population decline from earlier studies (Forsman et al. 2011). The one exception was the GDR treatment areas, where the population appeared to be increasing and had nearly recovered to initial levels, in association with the removal of Barred Owls (Figure 5C). We observed declines in 3 (KLA, CAS, and HUP) of the 4 areas that had stable population trends through 2006 (TYE, KLA, CAS, and HUP; Forsman et al. 2011). The weighted mean estimate of $\hat{\lambda} = 0.962$ for all years and study areas (excluding GDR treatment areas) indicated an average rate of decline of 3.8% per year. This estimated rate of decline was nearly 1% higher than the estimate of Forsman et al. (2011), but was comparable with rates reported by Franklin et al. (1999) and Anthony et al. (2006; Table 26).

Consistent with previous studies of Spotted Owls (e.g., Anthony et al. 2006, Blakesley et al. 2010, Forsman et al. 2011) and birds in general (Clutton-Brock 1988, Sæther 1990), we found that annual fecundity was highest for adult females, intermediate for 2-yr-old females, and lowest for 1-yr-old females. One- and 2-yr-old Spotted Owls rarely nested, and comprised only 3% and 6%, respectively, of the territorial population. Our estimate of mean annual adult fecundity ($\bar{x} = 0.309 \pm 0.027$) was lower than any reported in previous meta-analyses of Northern Spotted Owls, including Burnham et al. (1996; $\bar{x} = 0.339 \pm 0.010$), Anthony et al. (2006; $\bar{x} = 0.372 \pm 0.029$), and Forsman et al. (2011; $\bar{x} = 0.330 \pm 0.049$). The estimated mean annual adult fecundity from our study was also lower than estimates of mean fecundity reported for 2 populations of Mexican Spotted Owl (*Strix occidentalis lucida*) by Seamans et al. (1999; $\bar{x} = 0.494 \pm 0.022$; $\bar{x} = 0.380 \pm 0.019$), and 4 California Spotted Owl (*S. o. occidentalis*) populations reported by Blakesley et al. (2010; adult females: $\bar{x} = 0.562 \pm 0.117$). As observed in previous studies (Anthony et al. 2006, Forsman et al. 2011), we found that fecundity in the CLE study area in Washington was higher than in other study areas. Whether this difference was related to life-history tradeoffs by a species at the northern edge of its range compared with populations from the center of the range (Anthony et al. 2006), unique climatic attributes (Hicks et al. 2003), or high prey biomass in Washington mixed-conifer forests (Forsman et al. 2011) remains unknown.

We found substantial annual variation in fecundity among study areas, with support for declining trends in 8 areas (CLE, COA, HJA, TYE, KLA, NWC, HUP, and GDR; Table 25). The biennial cycle of high fecundity in even-numbered years and low fecundity in odd-numbered years was still important in several study areas, although best models also included climate and habitat effects in some study areas. This pattern likely incorporated variation in the breeding propensity of individuals combined with some complex interaction between climate, prey cycles, and territory quality (Forsman et al. 2011, Stoelting et al. 2015). However, despite the importance and persistence of the even–odd year cyclical pattern of fecundity, we still do not know what causes this synchronization. This pattern has also been observed in California Spotted Owls (Franklin et al. 2004, Blakesley et al. 2010), but in this subspecies the costs of reproduction were generally not high enough to cause this reoccurring cycle in fecundity (Stoelting et al. 2015).

Results from individual study areas suggested that apparent annual survival rates were declining in 8 of 11 study areas, and that declines were most strongly

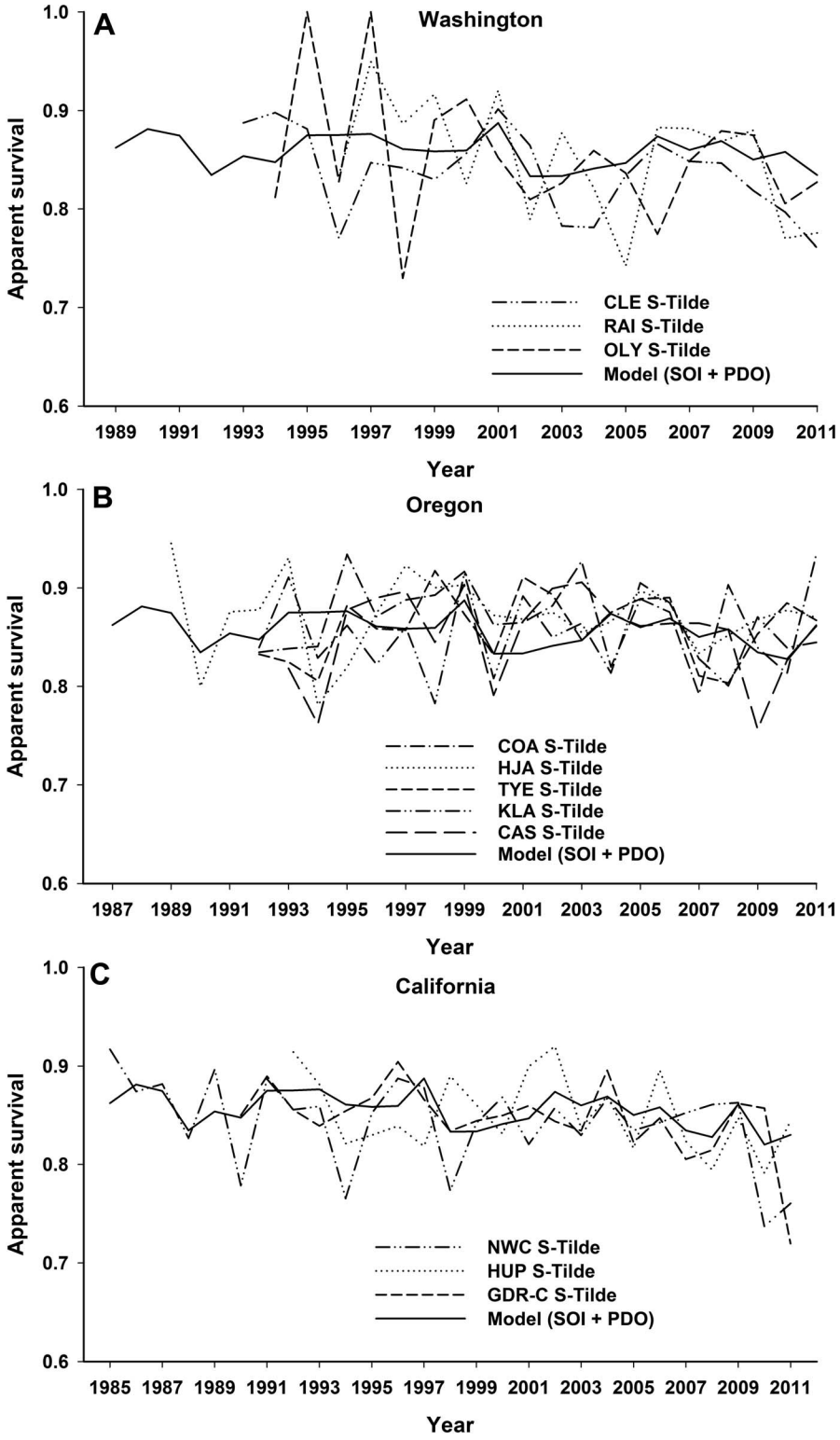

FIGURE 11. Estimates of the effects of the Pacific Decadal Oscillation (PDO) and Southern Oscillation Index (SOI) on apparent survival of Northern Spotted Owls generated from the best random effects (RE) model from the meta-analysis [RE ϕ(PDO + SOI)] based on the fixed effects model [ϕ(Area*t) p(sex*Area*t)] with study area (Area) and general time variation (t) on apparent survival (ϕ), and study area, time, and sex effects on capture probability (p). Random effects model estimates are plotted with shrinkage estimates (S-tilde) for the (**A**) 3 study areas in Washington, (**B**) 5 study areas in Oregon, and (**C**) 3 study areas in California, USA. Only sites where Barred Owls were not removed (control areas) were included for the Green Diamond study area (GDR-C). See Table 2 for study area abbreviations.

TABLE 22. Best model containing a climate effect on apparent survival of nonjuvenile Northern Spotted Owls for each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the specified climate effect(s) in each model.

Study area [a]	Best model [b]	ΔAIC_c [c]	Effect	$\hat{\beta}$	SE	LCL	UCL
Washington							
CLE	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(PDSI + SOI)	0.57	PDSI	0.015	0.008	−0.001	0.030
			SOI	−0.025	0.018	−0.060	0.010
RAI	$\phi(t)\ p(t)$ RE ϕ(PDO)	0.36	PDO	0.055	0.020	0.015	0.096
OLY	$\phi(t)\ p(t)$ RE ϕ(ENP + PDO)	1.23	ENP	−0.001	0.001	−0.003	0.001
			PDO	0.022	0.014	−0.006	0.049
Oregon							
COA	$\phi(t)\ p(t)$ RE ϕ(SOI*EDGE)	0.00	SOI	−1.398	0.358	−2.099	−0.697
			SOI*EDGE	6.684	1.743	3.268	10.101
HJA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(BO + WMT)	0.00	WMT	0.027	0.009	0.010	0.044
TYE	$\phi(t)\ p(t)$ RE ϕ(LNT + BO*HD)	0.60	LNT	0.008	0.008	−0.007	0.024
KLA	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(LNT*LNP)	0.00	LNT	0.046	0.019	0.008	0.084
			LNP	0.021	0.010	0.001	0.041
			LNT*LNP	−0.003	0.001	−0.006	0.001
CAS	$\phi(t)\ p(t)$ RE ϕ(WMT)	0.00	WMT	0.016	0.008	0.001	0.032
California							
NWC	$\phi(t)\ p(\text{sex} + t)$ RE ϕ(BO + ENT*ENP)	0.00	ENT	−0.021	0.020	−0.060	0.018
			ENP	−0.003	0.001	−0.005	−0.002
			ENT*ENP	0.002	0.001	0.001	0.003
HUP	$\phi(t)\ p(t)$ RE ϕ(WMT)	0.47	WMT	−0.014	0.009	−0.032	0.003
GDR	$\phi(\text{Trt}*t)\ p(\text{sex} + t + \text{Trt})$ RE ϕ(ENT + Trt)	3.17	ENT	0.016	0.007	0.003	0.029

[a] See Table 2 for study area codes.
[b] Model notation indicates structure for effects of total precipitation during the late nesting season (LNP), Pacific Decadal Oscillation (PDO), and Palmer Drought Severity Index (PDSI). See Table 19 and Table 20 for additional model covariate notation.
[c] See Table 18 for AIC_c value from top-ranked model for each study area.

associated with increased detections of Barred Owls in 7 areas. If this trend continues there should be increased concern regarding the continued persistence of the Northern Spotted Owl subspecies, because adult survival is the most important vital rate influencing the rate of population change in long-lived birds such as Spotted Owls (Franklin et al. 2000). Whereas Forsman et al. (2011) found that low rates of apparent survival were largely confined to Washington, we found that this trend extended to COA in Oregon and 2 study areas in California (NWC and GDR). Our results indicated that declines in apparent annual survival in the southern portion of the range of the Northern Spotted Owl may be reaching rates of decline previously observed only in Washington.

Barred Owls

The 2-species approach used in our occupancy analysis allowed us to investigate the effects of Barred Owl presence on colonization and extinction rates of territorial Northern Spotted Owls while accounting for both Barred Owl and Spotted Owl detection rates (Bailey et al. 2009, Yackulic et al. 2012, 2014). Our results suggested that Barred Owls were having substantial negative effects on occupancy dynamics of Northern Spotted Owls, which was consistent with previous findings (Kelly et al. 2003, Olson et al. 2005, Anthony et al. 2006, Dugger et al. 2011, Forsman et al. 2011, Sovern et al. 2014, Yackulic et al. 2014). The presence of Barred Owls was a predominant factor associated with increased extinction rates of Spotted Owls in all study areas, consistent with results from single-species occupancy studies where presence of Barred Owls was incorporated as a time-varying, individual covariate (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011, Sovern et al. 2014). Barred Owl presence had less consistent effects on colonization rates of Spotted Owls, which was also consistent with previous findings (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011, Sovern et al. 2014, Yackulic et al. 2014).

In addition to a strong association with occupancy dynamics, we observed a negative association between Barred Owl detections and apparent survival in more study areas in this analysis (7 with strong evidence, 3 with less support) than in the 2 previous meta-analyses that investigated this effect (2 of 11 areas, Anthony et al. 2006; 6 of 11 areas, Forsman et al. 2011). These results supported the conclusion that the negative effect of Barred Owls on apparent survival of Spotted Owls was increasing as Barred Owl populations increased in density farther south in Oregon and California (Forsman et al. 2011; Appendix A). We estimated *apparent* survival, i.e. mortality was not distinguished from

TABLE 23. Model selection criteria for a priori random effects models (RE) in the meta-analysis of apparent survival of adult Northern Spotted Owls in 11 demographic study areas in Washington, Oregon, and California, USA, 1985–2013. The best fixed effects model, which included the interaction between area and year on survival and interactions among sex, study area, and year on detection rates [ϕ(Area*t) p(Sex*Area*t)], was used for all random effects modeling. Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c). The model deviance (Deviance), number of parameters (*K*), difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), and Akaike model weights (w_i) are given for all models.

Model [a]	ΔAIC_c	*K*	w_i	Deviance
Random Effects				
RE ϕ(PDO + SOI)	0.00 [b]	706.40	0.35	19671.78
RE ϕ(LAT + PDO + SOI)	1.63	706.53	0.16	19673.14
RE ϕ(PREY + PDO + SOI)	1.68	706.58	0.15	19673.08
RE ϕ(Area + BO + PDO)	4.24	708.99	0.04	19670.55
RE ϕ(Area + BO*PDO)	4.62	709.11	0.03	19670.68
RE ϕ(Area + PDO*SOI)	5.07	709.31	0.03	19670.70
RE ϕ(Area + SPLINE)	5.09	709.39	0.03	19670.57
RE ϕ(Area + PDO + SOI)	5.18	709.26	0.03	19670.93
RE ϕ(Area + PDO)	5.37	709.55	0.02	19670.49
RE ϕ(BO + HAB)	5.86	710.41	0.02	19699.18
RE ϕ(Area + SOI)	6.28	709.59	0.02	19671.33
RE ϕ(BO*HAB)	6.48	710.85	0.01	19668.86
RE ϕ(Area + BO + R)	7.01	710.57	0.01	19669.98
RE ϕ(Area + ENT*ENP)	7.42	710.72	0.01	19670.08
RE ϕ(.)	7.52	710.73	0.01	19670.17
RE ϕ(Area + ENT + ENP)	7.52	710.77	0.01	19670.08
RE ϕ(R + HAB)	7.58	710.92	0.01	19669.83
RE ϕ(Area + T)	7.69	710.94	0.01	19669.88
RE ϕ(HAB)	7.77	710.98	0.01	19669.88
RE ϕ(CORE)	7.80	710.98	0.01	19669.91
RE ϕ(Area + BO + CORE)	7.90	711.18	0.01	19669.60
RE ϕ(Area + BO)	7.95	711.03	0.01	19669.97
RE ϕ(EDGE)	8.01	711.14	0.01	19669.79
RE ϕ(NWFP)	8.02	711.06	0.01	19669.97
RE ϕ(Area + BO + HAB)	8.02	711.25	0.01	19669.56
RE ϕ(HD)	8.17	711.04	0.01	19670.16
RE ϕ(AREA*PDO)	8.19	709.30	0.01	19673.84
RE ϕ(R*HAB)	8.32	711.40	0.01	19669.55
RE ϕ(Area + BO*CORE)	8.47	711.49	0.01	19669.51
RE ϕ(Area + BO*HAB)	8.58	711.56	0.00	19669.47
RE ϕ(CORE + EDGE)	8.62	711.31	0.00	19670.05
RE ϕ(Area + lnT)	8.82	711.42	0.00	19670.01
RE ϕ(Area + R + CORE)	8.82	711.70	0.00	19669.42
RE ϕ(Area + R + HAB)	8.85	711.80	0.00	19669.25
RE ϕ(LAT)	9.00	710.91	0.00	19671.26
RE ϕ(PREY)	9.09	710.92	0.00	19671.34
RE ϕ(Area + ENT)	9.44	711.74	0.00	19669.95
RE ϕ(Area + HAB)	9.53	712.13	0.00	19669.22
RE ϕ(Area + R*CORE)	9.54	712.18	0.00	19669.12
RE ϕ(Area + CORE)	9.58	712.09	0.00	19669.34
RE ϕ(Area + R*HAB)	9.57	712.28	0.00	19668.94
RE ϕ(REG)	10.11	712.14	0.00	19669.77
RE ϕ(Area + CORE + EDGE)	10.22	712.44	0.00	19669.25
RE ϕ(Area + ENP)	11.03	712.83	0.00	19669.24
RE ϕ(Area + WMT)	11.27	712.53	0.00	19670.12
RE ϕ(Area + WMT + WP)	11.67	712.62	0.00	19670.31
RE ϕ(Area + WMT*WP)	12.30	713.03	0.00	19670.08
RE ϕ(Area)	12.61	713.55	0.00	19669.30
RE ϕ(Area + EDGE)	12.62	713.81	0.00	19668.76
RE ϕ(Area + R)	12.68	713.63	0.00	19669.21
RE ϕ(Area + LNT)	12.74	713.44	0.00	19669.66
RE ϕ(Area + LNT*LNP)	12.83	713.58	0.00	19669.45
RE ϕ(Area + LNT + LNP)	12.83	713.38	0.00	19669.88
RE ϕ(Area + LNP)	12.89	713.68	0.00	19669.30
RE ϕ(Area + SOI + Area*SOI)	13.14	712.64	0.00	19671.76
RE ϕ(Area + WP)	13.17	713.91	0.00	19669.11
RE ϕ(Area + HD)	13.17	713.96	0.00	19669.00
RE ϕ(Area + PDSI)	13.23	713.96	0.00	19669.06
Fixed Effects				
ϕ(Area*t) p(sex*Area*t)	104.56	774	0.00	19633.41
ϕ(sex*Area*t) p(sex*Area*t)	106.68	775	0.00	19633.41
ϕ(t) p(t)	485.15	55	0.00	21497.47
ϕ(t) p(.)	567.53	29	0.00	21632.01
ϕ(.) p(t)	597.32	29	0.00	21661.80
ϕ(.) p(.)	694.58	2	0.00	21813.13

[a] Model notation indicates structure for effects of study area (Area), sex (sex), general time variation (*t*), no time variation (.), linear time trend (T), log-linear time trend (lnT), a 3-knot cubic spline time effect (SPLINE), reproduction (R), proportion of territories with Barred Owl detections (BO), indicator variable for geographic region (REG), biodiversity of prey species within study area (PREY), latitude of study area (LAT), Pacific Decadal Oscillation (PDO), Palmer Drought Severity Index (PDSI), southern oscillation index (SOI), mean monthly minimum temperature during the early nesting season (ENT), total precipitation during the early nesting season (ENP), mean monthly minimum temperature during the late nesting season (LNT), mean monthly minimum temperature during winter (WMT), total precipitation during winter (WP), percent cover of suitable owl habitat (HAB), a neighborhood focal statistic that defined the number of 30 m^2 pixels with $\geq$50% suitable habitat within 800 m of each pixel in each owl site (CORE), the amount of interface between suitable habitat and other cover types within each owl site (EDGE), percentage of suitable habitat that was disturbed (HD), and a binary covariate that distinguished the 8 Northwest Forest Plan study areas from the 3 nonfederal study areas (NWFP).

[b] The AIC_c value of the top model = 43570.63.

TABLE 24. Best random effects (RE) model that included the specified covariate in the meta-analysis of apparent survival of nonjuvenile Northern Spotted Owls in each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Model covariate coefficients ($\hat{\beta}$), standard errors (SE), and 95% confidence limits (lower: LCL; upper: UCL) are included for the effect listed ($\hat{\beta}$ [c] label).

Model [a]	ΔAIC_c [b]	$\hat{\beta}$ [c] label	$\hat{\beta}$	SE	LCL	UCL
RE ϕ(Area + BO + PDO)	4.24	BO	−0.0589	0.0295	−0.1167	−0.0010
RE ϕ(Area + BO + R)	7.01	R	−0.0248	0.0128	−0.0500	0.0004
RE ϕ(REG) [d]	10.11	Intercept	0.8488	0.0120	0.8243	0.8712
		REG1	0.0128	0.0145	−0.0156	0.0413
		REG2	−0.0064	0.0140	−0.0338	0.0210
		REG3	0.0125	0.0161	−0.0191	0.0441
		REG4	0.0124	0.0147	−0.0164	0.0413
		REG5	−0.0032	0.0188	−0.0400	0.0335
RE ϕ(NWFP)	8.02	NWFP	0.0065	0.0092	−0.0115	0.0245
RE ϕ(PREY + PDO + SOI)	1.68	PREY	−0.0020	0.0018	−0.0055	0.0015
RE ϕ(LAT + PDO + SOI)	1.63	LAT	0.0020	0.0017	−0.0013	0.0052
RE ϕ(PDO + SOI)	0.00	PDO	0.0112	0.0063	−0.0011	0.0235
RE ϕ(Area + PDSI)	13.23	PDSI	−0.0007	0.0020	−0.0045	0.0032
RE ϕ(PDO + SOI)	0.00	SOI	−0.0134	0.0075	−0.0281	0.0014
RE ϕ(Area + ENT*ENP)	7.42	ENT	0.0084	0.0055	−0.0023	0.0191
		ENP	−0.0008	0.0003	−0.0014	−0.0002
		ENT*ENP	0.0001	0.0001	–0.0001	0.0003
RE ϕ(Area + LNT)	12.75	LNT	0.0047	0.0031	−0.0014	0.0109
RE ϕ(Area + LNT*LNP)	12.83	LNT	0.0108	0.0058	–0.0005	0.0221
		LNP	0.0030	0.0019	−0.0008	0.0068
		LNT*LNP	−0.0003	0.0003	−0.0010	0.0003
RE ϕ(Area + WMT)	11.27	WMT	0.0083	0.0034	0.0017	0.0150
RE ϕ(Area + WMT + WP)	11.67	WP	−0.0002	0.0001	−0.0004	0.0001
RE ϕ(Area + T)	7.69	T	−0.0021	0.0006	−0.0033	−0.0009
RE ϕ(Area + lnT)	8.82	lnT	−0.0248	0.0077	−0.0398	−0.0098
RE ϕ(Area + SPLINE)	5.09	T	0.0073	0.0035	0.0005	0.0141
		TT	−0.2639	0.0903	−0.4409	−0.0869
		TTT	0.0263	0.0145	−0.0022	0.0548
		Knot1	0.0054	0.0039	−0.0022	0.0131
		Knot2	−0.0080	0.0042	−0.0163	0.0003
		Knot3	0.0041	0.0041	−0.0040	0.0121
		Knot4	0.0096	0.0045	0.0007	0.0184
RE ϕ(BO + HAB)	5.86	HAB	−0.0009	0.0417	−0.0826	0.0809
RE ϕ(CORE)	7.80	CORE	0.0170	0.0201	−0.0223	0.0564
RE ϕ(EDGE)	8.01	EDGE	0.0197	0.0898	−0.1564	0.1957
RE ϕ(HD)	8.17	HD	−0.2125	0.3136	−0.8272	0.4021

[a] Model notation indicates the structure of best random effects models based on the fixed effects model ϕ(Area**t*) *p*(sex*Area**t*). See Table 23 for model covariate notation.
[b] See Table 23 for AIC_c values.
[c] Labels designating covariate coefficients ($\hat{\beta}$) associated with continuous and categorical main effects and interactions.
[d] Geographic region was a categorical variable with 5 geographic regions coded as dummy variables relative to the sixth reference region as the intercept. Coding is as follows: Intercept = California Coast, REG1 = Oregon Cascades Douglas-fir, REG2 = Oregon–California mixed conifer, REG3 = Washington Douglas-fir, REG4 = Oregon coastal Douglas-fir, REG5 = Washington mixed conifer.

movements and/or behavioral changes that made birds unavailable to detection during our standard breeding season surveys. Thus, whether Barred Owls were associated with increased mortality of Spotted Owls (which we could not rule out) or increased permanent emigration through displacement of breeding birds from territories (where they become undetectable floaters) or from entire study areas remains unknown. However, the reoccupation of territories by Spotted Owls that had been missing prior to removal of Barred Owls in the GDR study area (L. Diller personal observation) suggests that displacement from territories into a nonbreeding floater population was at least one mechanism by which apparent survival and occupancy rates were negatively affected by Barred Owls. We do not know how long Spotted Owls can survive as nonterritorial floaters, but anecdotal evidence suggests that individuals can remain undetected for as long as 7 yr, yet recolonize their original or adjacent territories after Barred Owls are removed (L. Diller personal observation).

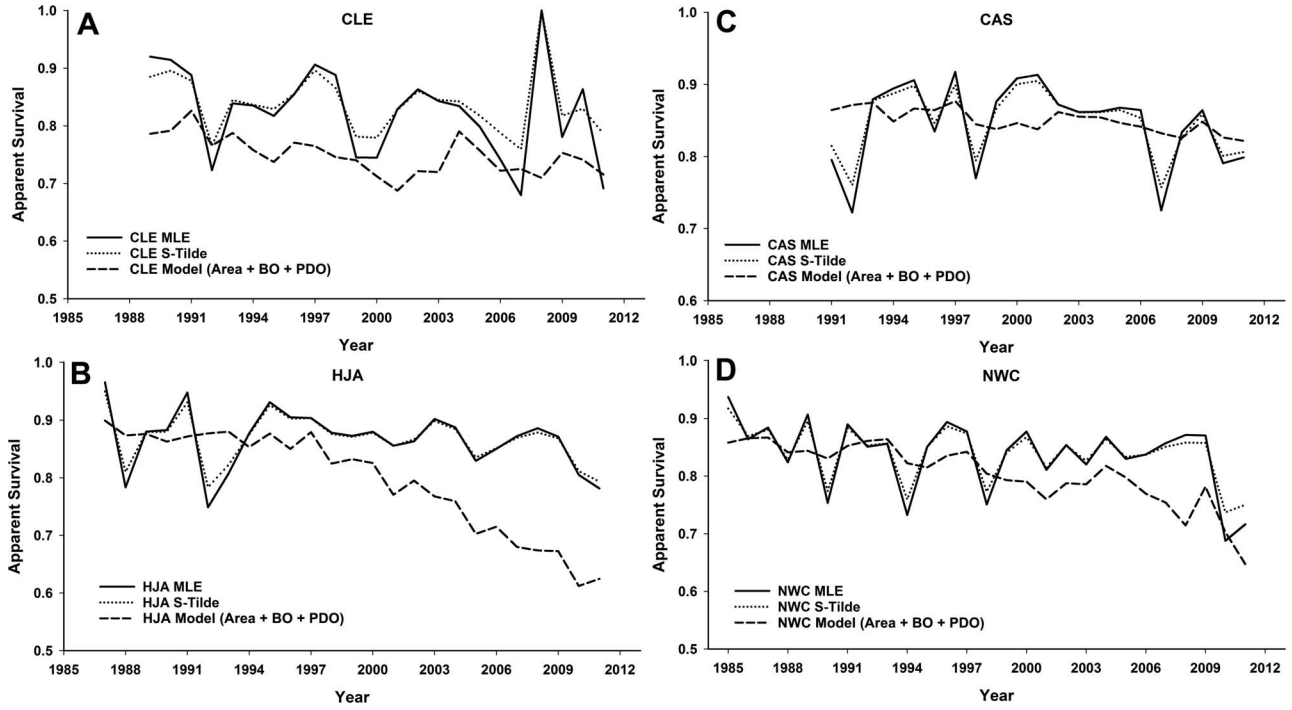

FIGURE 12. Estimates of the effects of Barred Owls (BO), the Pacific Decadal Oscillation (PDO), and study area (Area) on apparent survival (ϕ) of Northern Spotted Owls generated from the best meta-analysis random effects model (RE; ranked 4th) that included a Barred Owl effect [RE ϕ(Area + BO + PDO)] and was based on a fixed effect model [ϕ(Area*t) *p*(sex*Area*t)] with study area and general time variation (*t*) on apparent survival, and study area, time, and sex on capture probability (*p*). Random effects model estimates are plotted with original time-dependent survival estimates (MLE) and shrinkage estimates (S-tilde) for (**A**) 1 study area in Washington (CLE), (**B**, **C**) 2 study areas in Oregon (HJA, CAS), and (**D**) 1 study area in California (NWC). See Table 2 for study area abbreviations.

We observed little evidence that temporal variation in fecundity in individual study areas or recruitment across all areas (meta-analysis) was strongly associated with the presence of Barred Owls, which was consistent with results for fecundity but contradicted results for recruitment from previous meta-analyses (Forsman et al. 2011). However, our meta-analysis of fecundity suggested that Barred Owl presence had a weak negative effect on fecundity across all study areas, again consistent with the findings of Forsman et al. (2011). Weak relationships between Spotted Owl fecundity and Barred Owl presence likely represented the complex competitive and displacement interactions that occurred between these 2 species (Wiens et al. 2014). For example, Barred Owls can displace territorial Spotted Owls (see occupancy results), and displaced birds may then exist as nonterritorial nonbreeders that are difficult to detect and hence are no longer part of the territorial population, which is what we monitored. In addition, while the per capita rate of production (NYF) was not directly associated with Barred Owl presence, our results showed that the total number of pairs occupying territories had declined. Thus, the total number of young produced per study area declined in association with the expansion of Barred Owls.

Habitat

We observed strong positive associations between habitat characteristics, especially increased amounts of nesting and roosting habitat, and territory colonization rates by Northern Spotted Owls across all study areas, as reported elsewhere (Sovern et al. 2014). An increased amount of nesting and roosting habitat (HABa) was associated with decreased extinction rates in many areas, as was also reported by Dugger et al. (2011) and Sovern et al. (2014). Results were counterintuitive for the GDR study area in northern California, where we observed higher estimates of habitat disturbance (HD) and edge habitat associated with higher colonization rates, and more core habitat associated with increased extinction rates. Northern Spotted Owls occupied younger-aged stands in the GDR study area compared with most other study areas, and it is possible that they responded differently to habitat disturbance and the amount of edge and core habitat in these study areas because of their local dependence on dusky-footed woodrats (*Neotoma fuscipes*) as prey (Sakai and Noon 1993, Hamm and Diller 2009).

The effects of habitat were not strongly supported in our fecundity analyses (individual study areas and the meta-analysis), although in some study areas increasing amounts

TABLE 25. Summary of trends in demographic parameters including fecundity, apparent survival (ϕ), occupancy rates (Ψ), and lambda (λ) for Northern Spotted Owls from 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Mean lambda ($\hat{\lambda}$) and percent population change (%Δ) based on estimates of realized population change ($\Delta\lambda$) from the best random effects models with temporal trends on lambda are also included. Evidence of trends in parameters denoted below if ΔAICc < 2.0 for models with time trends or Barred Owl effects, and/or if the 95% confidence limits on regression coefficients for the time trend or the Barred Owl effect did not include zero.

Study Area [a]	Fecundity	ϕ	Ψ	λ	$\hat{\lambda}$	%Δ [b]
Washington						
CLE	Declining	Declining	Declining	No trend	0.916	–77%
RAI	No trend	Declining	Declining	No trend	0.953	–61%
OLY	No trend	No trend	Declining	No trend	0.961	–59%
Oregon						
COA	Declining	No trend	Declining	Declining	0.949	–64%
HJA	Declining	Declining	Declining	Declining	0.965	–47%
TYE	Declining	Declining	Declining	Declining	0.976	–31%
KLA	Declining	No trend	Declining	Declining	0.972	–34%
CAS	No trend	Declining	Declining	No trend	0.963	–44%
California						
NWC	Declining	Declining	Declining	Declining	0.970	–55%
HUP	Declining	Declining	Declining	Declining	0.977	–32%
GDR-CB	Declining	Declining	Declining	Declining	0.988	–31%
GDR-TB	Declining	Declining	Declining	Declining	0.961	–26%
GDR-CA	**	**	Declining	**	0.878	–41%
GDR-TA	**	**	N/A [c]	**	1.030	–9%

[a] See Table 2 for general study area codes and Table 4 for GDR study area notation.
[b] With the exception of the GDR study area, percent population change (%Δ) was based on estimates of $\Delta\lambda$ in 2011, the last year for which an estimate of λ could be generated.
[c] Data used for occupancy modeling in the GDR study area excluded treatment areas after Barred Owl removals began in 2009.
** Too few years since Barred Owl removal to evaluate a trend.

of suitable nesting and roosting habitat had positive effects on the number of young fledged (NYF). We observed almost no relationship between NYF and the amount of edge habitat, which was contrary to our prediction that the EDGE covariate would be a measure of woodrat (*Neotoma* spp.) habitat and would therefore be important in areas in the southern portion of the Spotted Owl's range (Franklin et al. 2000, Olson et al. 2004). However, we defined EDGE differently (at the population level) than other studies (individual territory level; Franklin et al. 2000, Olsen et al. 2004, Dugger et al. 2005), which might explain why we found few strong habitat effects on fecundity. This finding may be important, because it implies that managing the amount of edge habitat at the individual territory scale rather than at the study area scale may be most relevant for managing Spotted Owl reproductive rates. Finally, as we have noted in the past, the amount of temporal variation in fecundity was large, and none of the covariates that we investigated explained much of the variation in this parameter (Anthony et al. 2006, Forsman et al. 2011).

Adoption of the Northwest Forest Plan (NWFP), which included a network of late-successional reserves on federal lands, was expected to eventually reverse the declines of species associated with old-growth forests (USDA Forest Service and USDI Bureau of Land Management 1994). The Northern Spotted Owl was expected to continue its decline in the short term, and then stabilize or increase after 50–100 yr (Thomas et al. 1990, Lint et al. 1999). Previous demographic analyses suggested that Spotted Owl populations continued to decline range-wide after the NWFP was implemented, but that the rates of decline began to slow through 2009 (Table 26), although there was still much variation among study areas (Anderson and Burnham 1992, Burnham et al. 1996, Franklin et al. 1999, Anthony et al. 2006, Forsman et al. 2011). Our results suggested that rates of decline have now increased range-wide compared with the previous meta-analysis (Forsman et al. 2011), and that the proximate causes of population

TABLE 26. Comparison of estimate of annual rate of population change from reverse Jolly-Seber models (λ_{RJS}) from this study with estimates from previous analyses of long-term demographic data for Northern Spotted Owls in Washington, Oregon, and California, USA.

Study year range	No. study areas	$\bar{\lambda}$ (SE)	Annual decline (%)	Citation
1985–1998	15	0.961 (0.017)	3.9%	Franklin et al. (1999)
1985–2003	14	0.963 (0.009)	3.7%	Anthony et al. (2006)
1985–2008	11	0.971 (0.007)	2.9%	Forsman et al. (2011)
1985–2013	11	0.962 (0.019)	3.8%	This study

declines included both recruitment (including fecundity) and survival, which were declining in most study areas.

Local Weather and Regional Climate

Our meta-analysis of λ suggested that recruitment into the population of territorial owls for all study areas was most affected by the interaction between total winter precipitation (WP) and mean monthly minimum temperature during winter (WMT), with the lowest levels of recruitment occurring when conditions during the previous winter were cold and wet, and the highest levels of recruitment occurring when the previous winter was cold and dry. There was no support for a lag effect of these covariates, so the relationships likely reflected direct effects on survival of nonterritorial birds (potential recruits), particularly first-year birds, in the previous winter. The survival rate of nonterritorial or nonbreeding birds is usually difficult to measure, and, when estimated, is usually lower than the survival of territorial birds (Lenda et al. 2012). For example, nonterritorial Crested Caracaras (*Caracara cheriway*) experienced lower apparent survival than territorial breeding birds (Dwyer et al. 2012). In addition, Rohner (1996) found that survival of nonterritorial Great Horned Owls (*Bubo virginianus*) was substantially lower than for individuals holding territories during years when food resources were reduced, and that nonterritorial birds were negatively affected by a decline in prey resources before territorial birds were affected.

We also observed evidence of an association between climate and apparent adult survival rates for more study areas than previously reported (Forsman et al. 2011), with important covariates including both regional climate indices and local weather covariates. The meta-analysis of survival suggested that regional climate cycles were strongly associated with apparent survival across all study areas, consistent with previous findings for Northern Spotted Owls (Forsman et al. 2011) and other raptors (e.g., Peregrine Falcon [*Falco peregrinus*]; Franke et al. 2011, Tawny Owl [*Strix aluco*]; Millon et al. 2014). We observed higher survival rates when winters were warm (positive association with PDO) and dry (negative association with SOI), rather than higher survival when conditions were warm (positive association with PDO) and wet (positive association with SOI) as observed in a meta-analysis of 6 Northern Spotted Owl study areas by Glenn et al. (2011a). Regional climate cycles have been associated with vital rates for other birds (e.g., Wright et al. 1999, Sillett et al. 2000, LaManna et al. 2012, Wolfe et al. 2015), including other raptors (e.g., Franke et al. 2011, Jonker et al. 2014), but in most cases a clear understanding of the environmental change that climatic cycles represent (i.e. prey densities or habitat conditions) and the causal relationships that link that change to avian demographics is poorly understood.

Conclusions

Our results indicate that competition with Barred Owls may be the primary cause of Northern Spotted Owl population declines across their range. We observed declines in apparent survival and increased local extinction rates of Spotted Owls in sites where Barred Owls were present, and a positive association between Barred Owl removals and Spotted Owl vital rates. Apparent survival and local extinction rates appeared to be the key vital rates through which Barred Owls influenced Northern Spotted Owl populations, but both parameters reflected some combination of mortality, movements of owls off territories into an undetectable, nonbreeding floater population, and permanent movements out of study areas. In the Coast Range of Oregon, Wiens et al. (2014) observed lower survival rates for Spotted Owls (0.81) compared with Barred Owls (0.92) based on telemetry data where fates were known for individuals that co-occurred spatially, and where no permanent emigration of Spotted Owls was observed. Conversely, Spotted Owls that had not been detected in the GDR study area for many years sometimes reappeared in historical territories after the removal of Barred Owls (L. Diller personal observation). Given the high densities of Barred Owls that have been observed across most of the range of the Spotted Owl, our estimated declines in survival and increased local extinction rates of Spotted Owl territories likely reflected mortality rather than movement, but clearly both processes were occurring and likely interacted (i.e. displacement from territories may have increased Spotted Owl mortality). In addition, the relative importance of each process likely will continue to vary by study area relative to how long Barred Owls have been present and at what density.

While results from our study supported the hypothesis that competition with Barred Owls is an important stressor of Spotted Owl populations, nesting and roosting habitat loss and climatic patterns also were related to survival, occupancy, recruitment, and, to a lesser extent, fecundity, although there was little consistency in regard to which covariates were important for particular demographic parameters or across study areas. Our findings were consistent with other studies that have found links between habitat and demographic rates of Northern Spotted Owls (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, 2011, Forsman et al. 2011, Yackulic et al. 2014), and provided support for previous recommendations to preserve as much high-quality habitat in late-successional forests as possible across the range of the subspecies (Forsman et al. 2011). However, Barred Owl densities may now be high enough across the range of the Northern Spotted Owl that, despite the continued management and conservation of suitable owl habitat on federal lands (Davis et al. 2011, 2015), the long-term prognosis for the persistence of Northern Spotted Owls

may be in question without additional management intervention. For example, based on our study, the removal of Barred Owls in the GDR study area had rapid, positive effects on Northern Spotted Owl survival and rates of population change, suggesting that, along with habitat conservation and management, Barred Owl removal may be able to slow or reverse Northern Spotted Owl population declines on at least a localized scale (Diller et al. 2014).

We observed relationships between climate and survival rates for more study areas than previously reported (Forsman et al. 2011), and, in our analysis, recruitment was more strongly associated with climatic factors than the presence of Barred Owls. These relationships likely reflected the longer time series available for our analysis, rather than new relationships between owl demographics and climate, and, given predictions regarding climate change in the Pacific Northwest (warmer, wetter winters), these relationships warrant further exploration. Because rates of population change were a function of both survival and recruitment, lowered survival due to Barred Owls coupled with reduced recruitment due to climate change could lead to steeper future declines in Spotted Owl populations.

ACKNOWLEDGMENTS

This paper is the culmination of many years of work and dedication by a large number of biologists and researchers, one of whom we lost suddenly just before this analysis. Few had a greater impact on Spotted Owl conservation and management than Dr. Robert G. Anthony. His intelligence, energy, professionalism, and contagious sense of humor will be sorely missed. He was a good friend and mentor and we are grateful for having known him. This paper is dedicated to his memory. In addition, we are particularly indebted to Rich Fredrickson, Rocky Gutiérrez, Patti Happe, Lorin Hicks, Pete Loschl, Chuck Meslow, Gary Miller, Bruce Moorhead, Frank Oliver, Len Ruggiero, Erran Seaman, and Pat Ward, who were instrumental in the initiation of one or more of the demographic studies. Frank Oliver shaped, drilled, and polished over 12,000 color bands that we used to mark Spotted Owls. This study would not have been possible without the assistance of a small army of dedicated field biologists who helped collect the data. There have been so many of them that we can't remember all their names, but the ones who contributed the most were: Steve Adams, Steve Adey, Garth Alling, Meg Amos, David Anderson, Scott Armentrout, Duane Aubuchon, Keith Bagnall, Doug Barrett, Greg Bennett, Ryan Besser, Wendi Bonds, John Bottelli, Robin Bown, Cheryl Broyles, Mathew Brunner, Erin Burke, Tim Burnett, Joe Burns, Patty Buettner, Sue Canniff, Adam Canter, Chris Cantway, Bruce Casler, Doug Chamblin, Rita Claremont, David Clarkson, Billy Colegrove, Alan Comulada, Caroline Crowley, Ron Crutchley, Sam Cuenca, Natalie Cull, Amy Cunkelman, David Delaney, Glenn Desy, Diane Doersch, Michelle Dragoo, Desiree Early, Amy Ellingson, Roli Espinosa, Thomas Evans, Annie Farris, Mark Fasching, Tim Fetz, Helen Fitting, David Fix, Ernest Fliegel, Tracy Ford, Ray Forson, Gila Fox, Tim Fox, Shawna Franklin, Laura Friar, Ken Fukuda, Rudy Galindo, Dawn Garcia, Daniel George, Alan Giese, David Giessler, Charles Goddard, Teresa Godfrey, Jim Goode, Scott Graham, Eric Grant, Ashley Green, Allison Greenleaf, Tim Grubert, Gillian Hadley, Terry Hall, Tammy Hamer, Andy Hamilton, Keith Hamm, Timothy Hanks, Rick Hardy, Megan Harrigan, Steve Hayner, Amanda Heffner, Thomas Heinz, Marisa Herrera, Connie Holloway, Taryn Hoover, Eric Hopson, Scott Horton, Gay Hunter, John Hunter, Elizabeth Hurkes, Mark Irwin, Eugene Jackson, Ryan Jackson, Colin Jewett, Aaron Johnston, Jennifer Jones, Leilani Jones, Timm Kaminski, Marc Kasper, Tom Kay, Debaran Kelso, Leah Kenney, Wendy King, Wes King, Charles Knight, Mike Koranda, Richard Kosteke, Stan Kott, Amy Krause, David Lamphear, Chris Larson, Megan Larsson, Kurt Laubenheimer, Richard Leach, Rich Lechleitner, Doug Leslie, Krista Lewicki, Jeff Lewis, Patrick Loafman, Dan Loughman, Joanne Lowden, Rich Lowell, Hunter Lowry, Jessica Lux, Devin Malkin, Dave Manson, Kevin Maurice, Aaron McKarley, Dawn McCovey, Andrew McLain, Brian Meiering, Larry Melampy, Merri Melde, Joel Merriman, William Meyer, Christine Moen, Sean Mohren, Jason Mowdy, Ellen Meyers, Ben Murphy, Michael Murray, Suzanne Nelson, Matt Nixon, Timothy Parker, Heidi Pederson, Kim Pederson, Nicole Nielson-Pincus, Melanie O'Hara, Mary Oleri, Eduardo Olmeda, Michell O'Malley, Ivy Otto, Rob Owens, Antonio Padilla, Lyle Page, David Pavlackey, John Perkins, Jim Petterson, Mark Phillip, Tom Phillips, Tim Plawman, Aaron Pole, Andrew Pontius, Clayton Pope, Amy Price, Laura Quattrini, Laura Ratti, Elise Raymond, Mary Rasmussen, Reba Reidner, Angela Rex, Gail Rible, Kurt Richardson, Melanie Roan, Ana Roberts, Susan Roberts, Rob Roninger, Trish Roninger, Jen Sanborn, Jim Schaberl, Ted Schattenkerk, Anthony Scheiff, Britta Schielke, Jason Schilling, Matthew Schlesinger, Kary Schlick, Doreen Schmidt, Michael Schwerdt, Tim Selim, Shawn Servoss, Paula Shaklee, Erica Sisson, Gail Sitter, Kristian Skybak, Steve Small, Denise Smith, Don Smith, Spencer Smith, Alexis Smoluk, Tom Snetsinger, Maurice Sommé, Noel Soucy, Susannah Spock, Amy Stabins, Peter Steele, Cynthia Stern, Lori Stonum, Michael Storms, Bob Straub, Denise Strejc, Keith Swindle, Jim Swingle, Margy Taylor, Campbell Thompson, Joel Thompson, Jim Thrailkill, Trinity Tippin, Sheila Turner-Hane, Shem Unger, Jennifer Van Gelder, Andrew Van Lanen, Nick Van Lanen, Veronica Vega, Frank F. Wagner, Fred Wahl, Stephanie Waldo, Abe Walston, Fred Way, Kevin White, Mark Williams, Kari Williamson, Heather Wise, Jim Woodford, Sarah Wyshynski, Lance Wyss, Bryan Yost, Kendall Young, Jessica Zeldt, and Joe Zisa. Brooke Morris at the Oregon Cooperative Wildlife Research Unit, and Ann Leen and Kim Howard at the Department of Fisheries and Wildlife, Oregon State University, provided administrative support for the workshop, and we could not have hosted this event without their help.

Funding statement: Funding for demographic studies of Northern Spotted Owls on federal lands was provided

primarily by the USDA Forest Service, USDI Bureau of Land Management, and USDI National Park Service. Funding for studies on nonfederal lands came from the Green Diamond Resource Company, Plum Creek Timber Company, Louisiana Pacific Lumber Company, Hancock Forest Management, and the Hoopa Tribe. Funding for the workshop was provided by the USDA Forest Service and USDI Bureau of Land Management via a Cost Reimbursable Research Agreement with Oregon State University. The U.S. Geological Survey and USDA Forest Service required approval of the final manuscript before publication, but none of the funding agencies associated with this meta-analysis had any influence on the content of the submitted or published manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Ethics statement: All data from study areas in which K.M.D., E.D.F., and A.B.F. were principal investigators (CLE, OLY, COA, HJA, TYE, CAS, and NWC) were collected following protocols approved under animal care and use permits overseen by Oregon State University's and Colorado State University's Institutional Animal Care and Use Committees. These protocols were followed and all relevant state and federal permits were acquired and maintained for all study areas included in this meta-analysis.

Author contributions: (1) K.M.D., E.D.F., A.B.F., R.J.D., G.C.W, C.J.S., K.P.B., J.D.N., J.E.H., C.B.Y., P.F.D., L.B., L.V.D., D.R.H., J.M.H., and T.M. conceived the idea, design, and experiment; (2) K.M.D., E.D.F., A.B.F., R.J.D., S.H.A., L.S.A., B.L.B., J.B., P.C.C., L.V.D., E.M.G., S.A.G., D.R.H., J.M.H., J.H., R.B.H., C.M., J.A.R., J.R., and S.G.S. conducted the research; (3) K.M.D., E.D.F., A.B.F., R.J.D., K.P.B., G.C.W., J.D.N., C.J.S., C.B.Y, D.A.C., M.J.C., and P.C.C. wrote the paper; (4) K.M.D., E.D.F., A.B.F., R.J.D., G.C.W., C.J.S., K.P.B., J.D.N., J.E.H., C.B.Y., P.F.D., L.B., T.M., and J.A.R. developed and designed the methods; (5) R.J.D., G.C.W., C.J.S., J.E.H., C.B.Y., L.B., B.A., J.B., P.C.C., M.J.C., E.M.G., A.G., J.M.H., J.H., K.P.H., T.M., K.M., G.S.O., J.R., V.R., and J.S. analyzed the data; and (6) R.J.D. contributed substantial materials, resources, and funding.

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APPENDIX A

Study Area Characteristics

Study areas in the Cascade Mountains and on the Olympic Peninsula (Olympic [OLY], Rainier [RAI], Cle Elum [CLE], H. J. Andrews [HJA], and South Cascades [CAS]) were characterized by rugged mountains where forests extended from the lowlands (~180–1200 m elevation) up to the timberline (>1500 m elevation). Study areas in the Oregon Coast Ranges (Coast Ranges [COA] and Tyee [TYE]) and Klamath Mountains in southwestern Oregon and northwestern California (Klamath [KLA], NW California [NWC], Green Diamond Resources [GDR], and Hoopa [HUP]) also were mountainous, with elevations ranging from ~120 to 760 m. Mean annual precipitation was variable among and within study areas, ranging from ~120 cm per year in the Klamath study area to >350 cm per year on the western side of the Olympic Peninsula (Table 3). Variation in precipitation within a study area was most pronounced on the Olympic Peninsula, where average annual precipitation was ~350 cm yr^{-1} on the west side of the Olympic Mountains, but only ~41 cm yr^{-1} on the east side of the Olympic Mountains. Most precipitation occurred as rain during fall and winter in study areas in the Coastal Mountains of western Oregon and northwestern California (COA, TYE, KLA, NWC, GDR, and HUP), whereas precipitation in study areas in the Cascade Mountains (CLE, RAI, HJA, and CAS) and on the Olympic Peninsula (OLY) occurred as a mixture of snow in winter and rain in spring and fall.

The vegetation in all study areas was predominantly coniferous forest, but the age and species composition of forests varied widely among areas depending upon latitude, climate, and management history. In Washington, the OLY study area was dominated by coastal forests of western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*), and the CLE study area was

dominated by mixed conifer and ponderosa pine (*Pinus ponderosa*) forests that included mixtures of Douglas-fir, grand fir (*Abies grandis*), ponderosa pine, and western larch (*Larix occidentalis*). The RAI study area in the western Washington Cascades and the COA and HJA study areas in northwestern Oregon were dominated by mesic forests of Douglas-fir, western hemlock, and western redcedar.

In southwestern Oregon, the TYE and KLA study areas were dominated by Douglas-fir and incense cedar (*Calocedrus decurrens*), with highly variable amounts of ponderosa pine, white fir (*Abies concolor*), western white pine (*Pinus monticola*), sugar pine (*P. lambertiana*), canyon live oak (*Quercus chrysolepis*), Oregon white oak (*Q. garryana*), Pacific madrone (*Arbutus menziesii*), giant chinquapin (*Chrysolepis chrysophylla*), and California laurel (*Umbellularia californica*). Vegetation in the CAS study area in the southern Oregon Cascades was similar to vegetation in the TYE and KLA areas, except at higher elevations, where forests were dominated by Shasta red fir (*Abies magnifica* var. *shastensis*), Douglas-fir, and western hemlock.

Study areas in northwestern California were dominated by mixed conifer or mixed evergreen forests in which the overstory conifers were typically Douglas-fir, grand fir, white fir, or coastal redwood (*Sequoia sempervirens*), and common understory trees were tanoak (*Notholithocarpus densiflorus*), Pacific madrone, California laurel, Oregon white oak, and California black oak (*Quercus kelloggii*; Franklin and Dyrness 1973).

The age distribution and structure of forests varied widely among study areas depending on the history of fire and timber harvest. Most study areas (OLY, RAI, HJA, COA, TYE, CAS, KLA, NWC, and HUP) were characterized by a mixture of mature forest (100–200 yr old) and old-growth forest (>200 yr old) interspersed with young forests regenerating in areas that had been clear-cut or burned. Dominant overstory trees in mature and old-growth forests commonly exceeded 100 cm in diameter at breast height (DBH), and occasionally exceeded 200 cm DBH in the more mesic study areas. Portions of the CAS, OLY, and RAI study areas were inside National Parks, where forests had never been harvested and were mostly mature and old-growth stands that had developed after historical fires and windstorms. In several study areas, where thinning or partial overstory removal was a common method of forest management (CLE, KLA, and CAS), the age structure both within and among stands was highly variable because of the removal of selected trees in the overstory or understory. This was particularly the case in the CLE study area, where many stands had been entered to "high-grade" the large overstory trees, leaving stands dominated by small trees and scattered old, dominant trees. In the GDR study area in California, nearly all stands of old trees had been clear-cut and converted to young forests that were <70 yr old (Diller and Thome 1999).

As described in previous publications, the 11 study areas in our analysis were not selected randomly (Franklin et al. 1996, Anthony et al. 2006, Forsman et al. 2011). They were initially selected based on many different factors, including lobbying by local interest groups, opportunistic funding sources, land ownership boundaries, and agency attempts to improve sampling coverage by adding study areas in different regions within the range of the Northern Spotted Owl. Although the study areas were not randomly selected, they did include samples from most of the geographic provinces within the range of the Northern Spotted Owl (Figure 1), and they covered a total area of 19,813 km^2, or ~9% of the range of the Northern Spotted Owl, which has been estimated at 230,690 km^2 (USDA Forest Service and USDI Bureau of Land Management 1994). In addition, the percentage of suitable Spotted Owl habitat in the 8 study areas that were part of the Northwest Forest Plan (NWFP) effectiveness monitoring program (OLY, CLE, COA, HJA, TYE, KLA, CAS, and NWC) was similar to that in surrounding areas (Anthony et al. 2006; Appendix F); thus, we believe that the habitat conditions within these study areas characterized the range of forest conditions on federal and matrix forest lands within the range of the owl, and likely reflected conditions on federal forest lands in general. We were less certain that our sample reflected general patterns on nonfederal lands because managers on the 3 nonfederal study areas in our sample (RAI, GDR, and HUP) were actively managing to protect Spotted Owls and their habitat. This differed from practices on most nonfederal lands in the range of the owl, where management of habitat for Northern Spotted Owls was not a high priority.

APPENDIX B

Survey Methods and Workshop Protocols

Survey methods. Surveys were conducted during the breeding season (March through August) using vocal imitation or playback of owl calls to elicit territorial vocalizations from Spotted Owls, thereby revealing their presence (Reid et al. 1999). The number of surveys of each owl territory in each year was normally ≥3, although the survey protocol allowed for fewer visits in cases in which a pair was detected and the female had no brood patch or showed no evidence of nesting during the period when she should have been incubating or brooding young. After surveyors became familiar with the distribution of owl territories in their study areas, it was often possible to locate owls by simply calling quietly while visually searching the historical roost or nest areas during the day. If owls were not located during diurnal visits, surveyors searched the entire territory at night by calling

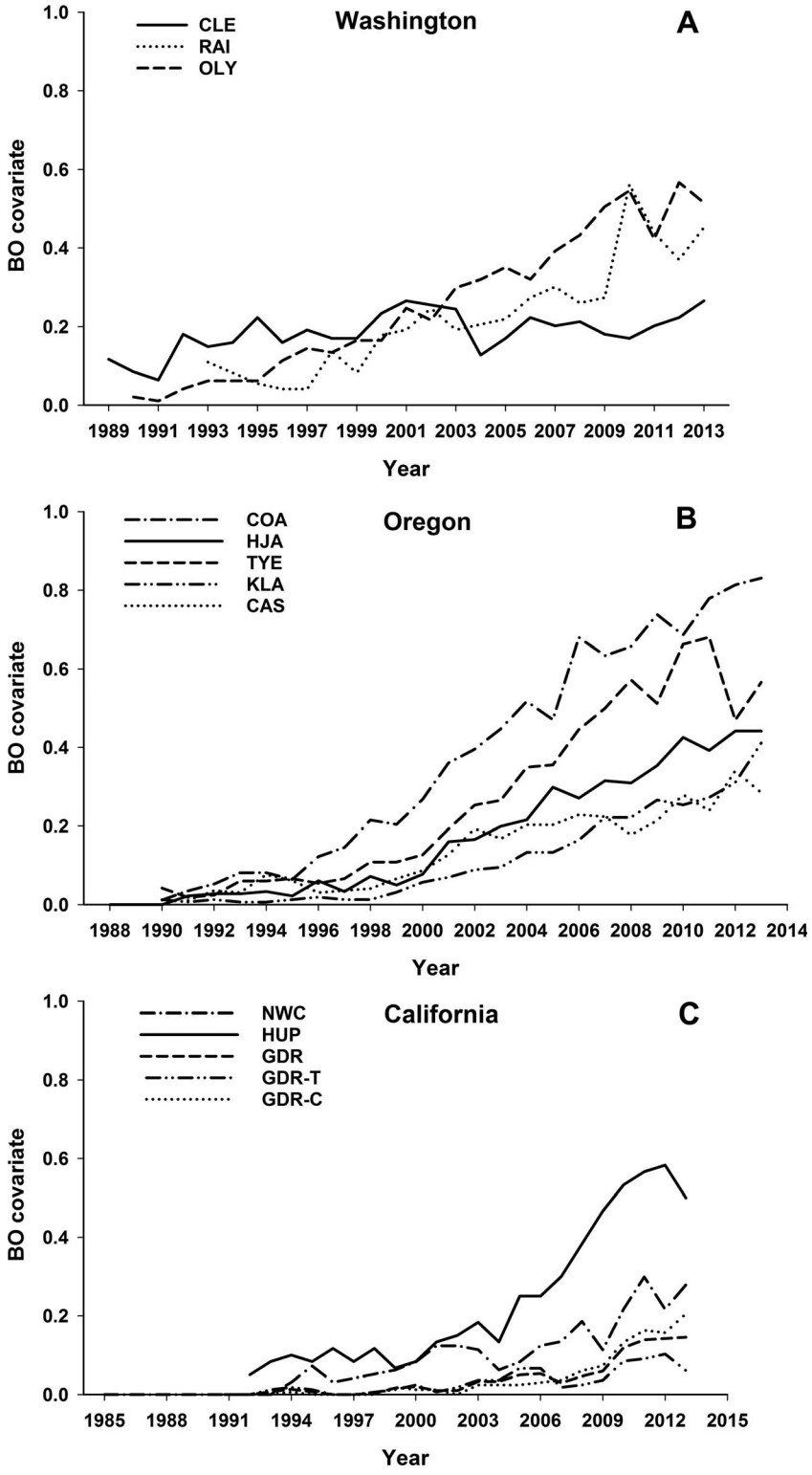
from survey stations distributed throughout the area (Lint et al. 1999).

When nonjuvenile owls were first located, they were captured and banded with a U.S. Geological Survey (USGS) numbered band on one leg and an acrylic band that was uniquely patterned and colored on the other leg (Forsman et al. 1996b). Juveniles were banded with identical acrylic color bands on one leg and a numbered USGS band on the opposite leg. If a bird banded as a juvenile was detected holding a territory in later years, it was retrapped, and its color band was replaced with a uniquely patterned color band used for nonjuveniles. The uniquely patterned color bands made it possible to identify owls visually without retrapping them. The procedure for identifying marked owls without recapturing them was to lure them in with a live mouse or artificial lure and examine their bands at close range with binoculars (Franklin et al. 1996, Reid et al. 1999).

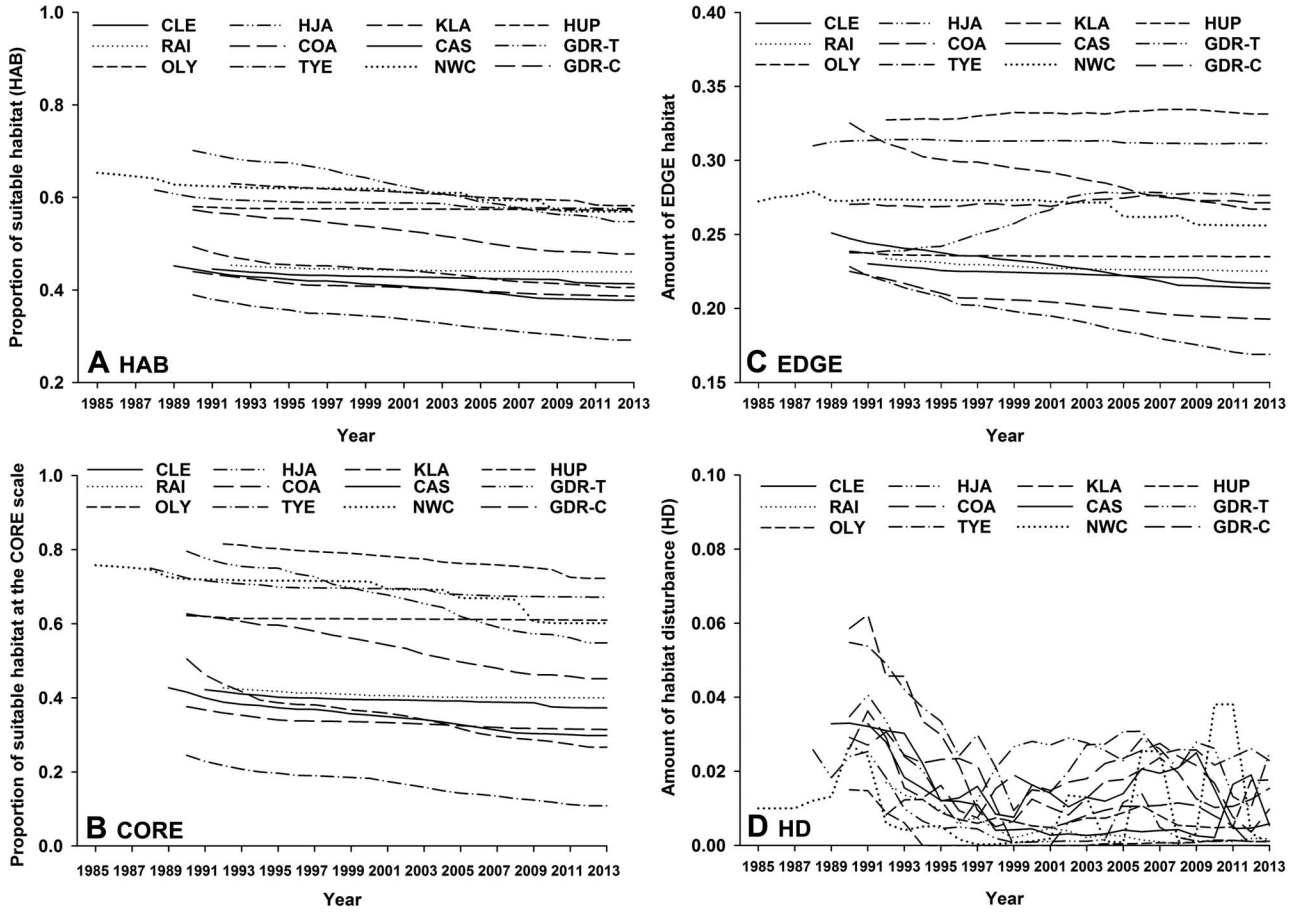
Because it often took several years for surveyors to become familiar with their study areas and to settle on study area boundaries that could be effectively surveyed, we truncated the data to remove the first 1–5 yr of survey data from the individual study areas. The number of years included in the analysis of individual study areas ranged from 22 to 29. Once owls were located each year, we followed a standard protocol to determine whether they were attempting to nest and to estimate the number of young produced by each female (Franklin et al. 1996, Lint et al. 1999, Reid et al. 1999). This protocol involved either feeding live mice to owls (majority of cases) or examining the brood patches of captured females during the nesting season (see details in Franklin et al. 1996). The number of young fledged per female (NYF) was defined as the maximum number of young detected during at least 2 visits after the young had left the nest tree. We included some exceptions to this protocol in order to reduce bias in estimates of NYF. For example, females were given a "0" for NYF if they: (1) did not appear to be nesting during 1 or more visits during early spring and then could not be relocated on multiple return visits, or (2) appeared to be nesting, but then could not be relocated on multiple return visits to the nest area. These exceptions were allowed because females that did not nest or whose nesting attempts were unsuccessful sometimes quickly disappeared and could not be relocated before the full protocol could be met, and we were concerned that we would overestimate NYF if we excluded these females from the data.

Workshop protocols. Instructions and protocols for data formatting were developed and reviewed several months before the workshop and then implemented by participants to create datasets for all analyses. Data from each study area were then checked for errors by randomly drawing a sample of 10 records from the files submitted and checking the original data sheets to ensure that the data were correctly entered and that field personnel had followed established protocols for locating, banding, and identifying individual Northern Spotted Owls, and for documenting the number of young produced. If the data were correctly formatted and the field forms for the 10 randomly sampled records supported the data coding, then the data were approved for analysis. If there were problems with the data or formatting, the study area leader was apprised of the problem, and told to review and correct their files and then resubmit another set of 10 randomly selected records for a second round of error-checking. This correction, resampling, and review process continued until the data passed inspection.

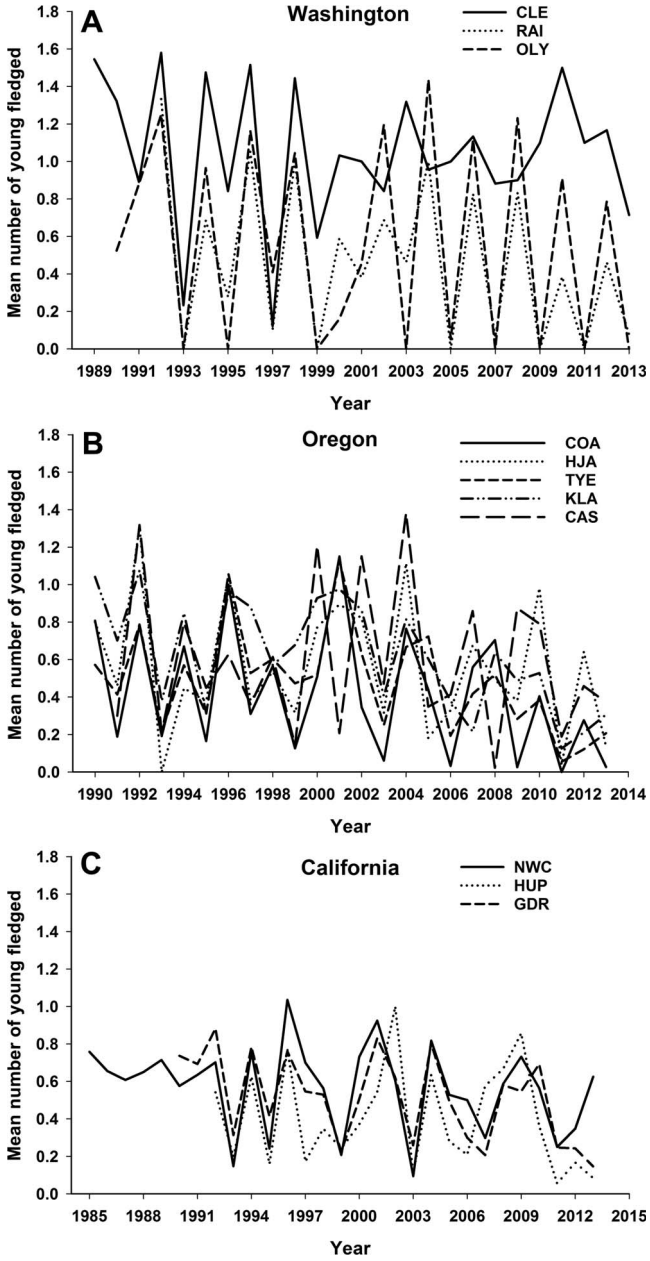
After participants arrived at the workshop, for the first 2 days the entire group of biologists and analysts met to discuss and agree on plausible hypotheses, analytical protocols, and a priori models that would be used in the analysis (Anderson et al. 1999). Once these discussions were concluded, and everyone was in agreement regarding hypotheses and protocols, study area leaders were required to sign a form stating that their data had passed the error-checking process and were ready for analysis. This form also stipulated that once the participant released their data for analysis during the workshop, it could not be withdrawn, regardless of the outcome of the analysis. Once the analysis began, any refinements to models or analysis protocols were discussed and agreed upon by all participants as the workshop progressed.



APPENDIX C FIGURE 13. Annual proportion of Northern Spotted Owl territories with Barred Owl detections (BO covariate) in study areas in (**A**) Washington, (**B**) Oregon, and (**C**) California, USA, 1985–2013. See Table 2 for study area abbreviations.



APPENDIX D FIGURE 14. Habitat covariates, including (**A**) the percent cover of suitable owl habitat within a 2.4-km radius of owl activity centers (HAB), (**B**) a neighborhood focal statistic defined as the proportion of 30 m^2 pixels with $\geq$50% suitable habitat within 800 m of each pixel (CORE), (**C**) the amount of interface between suitable owl nesting habitat and other cover types (EDGE), and (**D**) the percentage of suitable habitat that was disturbed (HD), used to model fecundity, survival, recruitment, lambda, and occupancy of Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013. See Table 2 for study area abbreviations.



APPENDIX E FIGURE 15. Reproductive covariate (mean number of young fledged per pair per year) used to model survival and recapture probabilities of Northern Spotted Owls in 11 study areas in (**A**) Washington, (**B**) Oregon, and (**C**) California, USA, during 1985–2013. See Table 2 for study area abbreviations.

APPENDIX F

The Why and What of Random Effects (by Kenneth P. Burnham)

Standard likelihood inference treats parameters as fixed effects; hence, all inference is based only on sampling variation, which is estimated from the likelihood function. However, that source of variation ignores the "process" variation (σ^2) in a set of parameters, such as annual survival probabilities. Hence, a linear model for trend, such as $S_i = a + b^*i + \epsilon_i$, embedded into the likelihood results in inference being based only on conditional sampling variation. The expected value of $(\epsilon_i)^2$ is $var(\hat{S}_i \mid S_i)$, but its sampling variation excludes process variation. Process variation is the conceptual, unexplained ("random") variation in the true, unknown set of S_i beyond any variation explained by a model structure. Viewed this way, S_i is considered a random variable, not a fixed constant.

Now, rather than using $S_i = a + b^*i + \epsilon_i$ for inference, the correct model for proper inference must involve $S_i = a +$

$b^*i + \delta_i$, where the expected value of $(\delta_i)^2$ is σ^2. However, process variation cannot be estimated from the likelihood. Moreover, ignoring process variation when making inference about parameters a and b is a logical mistake and can result in the seriously flawed inference of unjustifiably claiming "significance." So, what to do?

It is not generally correct to do standard regression on the maximum likelihood estimates (MLEs) $\hat{S}_i$ to make inference about the effect of a covariate, X_i, or about time trends, $X_i = i$. The model structure one needs is $\hat{S}_i = a + b^*X_i + \delta_i + \epsilon_i$, and the variance–covariance structure must now account for any sampling covariances among the MLEs. The sampling variances and covariances are estimated based on the model likelihood that produces the MLEs. Let that conditional sampling variance–covariance (VC) matrix be denoted as W. Also, we use here vector notation for the parameters in the likelihood $\underline{S}$. If interest is in a general linear model such as $\underline{S} = X\underline{\beta} + \underline{\delta}$, the actual model we must use is represented as:

$$\underline{\hat{S}} = X\underline{\beta} + \underline{\delta} + \underline{\epsilon}, \mathrm{VC}(\underline{\delta} + \underline{\epsilon}) = D = \sigma^2 I + W.$$

(Note: Full mathematical rigor is not being used here as this material focuses on concepts.) A further complication can be overdispersion in the data, estimated as $\hat{c}$. If overdispersion must be allowed for, then W is replaced by $\hat{c}W$.

Given this framework for correct frequentist inference about population-level parameters, $\underline{\beta}$, all the requisite theory is known and can be used in program MARK. For details, the interested reader is referred primarily to Burnham (2013), which is freely available. Burnham (2013) presents the full relevant theory when random effects issues arise for sets of capture–recapture parameters, as well as additional concepts such as shrinkage estimates. See also Burnham and White (2002), Franklin et al. (2002), and White et al. (2009) for additional discussion.

Now we look further at the issue of overdispersion. Consider the simplest case, wherein the $\hat{S}_i$ are independent and all with the same sampling variation, *var*; hence:

$$\mathrm{VC}(\underline{\delta} + \underline{\epsilon}) = D = \sigma^2 I + c(var)I = (\sigma^2 + c(var))I.$$

The linear model is now a standard one: The $\hat{S}_i$ are uncorrelated, with equal variability, and therefore standard regression can be used. The issue of overdispersion is then irrelevant, and inference can be based on the observed empirical variation among the set of $\hat{S}_i$. In this case, there is total robustness to overdispersion. In the general case (correlated $\hat{S}_i$ and unequal sampling variances), there is considerable robustness to overdispersion because the observed variation among the $\hat{S}_i$ is central to estimation of σ^2 and somewhat compensates for imperfect information about c. In fact, conceptually, scaled total variation in the set of $\hat{S}_i$ equals $\sigma^2 I + cW$. Consequently, as $\hat{c}$ increases, $\hat{\sigma}^2$ decreases, and this inverse relationship is what provides some robustness of inference about $\underline{\beta}$ to overdispersion using the random effects approach. However, we note that $\hat{\sigma}^2$ is quite sensitive to $\hat{c}$, but its isolated value is not central to inference about $\underline{\beta}$.

It appears that evidence (such as a t-statistic) about a covariate parameter (such as a linear time trend) is minimized at $c = 1$; thus, use of $\hat{c} = 1$ is conservative. For any random effects analysis it is easy to check this supposition by trying several values of $\hat{c}$. Program MARK is distributed with a lot of examples. The files denoted MPM14.* have real data on adult male Mallards (*Anas platyrhynchos*) banded preseason over 42 yr. For these data, the best estimate of the overdispersion factor is $\hat{c} = 1.195$. Below are some results for these data, using the random effects method in program MARK with a linear time-effects model on annual survival probability (detailed results using the Mallard banding data are available from K. P. Burnham):

c	$\hat{b}$	$\hat{se}$	t	$\hat{\sigma}$
1.000	0.00316	0.00111	2.85	0.0781
1.195	0.00321	0.00103	3.12	0.0707
1.250	0.00322	0.00101	3.19	0.0686
1.500	0.00328	0.00092	3.57	0.0593

Additional exploration has supported the idea, and observation, that use of $\hat{c} = 1.0$ is conservative for inference about population-level structural parameters, and that there is robustness of such inference to the numerical value of c.

We note that $\hat{c} = 1.0$ was used with the analyses of these extant Northern Spotted Owl data because estimation of c strongly supported this value. Nonetheless, it is worth knowing that this choice will have led to conservative inferences. The answer, then, to the implied question of why to use random effects analysis is: because it is the correct analysis for using the MLE estimates for inference on structural parameters in population-level models. "What" this also gives us is robustness to the overdispersion issue, as well as conservative inferences with $\hat{c} = 1.0$.

APPENDIX G

Study Area Selection, Potential Biases, and Survey and Analysis Considerations

It is important to acknowledge possible biases associated with estimates of vital rates for Northern Spotted Owls from long-term demographic studies. Other authors have discussed these possible biases (Raphael et al. 1996, Van Deusen et al. 1998, Manly et al. 1999, Boyce et al. 2005, Loehle et al. 2005, Forsman et al. 2011), some of which

have been rebutted (Franklin et al. 2006). Regardless, we believe that the most important sources of bias to consider are as follows:

Study area selection. We note that, because we did not randomly select our study areas, we make formal statistical inference only from the sample of marked, territorial owls used in our analysis to the population of owls in our study areas. However, we believe that our results are representative of Northern Spotted Owl populations on federal and mixed federal and private lands because our study areas: (1) encompassed 9% of the total range of the Northern Spotted Owl, (2) contained most habitat types used by the species, and (3) contained elements of most of the physiographic provinces in which the species occurs.

Habitat covariates. After investigating the habitat covariates more closely, we found that, despite a predicted negative relationship between the amount of nesting and roosting habitat (HAB) and the amount of edge habitat (i.e. as HAB declines, EDGE increases), these two covariates were strongly positively correlated on many study areas. This was because EDGE was defined in relation to HAB, so as HAB declined, in some cases dramatically over time, the amount of EDGE relative to HAB also declined.

Potential biases in estimates of demographic parameters. *Rate of population change (λ).* Key assumptions that must be met to use Pradel's (1996) model to estimate the finite rate of population increase (λ) are: (1) similar detection probabilities for all territorial birds, (2) similar areas sampled each year of study, and (3) no band loss. Two sources of variation in detection probabilities potentially relevant to Spotted Owls are "trap response" and heterogeneity (Hines and Nichols 2002). Trap response refers to the situation in which new, unmarked birds have different (typically lower) probabilities of detection than previously marked birds. Heterogeneity refers to variation in detection probability among individuals that cannot be attributed to trap response or to a measurable individual covariate. Sampling methods in our study were designed to minimize sources of variation in detection probabilities, and we do not believe that such variation led to substantive bias in our estimates of λ. In some cases, study areas surveyed for Spotted Owls were expanded, but we eliminated any associated bias in estimates of λ by accounting for these changes in our modeling. Finally, as reported above, Franklin et al. (1996) provided evidence that band loss in Northern Spotted Owls was negligible.

Occupancy. Three potential sources of bias in our parameter estimates for the occupancy analysis were: (1) the effects of unmodeled heterogeneity in capture probability, (2) the potential for small-sample bias in some study areas, and (3) the way we defined occupancy for Barred Owls. The only prior multispecies, multiseason modeling of Northern Spotted Owls and Barred Owls was completed in one study area (TYE), during an overlapping time period, and using a different definition of owl territories and different habitat covariates, in addition to including more covariates to explain heterogeneity in detection probabilities (Yackulic et al. 2014). Despite these methodological differences, the results reported by Yackulic et al. (2014) are similar to ours, suggesting that any heterogeneity that was unmodeled in our analysis may have been unimportant. The potential for small-sample bias has been explored in single-species, multiseason occupancy models (e.g., Mckann et al. 2013), but has not been explored for 2-species, multiseason occupancy models. Assuming that conditions identified by Mckann et al. (2013) can be generalized to 2-species models, it is possible that the smaller number of sites in some study areas (RAI, NWC, and HUP) led to bias in parameter estimates. However, Mckann et al. (2013) assumed a relatively short time series (5 yr) in their simulations, as compared with 19 yr for most territories in our analysis, and longer time series may compensate for fewer territories in some areas. Lastly, we defined Barred Owl occupancy in terms of one or more Barred Owls because the incidental detection data that we had available did not distinguish single owls from pairs (Yackulic et al. 2012, 2014). Moreover, as Barred Owl densities increase there may be multiple pairs of Barred Owls occupying each individual Spotted Owl territory (Wiens et al. 2014). Both of these factors suggest that the impacts of Barred Owl presence on Spotted Owl colonization and extinction may not be constant across territories or time. Given increasing Barred Owl densities in most study areas, the estimated effect of Barred Owl presence on Spotted Owl extinction and colonization in this study may have underestimated actual effects. However, the strength of the Barred Owl effect on extinction probabilities of Spotted Owls did not appear to increase through time in the TYE study area when prior data analyses were performed (C. Yackulic personal communication), so this negative bias may be small.

Fecundity. Although differences in the detectability of nesting and nonnesting owls could cause positive or negative biases in estimates of fecundity (Anthony et al. 2006), we believe that our estimates of fecundity were reasonably accurate because they pertained only to territorial owls and annual detection probabilities of territorial owls in our studies were high (>75%), regardless of nesting status. If anything, we suspect that our estimates may have been biased slightly high because nonbreeding territorial females might be harder to detect, but this should not have affected our comparisons of long-term trends, assuming that any such bias was consistent among years.

Apparent survival. Heterogeneity in recapture probability, temporary or permanent emigration, and band loss are the primary factors associated with bias or decreased

precision in estimates of survival from marked individuals in Cormack-Jolly-Seber open population models (Lebreton et al. 1992). Two of these potential sources of bias, heterogeneity in recapture rates and temporary emigration, were investigated by Manly et al. (1999) for Northern Spotted Owls in the eastern Cascades of Washington using computer simulations. In their analysis, lack of independence between capture probabilities of paired males and females, variation in recapture rates, and temporary emigration had little effect on estimates of apparent survival. Potential bias associated with heterogeneity of recapture rates was likely low because both survival and detection probabilities were generally high (Carothers 1973, Pollock et al. 1990, Hwang and Chao 1995). As noted above, annual detection probabilities observed in our study were generally very high (>75%), suggesting little unmodeled heterogeneity in recapture rates. Dispersal of resident, territorial Northern Spotted Owls in a subset of the study areas included in our analysis was estimated at ~7% each year (Forsman et al. 2002), and most of the individuals that dispersed were relocated in adjacent territories within the study area boundaries. Thus, while some undetected movements outside each study area almost certainly occurred each year, the negative bias in apparent survival associated with permanent emigration beyond the boundaries of our study areas was likely quite low when these studies were initiated. However, as noted above, the increased displacement of Spotted Owls into undetectable, nonterritorial floater populations due to increasing Barred Owl densities may be occurring in all our study areas. Thus, decreasing trends in apparent survival of Spotted Owls may not reflect increased mortality, but rather increased permanent emigration due to competition with Barred Owls.

Lastly, Franklin et al. (1996) examined records from >6,000 Northern Spotted Owls that were double-banded with colored bands and numbered metal bands, and found only 2 cases in which the color band was lost and 2 cases in which the numbered metal band was lost (<0.07% total band loss). Based on this evaluation, we believe that negative bias in estimates of apparent survival associated with band loss in our study was extremely low.

Survey and analysis considerations. Previous Spotted Owl meta-analyses have taken advantage of both refinements in existing estimation methodology and development of new methods. Major changes in analytical approaches in our analyses included the addition of 2-species dynamic occupancy analyses (this study) and a shift from projection matrices to capture–recapture approaches for estimation of λ (Franklin et al. 2004, Anthony et al. 2006). As noted above, possible differences in detection probabilities of territorial breeders and nonbreeders is a potential source of bias in fecundity analyses that we do not believe to be substantial. However, we note that such variation in detection probabilities can now be addressed using multistate occupancy models (Nichols et al. 2007, Stoelting et al. 2015). In addition to dealing with detection probabilities of Spotted Owls, the dynamic 2-species occupancy modeling used in our analyses could be expanded to include the 2 Spotted Owl occupancy states of breeding and nonbreeding, thus permitting direct inference about territory-level effects of Barred Owls on Spotted Owl fecundity. The addition of one state to the dynamic occupancy analysis admittedly would complicate the modeling, but the following benefits merit consideration of this approach: (1) addressing detection probabilities that may vary between breeders and nonbreeders, (2) permitting direct inference about Barred Owl presence on fecundity, and (3) incorporating into the analysis the extra information of territory-level occupancy state and fecundity in the previous year. One additional approach that may merit consideration is a joint analysis of Spotted Owl survival with territory-level Barred Owl presence (based on occupancy modeling) as a "covariate."

Improvements to the current study design might also include changes to field survey protocols to include Barred Owl–specific surveys during each breeding season, which would increase detection rates of Barred Owls in our study areas (Wiens et al. 2011). The additional cost of Barred Owl surveys might not outweigh the benefits, although incorporating such surveys into the current Spotted Owl protocols might be possible with only relatively minor increases in survey cost (Diller et al. 2014).

APPENDIX H

Analytical Approach

Annual rates of population change. In addition to derived annual estimates of lambda (λ_t), the Pradel reverse Cormack-Jolly-Seber (CJS) model (Pradel 1996) allowed for the decomposition of annual estimates of λ_t into 2 components, apparent survival (ϕ_t) and recruitment (f_t), where:

$$\lambda_t = \phi_t + f_t.$$

In this case , ϕ_t was local apparent survival and reflected both survival and retention of territory holders within the study area. Recruitment (f_t) was the number of new animals in the population at time $t + 1$ per animal in the population at time t, and reflected both in situ recruitment and immigration of recruits from outside the study area. Thus, estimates of λ_t included all losses and gains to the study area population during each year and were used to generate estimates of realized population change in each study area.

We changed from f-parameterization to λ-parameterization before running random effects models on λ_t in

program MARK because, in order to obtain model selection results for random effects on λ, it is necessary for the parameter to be in the model (i.e. not derived; Pradel 1996, Hines and Nichols 2002). We used $\hat{c} = 1$ for analyses of the rate of population change, because overdispersion in this parameter in previous analyses of Spotted Owl population data was negligible (Anthony et al. 2006, Forsman et al. 2011). We initially investigated fixed effects models with general time dependence on survival (ϕ_t) and recruitment (f_t), and combinations of annual time and sex effects on recapture rates (p). The best structure of p from the model with the lowest Akaike's Information Criterion corrected for small sample size (AIC_c) was retained and used as the base fixed effects model for 5 random effects models of λ_t. The 5 random effects models included the intercept-only (no effect), general time (t), linear time trend (T), log-linear time trend (lnT), and spline models (SPLINE, with knots every 5 yr backward from 2013, such that the first interval was $\geq$5 years; Bonner et al. 2009). The log-link function was used for lambda or recruitment in fixed effects models, and the identity link function was used for lambda in the random effects models.

Occupancy analysis. We used an iterative model selection process that allowed us to explore different structures for each of the 8 model components (initial occupancy, colonization, extinction, and detection probability, for each of the 2 species). For detection probabilities, we considered within- and among-year variation for both species, as well as temporal trends. We also considered models in which Barred Owl detection probabilities differed when Spotted Owls were present, and models in which Spotted Owl detection probabilities differed when Barred Owls were either: (1) present, but not necessarily detected by survey during that specific survey period, or (2) present and detected during the same survey period. We hypothesized that Spotted Owl detection probabilities would be lower when Barred Owls were present, and lower still when Barred Owls were present and detected, because of the aggressiveness of Barred Owls (Van Lanen et al. 2011). At the same time, the presence of Spotted Owls could have led to lower detection rates of Barred Owls because surveyors ceased calling once Spotted Owls were detected. Field survey protocols were solely focused on detecting Spotted Owls, so only Spotted Owl calls were used to conduct surveys (Forsman et al. 1996a), and the detection of Barred Owls was incidental to that effort. Therefore, we also included a "trap response" model on detection probabilities for each species. For example, if Spotted Owls were detected during a previous visit, detection probabilities for Spotted Owls were predicted to increase during subsequent visits due to knowledge gained by surveyors regarding Spotted Owl locations within a territory, resulting in a more focused calling effort around those previous locations (Tempel and Gutiérrez 2013). Conversely, this same process might be expected to result in decreased detection probabilities for Barred Owls as surveys were then potentially focused on a smaller area within the Spotted Owl territory.

Fecundity. We used the normal distribution regression model on annual averages for the analysis of the number of young fledged per female (NYF) by age class in each study area (Anthony et al. 2006, Forsman et al. 2011). We averaged across owl territories by year in each area to equalize the variance-to-mean relationship for NYF in order to meet the homoscedasticity assumption inherent in the normal distribution model. Covariates of interest (Barred Owls [BO], habitat, and weather) were measured at the population (study area) level. Thus, the appropriate sample unit for this analysis was not owl territories but study area and age class combinations that responded to yearly effects that influenced entire study areas. In addition, by averaging NYF and treating study areas as sampling units, we avoided autocorrelation issues over time for individual owl territories. The pattern of the variance-to-mean ratio was consistent with a truncated Poisson distribution because Spotted Owl pairs seldom raise more than 2 young (underlying data structure = 0, 1, 2). However, the mean NYF per year by age class and study area was not Poisson distributed (Forsman et al. 2011). Normal models are more accurate than Poisson models when data depart from a Poisson distribution (White and Bennetts 1996), and are just as accurate as multinomial models when averages are analyzed (McDonald and White 2010). Thus, we used a regression model based on a normal distribution to model mean annual NYF in each study area as:

$$\text{PROC MIXED; MODEL MEAN\_NYF} = \text{fixed effects}.$$

Residual variation was a combination of year-to-year variation and estimated variation around the actual mean and was approximately equal to:

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

where n = number of territorial females checked in a particular year. We performed several diagnostics to justify this approach. First, we conducted a variance components analysis on individual NYF records for adult females (adjusted for obvious even–odd year affects) to confirm that spatial variance among territories tended to be small relative to temporal variance among years and other residual effects. This negated the need to include owl territories as a random effect, because ignoring spatial variance within study areas would not bias results. In addition, we were able to support the key assumption that residual variation (var(residual)) was relatively constant based on the following: (1) var(NYF)/n was small relative

to var(year effects), (2) relatively few (<10%) territorial subadults were encountered, such that var(NYF)/n was also approximately constant, even though var(NYF) may decline with increasing age class, and (3) there was no evidence of heterogeneous variances based on a Levene's test (Ramsey and Schafer 2002). Finally, we assumed that residual effects were approximately normally distributed based on the central limit theorem, which states that the average of the measurements will have an approximately normal distribution with large sample sizes even if the individual measurements are discrete.

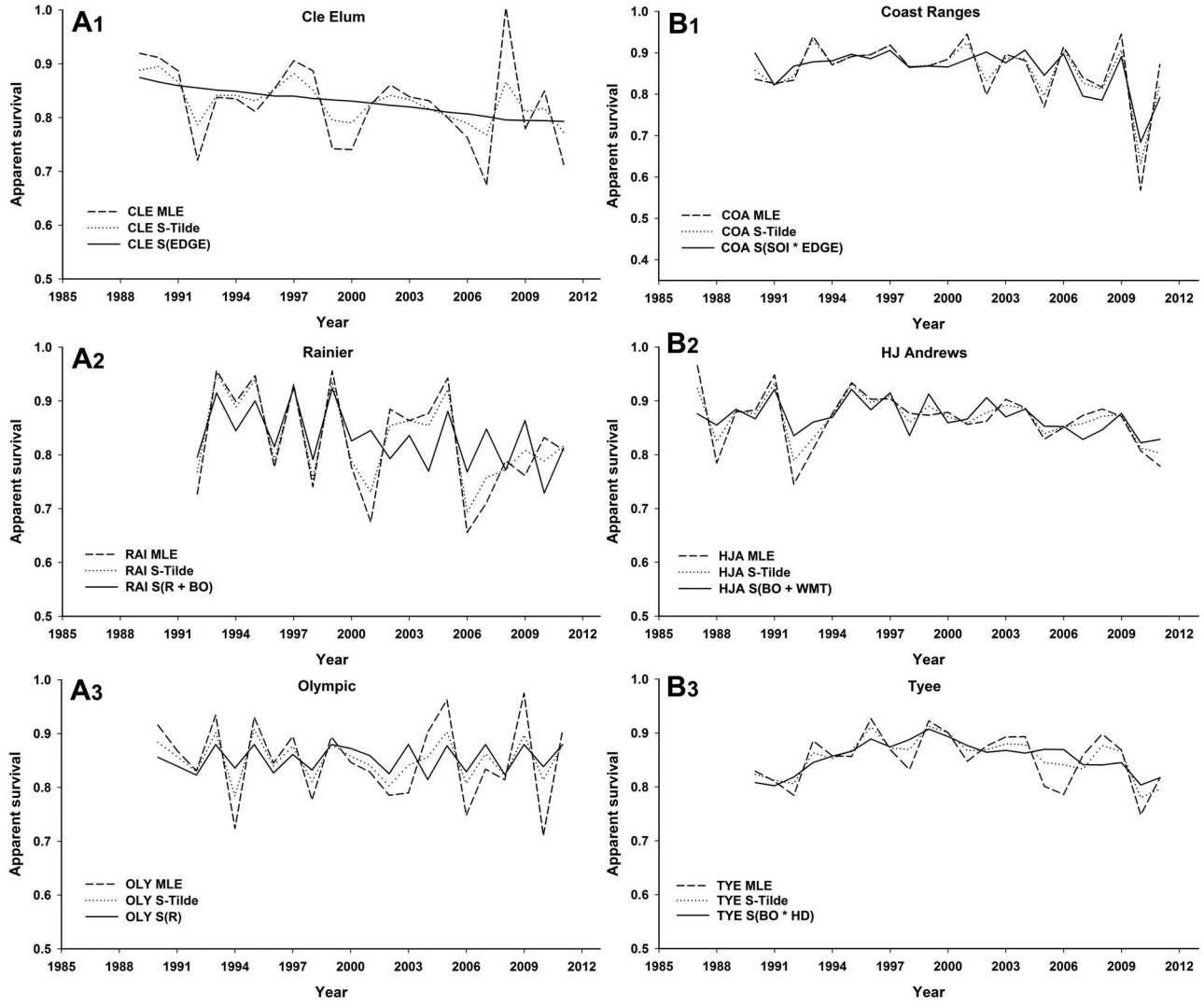
Apparent survival. We did not estimate juvenile survival rates because high rates of permanent emigration bias estimates of apparent survival for juveniles (Burnham et al. 1996). We assumed that permanent emigration did not result in a large difference between apparent survival (estimated here) and true survival of nonjuveniles, because previous studies have indicated that permanent emigration by adult Spotted Owls is uncommon, and that most cases of breeding dispersal in adult Northern Spotted Owls involve short movements between adjacent territories (i.e. within a study area; Forsman et al. 2002, Zimmerman et al. 2007).

In contrast to previous survival analyses, we excluded captures of birds when they were first captured as S1 (1 yr old), but retained the S2 (2 yr old) and adult (≥3 yr old) portions of their capture histories. We also combined the S2 and adult age classes into a single age class, and used this combined age class (S2 + Adults) in the survival analysis for individual study areas and in the meta-analysis (5,090 individuals). We did this for the following reasons: (1) survival of the S2 and adult age classes was similar, whereas survival for the S1 age class was lower than for the older age classes (Burnham et al. 1996, Anthony et al. 2006, Forsman et al. 2011), (2) the number of S1 owls in the territorial population was small and therefore unimportant for estimating trends, (3) S1 owls were more likely to permanently emigrate compared with S2 and adult owls (Forsman et al. 2002); thus, excluding them resulted in estimates that were closer to true survival, and (4) excluding S1 owls and combining the S2 and adult age classes made the survival analyses in individual study areas and the meta-analysis directly comparable as they relied on the same data.

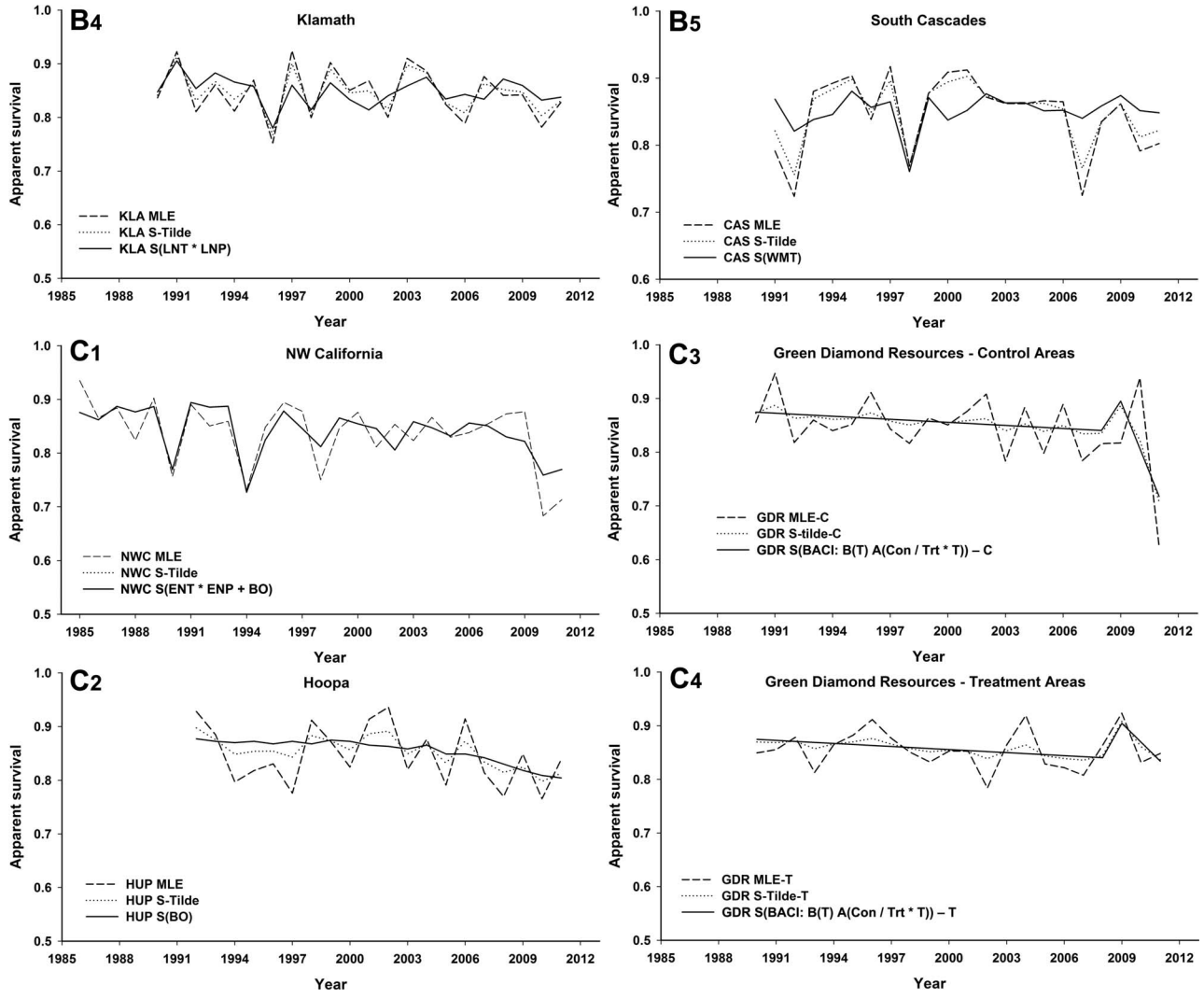
We used $\hat{c} = 1$ to estimate overdispersion in all study areas because: (1) this was very close to the mean $\hat{c}$ across all study areas in previous analyses (Anthony et al. 2006, Forsman et al. 2011), and (2) regression inferences about covariate effects on parameters such as ϕ and λ based on random effects models are robust to overdispersion (Burnham and White 2002; Appendix F).

To avoid developing a large a priori model set by investigating all possible covariate combinations of model structures on each parameter for each study area, we used an ad hoc, hierarchical strategy to develop model sets, which generally results in model selection results comparable to an "all possible combinations" strategy (Doherty et al. 2012). Our strategy for analyses of apparent survival included initially modeling recapture probabilities (p) to first determine the best structure for p. We used a general time structure on survival [$\phi(t)$] and investigated 3 recapture probability models for each study area: p(sex*t), p(sex + t), and $p(t)$. The recapture probability structure from the fixed effects model with the lowest AIC_c was retained, and we fit the annual time plus sex fixed effects model [$\phi(t + \text{sex})$] to survival using the best structure for recapture probabilities to determine whether sex effects were important. If the ratio of the weight of the sex effect model [$\phi(t + \text{sex})$ p(best)] divided by the weight of the model without sex effects [$\phi(t)$ p(best)] was >10, we considered the weight of evidence strong enough to retain the sex effect in the base fixed effects model used for the random effects modeling of covariates (Burnham and Anderson 2002).

Meta-analysis of apparent survival. We removed S1 captures from the dataset and combined S2 and adult owls into a single age class, consistent with the apparent survival analysis in individual study areas. The fixed effects global model included the study area (g) by annual time (t) interaction on survival [$\phi(g*t)$] and the sex by study area by time interaction on capture rates [$p(g*\text{sex}*t)$]. We hypothesized that there would be a minimal effect of sex on survival (e.g., Anthony et al. 2006, Forsman et al. 2011), and verified this with an additional model that included an additive sex effect [$\phi(g*t + \text{sex})$]. If the ratio of the weight of the sex effect model divided by the weight of the model without sex effects was >10, we considered the strength of evidence strong enough to retain the sex effect in the base fixed effects model used for the random effects modeling of covariates (Burnham and Anderson 2002). We also used a binomial categorical variable (NWFP) to test the hypothesis that survival differed between the 8 primarily federally owned study areas and the 3 nonfederally owned study areas. If the ratio of the weight of the NWFP model divided by the weight of the model without the NWFP covariate was >10, we considered the weight of evidence strong enough to retain the NWFP effect for the random effects modeling (Burnham and Anderson 2002).



APPENDIX I FIGURE 16. Estimates from the best random effects models for each study area from the meta-analysis of apparent survival of Northern Spotted Owls during 1985–2013 plotted with estimates of survival from fixed effects base models (MLE) and shrinkage estimates (S-Tilde) in individual study areas in (**A**) Washington, (**B**) Oregon, and (**C**) California, USA. Control and Treatment areas in the GDR study area are plotted separately. Model notation indicates structure for effects of a linear time trend (T), the annual amount of interface between suitable habitat and other cover types within each owl site (EDGE), the annual percentage of suitable habitat that was disturbed (HD), reproduction (R), mean monthly minimum temperature during the early nesting season (ENT), total precipitation during the early nesting season (ENP), mean monthly minimum temperature during the late nesting season (LNT), total precipitation during the late nesting season (LNT), mean monthly minimum temperature during winter (WMT), the Southern Oscillation Index (SOI), proportion of territories with Barred Owl detections (BO), and, for GDR, a time trend on survival in both treatment and control areas before removal started (1992–2008; B(T)) and different time trends in treatment vs. control areas after removals began in 2009 [A(Trt*T)] in a BACI design.



APPENDIX I FIGURE 16. Continued.