Received: 12 January 2022 | Revised: 9 June 2022 | Accepted: 23 June 2022

DOI: 10.1002/eap.2726

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Range-wide sources of variation in reproductive rates of northern spotted owls

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Funding information
Green Diamond Resource Company; Hoopa Valley Tribe; National Park Service; Plum Creek; U.S. Bureau of Land Management; U.S. Forest Service; Weyerhaeuser Company

Handling Editor: Dianne Brunton

Abstract

We conducted a range-wide investigation of the dynamics of site-level reproductive rate of northern spotted owls using survey data from 11 study areas across the subspecies geographic range collected during 1993–2018. Our analytical approach accounted for imperfect detection of owl pairs and misclassification of successful reproduction (i.e., at least one young fledged) and contributed further insights into northern spotted owl population ecology and dynamics. Both nondetection and state misclassification were important, especially because factors affecting these sources of error also affected focal ecological parameters. Annual probabilities of site occupancy were greatest at sites with successful reproduction in the previous year and lowest for sites not occupied by a pair in the previous year. Site-specific occupancy transition probabilities declined over time and were negatively affected by barred owl presence. Overall, the site-specific probability of successful reproduction showed substantial year-to-year fluctuations and was similar for occupied sites that did or did not experience successful reproduction the previous year. Site-specific probabilities for successful reproduction were very small for sites

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that were unoccupied the previous year. Barred owl presence negatively affected the probability of successful reproduction by northern spotted owls in Washington and California, as predicted, but the effect in Oregon was mixed. The proportions of sites occupied by northern spotted owl pairs showed steep, near-monotonic declines over the study period, with all study areas showing the lowest observed levels of occupancy to date. If trends continue it is likely that northern spotted owls will become extirpated throughout large portions of their range in the coming decades.

KEYWORDS
barred owl, detection, misclassification, multistate, nondetection, occupancy, reproductive rate, spotted owl

INTRODUCTION

Most forest-adapted bird species have declining populations that increasingly rely on protected forests, but forest reserves alone may not prevent bird extinctions long-term (Phalan et al., 2019; Sekercioglu et al., 2019; Stouffer et al., 2021). While habitat loss is widely considered the most significant cause of bird species declines, invasive species have been implicated in 33% of animal extinctions worldwide (Blackburn et al., 2019; Rutt et al., 2019). In the Pacific Northwest (PNW) of the USA, birds associated with older forests have declined despite implementation of the Northwest Forest Plan (NWFP) in 1994 that protects remaining old-growth forest and enables broadscale development of old-forest characteristics (Phalan et al., 2019). The NWFP has made substantial progress toward meeting goals of old-forest recovery and reduced threats to biodiversity from habitat loss due to logging on public lands, but new stressors such as invasive species and climate change have emerged as important contributors to continued species declines (Davis et al., 2022; Franklin et al., 2021; Lesmeister et al., 2018; Spies et al., 2019).

Northern spotted owls (*Strix occidentalis caurina*) are old-forest obligates of the PNW and were listed as a threatened subspecies under the United States Endangered Species Act in 1990 and in 2020 were deemed to warrant uplisting to endangered due to continued population declines, but this decision was precluded citing a lack of resources (US Fish and Wildlife Service, 1990, 2020). The NWFP was adopted to aid in conservation of northern spotted owls and other old-forest obligate species on federally managed public lands (USDA Forest Service and US Bureau of Land Management, 1994), and a unique component of the NWFP was the establishment of an effectiveness monitoring program to estimate range-wide trends for northern spotted owl populations on those lands and assess the utility of the NWFP at regular intervals (Lint et al., 1999). Subsequently, and largely because of their conservation status and importance to land management decision-making, northern spotted owl populations have been intensively studied across their geographic range for more than three decades (Anthony et al., 2006; Burnham et al., 1996; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021). Continued population declines documented by these past analyses (e.g., Anthony et al., 2006; Burnham et al., 1996; Dugger et al., 2016; Forsman et al., 2011) and the most recent range-wide meta-analysis (Franklin et al., 2021) emphasize the need to better manage factors driving northern spotted owl population dynamics.

High temporal variation of reproductive rates is common in long-lived vertebrate species (e.g., Gaillard et al., 1998) and birds in particular (Millon et al., 2010; Newton, 1989; Pietiäinen, 1989), and has been a striking pattern observed in range-wide northern spotted owl meta-analyses (e.g., see Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021). Our focus in this paper is on large-scale temporal and spatial variation in spotted owl reproductive rates and on factors associated with this variation. Previous meta-analyses have focused on two different parameters that reflect reproduction: fecundity and recruitment rate. Fecundity is defined as the number of female young produced per territorial female per year and is based on multiple visits to territories to provide confidence in counts of the number of young produced. Recruitment rate is defined as the number of new territorial birds recruited to the population in year $t+1$ per territorial bird in the population in year t. This parameter therefore incorporates fecundity and survival of birds produced on the study area, as well as immigration of birds from outside the study system. Building upon findings of the most recent northern spotted owl meta-analysis (Franklin et al., 2021), we sought inferences about northern spotted owl reproductive rate, defined as the probability that an occupied site would fledge at least one young. One motivation for investigating reproductive rate was the opportunity to incorporate models of nondetection and misclassification (failure to record successful reproduction when it occurs), therefore permitting the use of all breeding season data for northern spotted owls (i.e., even single visits to a site; see Nichols et al., 2007). This approach to inference differs from approaches used in most other studies of reproductive rate that restrict analyses to sites at which sampling protocols (e.g., number of visits to nests) are deemed adequate to definitively determine reproductive success or failure and (in some studies) to identify all breeding pairs. Our inferential approach has been rarely used, and we hope to demonstrate its potential applicability to many other bird species, especially those that are territorial during the breeding season.

The other motivation for looking at reproductive rate was the ability to investigate questions about site-specific dynamics of successful reproduction (MacKenzie et al., 2009), including site-level factors that could contribute to its temporal and spatial variation. These questions are useful for northern spotted owl conservation, but also relevant to ecological hypotheses about avian population dynamics in general. One central question involved the influence of successful reproduction in one breeding season on (1) site occupancy the next season and (2) successful reproduction the next season, given site occupancy. We hoped to discriminate between two competing hypotheses about transitions to successful reproduction: a cost of reproduction hypothesis and a site/pair quality hypothesis (Lee & Bond, 2015; MacKenzie et al., 2009, 2012). The existence of reproductive costs can be an important factor in life history evolution (e.g., Williams, 1966), but our focus here is on phenotypic correlations (sensu Reznick, 1985) and on population-dynamic patterns and consequences. Under the cost of reproduction hypothesis, the energetic costs of reproducing in one year are so substantial that they lead to lower probabilities of successfully reproducing the next year. Therefore, we would expect lower probabilities of successfully fledging young for sites that were successful the previous year compared with sites that were occupied but did not fledge young the previous year.

The site/pair quality hypothesis states that site characteristics, and/or the reproductive abilities of the owls occupying the site, affect the likelihood of reproduction each year. Variation in site quality, combined with territorial behavior, is an important determinant of species distribution patterns (Fretwell, 1972) and a potentially important mechanism of population regulation (e.g., Rodenhouse et al., 1997). Variation in the quality of individuals and pairs has also been found to be substantial for multiple bird species, with important population-dynamic consequences (e.g., Newton, 1989). Under the site/pair quality hypothesis we would expect the highest reproductive rates for sites with successful reproduction in the previous year, intermediate rates for sites occupied but unproductive previously, and the lowest rates for sites that were unoccupied in the previous year (Lee & Bond, 2015). We could not distinguish between the site-level versus owl pair-level hypotheses because territorial northern spotted owls move infrequently and successful pairs exhibit high site fidelity (Forsman et al., 2002; Jenkins et al., 2021).

Site-specific models also enabled tests of effects of site-level environmental covariates on the dynamics of successful reproduction for spotted owls, such as habitat components and the presence of invasive barred owls (*Strix varia*). Landscape change and increasing competitive pressures from barred owls are considered the primary drivers for northern spotted owl population declines (Wiens et al., 2021). Habitat components, such as the availability of forest structure for nesting and roosting, are thought to influence nearly every vital rate of northern spotted owls: apparent survival (Dugger et al., 2005, 2016; Franklin et al., 2000; Olson et al., 2004), local colonization and extinction rates (Dugger et al., 2016; Yackulic et al., 2019), and reproduction (Dugger et al., 2005; Franklin et al., 2000; Olson et al., 2004). Barred owls, native to forests of eastern North America, are now present across the range of the northern spotted owl and are causing significant, negative impacts to northern spotted owl site occupancy, breeding propensity (Diller et al., 2016; Dugger et al., 2016; Mangan et al., 2019; Wiens et al., 2014; Yackulic et al., 2014, 2019), and breeding dispersal dynamics (Jenkins et al., 2019, 2021). The use of site-level cover type and barred owl covariates may help to explain some of the site-level spatial drivers of successful reproduction that were not discernible under the previous meta-analytic framework. Previous research has also suggested an association between northern spotted owl reproduction and climate (Dugger et al., 2005, 2016; Forsman et al., 2011; Franklin et al., 2000; Glenn et al., 2011; Olson et al., 2004), and for this reason we included region-wide climate covariates in our analysis. While our focus was on the influence of site-level factors that affected northern spotted owl demographic rates, general ecological interest in demographic effects of habitat (e.g., Holmes et al., 1996; Murphy, 2001), competition (Dhondt, 2012; MacArthur & Wilson, 1967) and climate variables (e.g., Iles et al., 2013; Payo-Payo et al., 2015) extend far beyond the northern spotted owl system and are areas of active interest among ecologists.

METHODS

This analysis was conducted in conjunction with the seventh northern spotted owl meta-analysis workshop that examined long-term population trends (Franklin et al., 2021) and followed the data preparation and sharing protocols of previous meta-analyses of northern spotted owl demographic data established by Anderson et al. (1999).

Study area

We used data from 11 long-term study areas: three in Washington (Olympic = OLY, Mount Rainier = RAI, and Cle Elum = CLE), five in Oregon (Coast Ranges = COA, HJ Andrews = HJA, Tyee = TYE, Klamath = KLA, and South Cascades = CAS), and three in California (Green Diamond = GDR, Hoopa = HUP, and NW California = NWC; Figure 1). Four study areas were located primarily on federally managed public lands (OLY, HJA, CAS, and NWC), five included a mixture of public and private lands (CLE, RAI, COA, TYE, and KLA), one was located on private industrial timberlands (GDR), and one was located on Native American lands (HUP). The 11 study areas ranged from 356 to 3922 km^2 and consisted of a broad range of forested cover types with dominant tree species that varied by study area (for details please see Anthony et al., 2006). Although these 11 study areas span a broad latitudinal range that encompasses a large portion of the northern spotted owl's range, the initial selection of study areas was not random. Therefore, any inferences made from this study should be limited to federally managed public lands within the range of the northern spotted owl (Anthony et al., 2006: appendix F).

Delineation of sites

We defined northern spotted owl territories (designated as "sites") based on the accumulation of annual site centers from 1993 to 2018 with the following criterion: (1) nest location, (2) location of fledglings, (3) primary roost location, or (4) nighttime location within 1 h of dusk. Therefore, by definition, a site could not enter the study until at least one owl was detected. We then used these annual site centers to develop Thiessen polygons for each spotted owl site that extended outward to a maximum of one-half median nearest-neighbor distance or midway between owl locations of adjacent sites, whichever was shorter. Median nearest-neighbor distances varied among study areas and were larger in the northern portions of the owl's range (1.75 km) relative to the southern portions of the range (0.60 km). These survey polygons were viewed as potential spotted owl territories but referred to as "sites" because they may or may not have been occupied by territorial spotted owls during any given year of the study.

While defining sites this way (based on the accumulation of owl locations) requires that only occupied, or once-occupied sites are included in our analysis and therefore could result in an artificial decline in site occupancy (i.e., occupancy must decline if all sites are occupied at the onset of a study), sampling at 8 of 11 study areas was initiated at least 3 years prior to 1993 and had initial occupancy estimates <1, and only one study area initiated in 1992 (RAI) had initial occupancy = 1. Therefore, we believe an adequate amount of time had passed between the initiation of these studies (1985–1992) and the time frame used in this analysis (1993–2018) for occupancy dynamics to move away from initial occupancy states, and that our results represent ecological processes rather than artifacts of study design. Additionally, because sites were defined based on the collection of annual locations, they did not change (i.e., were spatially invariant) over the course of the study and represented areas of potential use by spotted owls. Furthermore, and owing to the long history of surveying for owls in these study areas, the spatial coverage of Theissen polygons (sites) generally encompassed all areas of potentially suitable forest cover within a study area.

Our study included data from 1993 to 2018 for most study areas. A barred owl removal experiment was implemented on four study areas at various times during our study (US Fish and Wildlife Service, 2013; Wiens et al., 2019, 2020, 2021). To minimize confounding our results from the long-term spotted owl monitoring program, which was specifically designed to monitor spotted owl populations in their "natural environment" (Lint et al., 1999), with experimentally manipulated barred owl densities resulting from removal efforts, we censored all sites where barred owl removal occurred beginning with the year that removal began. Barred owls were removed from a subset of sites within the GDR study area from 2009 to 2013, from all monitored sites on the HUP study area from 2014 to 2018, and from a subset of sites on the CLE and COA study areas from 2016 to 2018. Because barred owls were removed from all monitored sites at the HUP study area, data from this area only covered the period 1993–2013.

Owl surveys

We surveyed sites within each study area multiple times annually during the breeding season to locate owls and document the number of young produced by each territorial female. Surveys were conducted either by walking in to known owl sites during daytime and

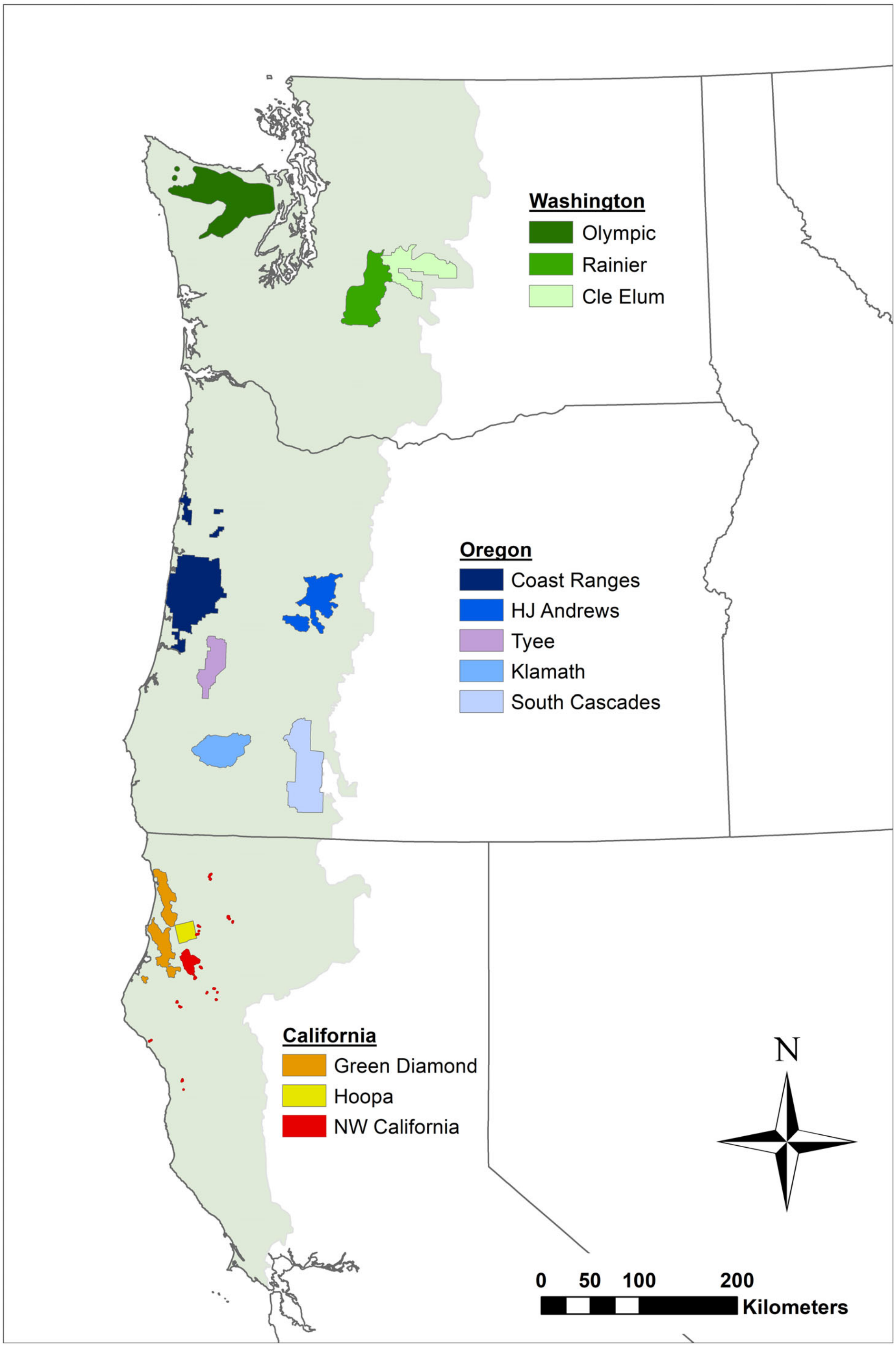

FIGURE 1 Location of 11 study areas used in the northern spotted owl reproductive rate analysis. Light green shaded area denotes the Northwest Forest Plan footprint.

assessing occupancy and reproductive status of the owls, or by roadside, or "nighttime" surveys in which an observer either mimicked or played recorded owl calls and listened for ≥10 min for a response from a resident owl (Franklin et al., 1996). Nighttime surveys were designed to establish occupancy of sites, whereas daytime walk-in surveys were designed to establish both occupancy of sites and reproductive status of the owls. Nighttime surveys that produced detections of spotted owls were followed up by secondary daytime visits to determine the reproductive status of the owls. Successful reproduction was determined by evidence of at least one fledged young observed outside the nest. Specific survey protocols have been described in greater detail elsewhere (Dugger et al., 2016; Franklin et al., 1996; Reid et al., 1999) and include the use of multiple visits to sites to determine pair and reproductive status.

We defined our primary sampling periods as the 6-month breeding season and our secondary sampling periods as the 12 bi-monthly intervals between 1 March and 31 August. Each site surveyed during a secondary sampling period was assigned to one of three observation states based only on information from that survey visit:

0—no detection of an owl pair,
1—detection of an owl pair but no evidence of successful reproduction,
2—detection of an owl pair with evidence of successful reproduction.

Data for each site were summarized as a detection history, a vector containing the observation states for each survey that occurred during a secondary sampling period. We assumed no false-positive detections or classifications of reproductive success, so if multiple surveys were conducted within a secondary sampling period, the greatest observation state number was used in the detection history. If no visit occurred during one of the secondary sampling periods, the site was assigned a dot (.) to denote that no survey was conducted. Surveys in which only a single owl was detected were classified as state = 0, and surveys that identified nest failures were classified as state = 1. For example, consider the detection history [01.1.0102220 0.0000.00000]. This detection history includes 2 years of observations at a site. In year 1, there were no pair detections in periods 1, 6, 8, or 12; a pair was observed with no evidence of successful reproduction in periods 2, 4, and 7; and successful reproduction (i.e., fledged young) was observed in periods 9–11. No surveys were conducted during periods 3 and 5. In year 2 there were no detections of a pair, and no surveys were conducted in periods 2 and 7. Summary statistics for numbers of sites surveyed and survey effort for each study area are presented in Table 1 and Appendix S1: Figure S1.

TABLE 1 Number of sites and survey effort across 11 study areas used to estimate occupancy and reproductive rates of northern spotted owls during 1993–2018.

Study area	Sites	Sites surveyed annually	Mean (SD) surveys per site per year
Washington			
CLE[a]	87	30–81	3.4 (0.27)
OLY	97	85–97	3.3 (0.30)
RAI	72	20–70	3.4 (0.41)
Oregon			
CAS	170	100–169	3.1 (0.23)
COA[a]	172	127–172	4.0 (0.40)
HJA	185	111–180	4.3 (0.47)
KLA	159	99–159	4.3 (0.34)
TYE	162	152–161	4.3 (0.23)
California			
GDR[a]	291	69–190	3.6 (0.42)
HUP[b]	57	50–57	4.8 (0.98)
NWC	59	50–59	3.4 (0.30)

Note: Study area acronyms are CAS, South Cascades; CLE, Cle Elum; COA, Coast Range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.
[a] The wide range in sites surveyed annually for CLE, COA, and GDR reflects sites that were censored because of their inclusion in a separate barred owl removal experiment (Appendix S1; Figure S1).
[b] HUP data include the years 1993–2013.

Environmental covariates

We selected covariates based on results of previous research on spotted owls (Appendix S1: Table S1). We generated an annual, site-specific covariate that described the proportion of suitable nesting and roosting forest cover ($PNR_{i,t}$) from maps developed for northern spotted owl habitat monitoring (Davis et al., 2016, 2022). A basemap of nesting and roosting (NR) cover in 1993 was developed using Maxent (Phillips et al., 2006) by correlating 1993 owl locations to a suite of forest structure and composition metrics derived from gradient nearest-neighbor imputation (Ohmann & Gregory, 2002). We then used an ensemble Landsat-based detection of trends in disturbance and recovery (LandTrendr) methodology to detect annual changes in those forest structure and composition metrics resulting from forest disturbance to create annual NR cover maps (Cohen et al., 2018; Healey et al., 2018). Because our NR maps were sensitive to changes in forest structure and composition, lower intensity disturbances that resulted in minimal changes to these metrics generally did not result in the loss of NR cover, whereas higher intensity disturbances that resulted in more substantial changes to these metrics were more likely to 'remove' NR cover (Davis et al., 2016, 2022). We calculated PNR for each site i in each year t based on the proportional amount of NR cover within habitat-capable land of each site, excluding nonhabitat cover types such as talus and open water. Satellite imagery used to estimate PNR was acquired at the end of the breeding season or shortly thereafter when cloud-free conditions prevailed. Accordingly, we used estimates of PNR at time t when modeling parameters governing transitions from year t to year $t + 1$, as we felt that conditions at the end of the breeding season would be more representative of conditions at the beginning of the subsequent breeding season ($t + 1$) than imagery acquired at the end of the next breeding season. We predicted that PNR would be positively associated with increases in northern spotted owl occupancy and reproductive success.

As part of a larger meta-analysis investigating demographic trends in northern spotted owls (Franklin et al., 2021), we generated an annual site-specific barred owl covariate ($\mathrm{BO}_{i,t}$) that was the forward conditional estimate (sensu Yackulic et al., 2020) that site i was occupied by a barred owl during the breeding season of year t. $\mathrm{BO}_{i,t}$ was estimated from a dynamic occupancy model of barred owl presence in which occupancy was defined as one or more barred owls being present. The model structure for detection, colonization, and extinction within a study area was based on the best-supported model from Dugger et al. (2016) that did not include habitat covariates. Barred owl models for each study area were fitted using program PRESENCE (http://www.mbr-pwrc.usgs.gov/software.html). We predicted that barred owl presence in either year t or $t+1$ would negatively affect all parameters reflecting spotted owl occupancy and successful reproduction (Dugger et al., 2016; Franklin et al., 2021; Yackulic et al., 2019).

Finally, we generated two annual climate covariates: the southern oscillation index (SOI_t) and Pacific decadal oscillation (PDO_t). We collected monthly values of SOI from the National Oceanic and Atmospheric Administration's Climate Prediction Center (https://www.cpc.ncep.noaa.gov/data/indices/soi; National Oceanic and Atmospheric Administration) and PDO from the University of Washington, Joint Institute for the Study of Atmosphere and Ocean (http://research.jisao.washington.edu/pdo/PDO.latest.txt; Mantua et al., 1997). We used the mean of the monthly values over each year t (July_t–June_{t+1}) as our covariate values. Climate covariates SOI_t and PDO_t have similar effects in the PNW, but they operate on different time scales (PDO_t operates on a longer time scale). Cooler, wetter winters in our study areas ($\mathrm{SOI}_t > 0$; $\mathrm{PDO}_t < 0$) have been associated with higher annual reproduction (Glenn et al., 2011), presumably related to associated increases in prey productivity. We predicted that reproduction would be positively correlated with SOI and negatively correlated with PDO (Glenn et al., 2011).

Modeling approach

Our analyses were based on the multiseason–multistate occupancy approach described by MacKenzie et al. (2009, 2012, 2018). These models are useful because: (1) they allow for different state-specific detection rates (p), (2) they include a classification parameter (δ) that accounts for the potential misclassification of sites, in our case the probability of failing to detect successful production of young given that it occurred, and (3) they allow for the comparison of estimates between studies that use different sampling protocols. A key assumption of our model is that uncertainty in state classification decreases with each successive state assignment. That is, sites observed in state 0 (no detection of an owl pair) could be in true states 0 (unoccupied by an owl pair), 1 (occupied by a nonreproductive owl pair) or 2 (occupied by an owl pair that fledges ≥1 young). Sites observed in state 1 (detection of an owl pair, but no evidence of successful reproduction) could be in true states 1 or 2, but not in state 0, and sites observed in state 2 (detection of an owl pair with fledged young) could only be in true state 2.

We used multiseason–multistate occupancy models to estimate the fraction of sites in each of these true states, as well as the transition probabilities from one state to another. Model parameters are defined as follows:

$\psi_{i,1}$: probability that site i is occupied by a pair in year 1 (first year of study).

$\psi_{i,t+1}^{[0]}$: probability that site i, not occupied by a pair in year t, is occupied in year $t+1$.

$\psi_{i,t+1}^{[1]}$: probability that site i, occupied by a pair, but with no successful reproduction, in year t, is occupied in year $t+1$.

$\psi_{i,t+1}^{[2]}$: probability that site i, occupied by a pair with successful reproduction in year t, is occupied in year $t+1$.

$R_{i,1}$: probability that site i, occupied by a pair in year 1 (first year of study), experiences successful reproduction.

$R_{i,t+1}^{[0]}$: probability that site i, unoccupied in year t and occupied by a pair in year $t+1$, experiences successful reproduction in year $t+1$.

$R_{i,t+1}^{[1]}$: probability that site i, occupied with no successful reproduction in year t and occupied by a pair in year $t+1$, experiences successful reproduction in year $t+1$.

$R_{i,t+1}^{[2]}$: probability that site i, occupied with successful reproduction in year t and occupied by a pair in year $t+1$, experiences successful reproduction in year $t+1$.

$\delta_{i,t,j}$: probability that evidence of successful reproduction is detected in visit j of year t at site i that is occupied by a pair that successfully reproduces in year t.

$p_{i,t,j}^{[1]}$: probability that a pair is detected in visit j of year t for a site i occupied by a pair that does not successfully reproduce.

$p_{i,t,j}^{[2]}$: probability that a pair is detected in visit j of year t for a site i occupied by a pair that successfully reproduces.

The above real parameters were included in the models we fitted to the data, and when covariates were used in the modeling, associated model coefficients (β parameters) were also estimated. We then used the real parameters to compute the following derived parameters (see MacKenzie et al., 2009, 2018):

$\phi_{i,t}^{[0]}$: probability of site i being in state 0 in year t.
$\phi_{i,t}^{[1]}$: probability of site i being in state 1 in year t.
$\phi_{i,t}^{[2]}$: probability of site i being in state 2 in year t.
$R_{i,t} = \phi_{i,t}^{[2]} / \left(\phi_{i,t}^{[1]} + \phi_{i,t}^{[2]} \right)$: the probability site i experiences successful reproduction in year t, given that it is occupied by a pair.

The site-specific summary statistics $\phi_{i,t}^{[m]}$ (state m) are useful in characterizing the site occupancy patterns of the studied system, and the derived parameter $R_{i,t}$ is useful for characterizing temporal dynamics of reproductive rate, a key fitness component, and driver of population dynamics. Together, these derived parameters characterize the overall dynamics of northern spotted owl populations across the 11 study areas.

Model set development

We used a model building strategy referred to as the sequential-by-submodel approach following Morin et al. (2020) and used Akaike's information criterion (AIC) for model ranking (Burnham & Anderson, 2002). Detection probabilities $\left(p_{i,t,j}^{[m]} \right)$ were modeled first, then the classification parameter ($\delta_{i,t,j}$), then occupancy transitions $\left(\psi_{i,t+1}^{[m]} \right)$, followed by reproduction transitions $\left(R_{i,t+1}^{[m]} \right)$. We did not investigate hypotheses on initial occupancy ($\psi_{i,1}$) or reproduction ($R_{i,1}$) and left them as intercept-only models because we wanted to ensure stable estimates for these parameters and found that their structure had little influence on the overall occupancy or reproductive transition estimates. In the earlier modeling stages, we allowed the classification parameter to vary by early versus late sampling periods and for full variation in the transition parameters (i.e., STATE × YEAR). To reduce the overall number of models, we initially retained only the top-ranked detection and classification structures (those with the lowest AIC) when modeling transition parameters. We retained all competitive occupancy transition structures ($\Delta\text{AIC} \leq 5$) when modeling reproduction transitions. The last modeling stage compared the final set of competitive models ($\Delta\text{AIC} \leq 5$) with the previously held out competitive detection and classification structures from stages 1 and 2 to ensure that we apportioned variation reasonably among parameters and covariate effects (see Appendix S2 for full model set development rules). We structured all models using state 0 as the common intercept.

We modeled spotted owl detection probabilities, $p_{i,t,j}^{[m]}$ as functions of state (m), probability of barred owl presence at site i in year t, ($\text{BO}_{i,t}$), YEAR, and trap response ($\text{TRAP}_{i,j,t}$), which permitted a different pair detection probability before and after initial detection within a year. The "trap response" terminology was borrowed from capture–recapture studies in which animals respond to initial capture by either an increase (e.g., because of positive response to bait) or a decrease (being in trap was an unpleasant experience) in capture probability during subsequent encounters with traps. The mechanism for occupancy sampling differs in that the response is by the investigators (prior detection of a pair provides information facilitating subsequent detections), but the effect on detection probabilities, and therefore the modeling, are the same. Detection probabilities were predicted to be higher for sites in state 2 than those in state 1 because of behaviors associated with feeding of young and nest attendance. Higher probabilities of barred owl presence ($\text{BO}_{i,t}$) were expected to decrease spotted owl detection probability (Bailey et al., 2009; Dugger et al., 2016; Yackulic et al., 2014). The trap response covariate $\text{TRAP}_{i,j,t}$ captured the prediction that the detection probability of a pair at site i should increase following the initial detection of the year because subsequent within year visits to a site typically began where the birds were last found. We had no specific predictions about the influence of YEAR on detection probability but wanted to allow for year-to-year variation.

The parameters denoting the correct classification of reproductive success, $\delta_{i,t,j}$, were modeled as functions of $\text{BO}_{i,t}$ and survey month (categorized as early or late). The early versus late categorization simply recognized the fact that successful reproduction frequently cannot be determined early in the breeding season (1 March–31 May) before nestlings leave the nest, leading to higher correct classification probabilities later in the season (1 June–31 August). The barred owl covariate ($\text{BO}_{i,t}$) was predicted to decrease classification probability either due to northern spotted owl pairs altering their feeding and nest attendance behaviors in the presence of barred owls, or by surveyors curtailing their activities when barred owls are detected to avoid potentially negative species interactions.

We considered multiple model structures for the state-specific occupancy transition probabilities, $\psi_{i,t+1}^{[m]}$. There is evidence that the previous year's occupancy state can strongly influence current year occupancy in northern spotted owls (Dugger et al., 2016; Yackulic et al., 2019), providing a motivation for distinguishing among $\psi_{i,t+1}^{[0]}$, $\psi_{i,t+1}^{[1]}$, and $\psi_{i,t+1}^{[2]}$ in our model structure. In addition, many bird species (e.g., Greenwood &

Harvey, 1982; Johnson et al., 1992), including spotted owls (Jenkins et al., 2021), show greater fidelity to breeding sites where they successfully reproduced the previous year. These considerations led to the prediction that $\psi^{[0]}_{i,t+1} \ll \psi^{[1]}_{i,t+1} < \psi^{[2]}_{i,t+1}$. Therefore, all model structures of occupancy transitions included an effect of previous year's state (i.e., we did not test the model with no state effect; $\psi_{i,t+1}$). We compared the model with only state-specific effects $\left(\psi^{[m]}_{i,t+1}; \text{STATE}\right)$ against 11 alternate model structures investigating potential effects of NR cover in site i, year t $\left(\psi^{[m+\text{PNR}_{i,t}]}_{i,t+1}\right)$, barred owl presence in site i, year t $\left(\psi^{[m+\text{BO}_{i,t}]}_{i,t+1}\right)$, and a linear effect of year (TIME). We predicted that higher proportions of NR cover (PNR) in year t would improve the likelihood of occupancy in year $t+1$. The recent range expansion of barred owls into the range of the northern spotted owl is associated with steep declines in northern spotted owl population size and site occupancy rates, as well as with high rates of northern spotted owl extinction from occupied sites (Dugger et al., 2016; Forsman et al., 2011; Yackulic et al., 2014, 2019). We predicted that the probability of a site being occupied by barred owls at time t ($\text{BO}_{i,t}$) would negatively affect northern spotted owl occupancy at $t+1$. We tested structures that allowed the previous year's state to influence the effect of $\text{BO}_{i,t}$ and $\text{PNR}_{i,t}$ on current year occupancy (e.g., $\psi^{[m\times\text{PNR}_{i,t}]}_{t+1}$, $\psi^{[m\times\text{BO}_{i,t}]}_{t+1}$). We predicted a negative time trend (TIME) based on documented population declines (e.g., Dugger et al., 2016). While a linear time effect is highly correlated with barred owl occupancy across our study areas, we fitted models with both $\text{BO}_{i,t}$ and TIME because our barred owl covariate was site specific and included spatial variation not represented in the time trend.

The probability of successful reproduction in year $t+1$, $R^{[m]}_{i,t+1}$, was modeled as a function of site state (m) at time t. We modeled reproduction transitions, $R^{[m]}_{i,t+1}$, in two steps to reduce the total number of model runs. We first determined which climate variable (SOI or PDO) was most influential based on AIC model ranking and retained the best-ranked climate covariate when continuing to step 2. In step 2, we examined 35 alternative $R^{[m]}_{i,t+1}$ model structures testing relative support for hypotheses about the influence of $\text{BO}_{i,t}$, $\text{PNR}_{i,t}$, and the top climate variable on reproductive rate (Appendix S2). We also examined both linear (TIME) and annual (YEAR) time effects on reproductive success transitions. Under the site/pair quality hypothesis we expected the highest reproductive rates for sites with successful reproduction (state 2) at time t, and the lowest reproductive rates for sites that were unoccupied (state 0) at time t, i.e., $R^{[0]}_{i,t+1} < R^{[1]}_{i,t+1} < R^{[2]}_{i,t+1}$. Under the cost of reproduction hypothesis, we expected lower probabilities of reproductive success for sites that fledged young the previous year, $R^{[2]}_{i,t+1} < R^{[1]}_{i,t+1}$. We hypothesized that the presence of barred owls at time $t+1$ ($\text{BO}_{i,t+1}$) would negatively influence the likelihood of successful reproduction at sites in $t+1$. We predicted $R^{[m]}_{i,t+1}$ would be positively associated with $\text{PNR}_{i,t}$. We also tested structures that allowed the previous year's state to influence the effect of $\text{BO}_{i,t}$ and $\text{PNR}_{i,t}$ $\left(\text{e.g.}, R^{[m\times\text{BO}_{i,t+1}]}_{i,t+1}, R^{[m\times\text{PNR}_{i,t}]}_{i,t+1}\right)$, therefore testing the hypothesis that sites where pairs successfully reproduced in year t may be more resilient to the negative effects of environmental conditions. We also hypothesized that $\text{PNR}_{i,t}$ could mitigate or exacerbate effects of barred owls in year $t+1$ $\left(\text{e.g.}, R^{[\text{PNR}_{i,t}\times\text{BO}_{i,t+1}]}_{i,t+1}\right)$ or poor winter climate $\left(\text{e.g.}, R^{[\text{PNR}_{i,t}\times\text{SOI}_{t}]}_{i,t+1}\right)$. Because climate varied annually and was not site specific, we did not include annual year effects and climate covariates in the same model. Previous meta-analyses have used first-order autoregressive models for fecundity at the level of a study area (Franklin et al., 2021), and we note that our first-order Markov model with $R^{[2]}_{t+1} < R^{[1]}_{t+1}$, when coupled with a synchronizing environmental effect (a year of very high or low reproduction; e.g., associated with an extreme in prey availability) provides a potential site-level mechanism that could underlie an autoregressive model.

We used the *RPresence* package (http://www.mbr-pwrc.usgs.gov/software.html) in R (R Core Team, 2020) to generate parameter estimates and model selection results. We ran all models 20–100 times with each model run using random initial value vectors to increase the likelihood of selecting the global maxima. We examined all coefficient estimates and standard errors for evidence of overfitting and model misspecification (e.g., very large standard errors). If there was evidence of overfitting, we removed interactions from either or both $R^{[m]}_{i,t+1}$ and $\psi^{[m]}_{i,t+1}$ and reexamined rankings. We also examined convergence statistics (output by PRESENCE) and standard errors for evidence of convergence failure. After determining final model rankings for each study area, we calculated our four derived parameters $\left(\phi^{[0]}_{i,t}, \phi^{[1]}_{i,t}, \phi^{[2]}_{i,t}, \text{and } R_{i,t}\right)$ based on top models ($\Delta\text{AIC} < 5$), then averaged those estimates based on model weights rescaled within the top model set for interpretation (Burnham & Anderson, 2002).

RESULTS

Model selection overview

Here we present the top-ranked final models ($\Delta\text{AIC} \le 5$), their likelihoods, number of parameters, ΔAIC values,

TABLE 2 Top-ranked multistate models of detection $\left(p^{[m]}_{i,t,j}\right)$, classification $\left(\delta_{i,t,j}\right)$, and state-specific occupancy $\left(\psi^{[m]}_{i,t+1}\right)$ and reproduction $\left(R^{[m]}_{i,t+1}\right)$ transition probabilities for northern spotted owl sites in 11 study areas in Washington, Oregon, and California, USA, 1993–2018.

Study area	$R^{[m]}_{i,t+1}$	$\psi^{[m]}_{i,t+1}$	$p^{[m]}_{i,t,j}$	$\delta_{i,t,j}$	−2lnL	K	ΔAIC[a]	w_i
Washington								
CLE[b]	STATE + BO + YEAR[c]	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	3902.17	40	0	0.37
	STATE + BO + YEAR[c]	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	3899.74	42	1.57	0.17
	STATE + PNR + BO + YEAR[c]	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	3901.94	41	1.77	0.15
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	3900.32	42	2.14	0.13
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	3898.61	43	2.44	0.11
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	3989.61	44	4.70	0.03
OLY	STATE × PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6709.75	41	0	0.25
	STATE × PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	6706.58	43	0.83	0.16
	STATE × PNR + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6713.30	40	1.55	0.12
	STATE × PNR + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	6709.64	42	1.89	0.10
	STATE × PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6715.01	40	3.25	0.05
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6719.38	38	3.63	0.04
	STATE × PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6711.93	42	4.18	0.03
	STATE × PNR + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6717.97	39	4.21	0.03
	STATE × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6716.42	40	4.66	0.02
	STATE × PNR + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6714.44	41	4.69	0.02
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	6716.61	40	4.85	0.02
RAI[b]	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	3135.30	41	0	0.39
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	3134.86	42	1.56	0.18
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	3135.26	42	1.96	0.15
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	3134.81	43	3.51	0.07
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	3134.86	43	3.56	0.07
	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	3135.22	43	3.92	0.06
Oregon								
CAS	STATE + PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	13626.32	45	0	0.43
	STATE + PNR × BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	13625.15	46	0.83	0.28
	STATE × BO + PNR + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	13624.38	47	2.05	0.15
	STATE × BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	13627.05	46	2.72	0.11
COA[b]	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	13858.29	41	0	0.51
	STATE + BO + YEAR[c]	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	13862.05	40	1.76	0.21
	STATE + BO + PNR + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	13858.25	42	1.97	0.19
	STATE + BO + PNR + YEAR[c]	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	13862.00	41	3.71	0.08
HJA	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE	17275.14	65	0	0.16
	STATE × BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE	17272.64	67	1.5	0.08
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE	17274.79	66	1.65	0.07
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE + BO	17275.14	66	2.00	0.06
	STATE × BO + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE	17269.26	69	2.12	0.06
	STATE + PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE	17271.44	68	2.30	0.05
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE + BO	17271.78	68	2.63	0.04
	STATE × BO + PNR + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE	17272.18	68	3.04	0.04
	STATE × BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE + BO	17272.64	68	3.50	0.03
	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE	17274.66	67	3.52	0.03
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + YEAR	LATE + BO	17274.79	67	3.65	0.03
	STATE × BO + PNR + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE	17269.26	70	4.12	0.02

(Continues)

TABLE 2 (Continued)

Study area	$R^{[m]}_{i,t+1}$	$\psi^{[m]}_{i,t+1}$	$p^{[m]}_{i,t,j}$	$\delta_{i,t,j}$	−2lnL	K	ΔAIC[a]	w_i
	STATE + PNR × BO + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE	17271.33	69	4.19	0.02
	STATE + PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE + BO	17271.44	69	4.30	0.02
	STATE × BO + YEAR	STATE × BO + TIME	STATE + TRAP + YEAR	LATE + BO	17269.67	70	4.53	0.02
KLA[b]	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	13587.06	43	0	0.58
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	13590.95	42	1.90	0.23
	STATE + PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	13585.70	45	2.64	0.16
TYE	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	10591.64	43	0	1
California								
GDR	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	15592.46	43	0	0.50
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	15596.98	42	2.52	0.14
	STATE + PNR × BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	15591.37	45	2.91	0.12
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	15599.84	41	3.38	0.09
HUP	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6023.44	36	0	0.20
	STATE × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6020.07	38	0.63	0.14
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6023.14	37	1.70	0.08
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6023.17	37	1.73	0.08
	STATE × BO + PNR + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6019.73	39	2.29	0.06
	STATE × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6019.81	39	2.37	0.06
	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6022.33	38	2.89	0.05
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6022.87	38	3.44	0.04
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6023.43	38	4.00	0.03
	STATE × BO + PNR + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6019.47	40	4.04	0.02
	STATE + BO + YEAR	STATE + TIME	STATE + TRAP + BO	LATE	6029.62	35	4.19	0.02
	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6022.01	39	4.58	0.02
	STATE × BO + YEAR	STATE + TIME	STATE + TRAP + BO	LATE	6026.03	37	4.60	0.02
	STATE × BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6020.06	40	4.63	0.02
NWC	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6406.96	40	0	0.20
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6403.23	42	0.27	0.17
	STATE + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6406.56	41	1.6	0.09
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6406.96	41	2.00	0.07
	STATE + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	6402.98	43	2.02	0.07
	STATE + PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6403.23	43	2.27	0.06
	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6406.33	42	3.37	0.04
	STATE + PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6406.56	42	3.60	0.03
	STATE + PNR × BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6402.67	44	3.71	0.03
	STATE × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6406.69	42	3.74	0.03
	STATE × BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE	6402.89	44	3.93	0.03
	STATE + PNR + BO + YEAR	STATE × BO + TIME	STATE + TRAP + BO	LATE + BO	6402.98	44	4.02	0.03
	STATE × PNR + BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE	6405.86	43	4.90	0.02
	STATE + PNR × BO + YEAR	STATE + BO + TIME	STATE + TRAP + BO	LATE + BO	6405.87	43	4.91	0.02

Note: m denotes state, i denotes site, t denotes year, and j denotes secondary sampling occasion. Models with interactions also included their main effects. $-2\ln L$ is the negative of twice the log likelihood, k is the number of model parameters, ΔAIC is the difference between the AIC of the focal model and that of the LOW-AIC model, and w_i is the AIC weight for the focal model. Covariates are described in Appendix S1: Table S1. CAS, South Cascades; CLE, Cle Elum; COA, Coast Range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.

[a] Akaike's information criterion (AIC) of top models: CLE 3984.17, OLY 6791.75, RAI 3217.30, CAS 13716.32, COA 13940.29, HJA 17405.14, KLA 13673.06, TYE 10677.64, GDR 15678.46, HUP 6095.44, NWC 6486.96.

[b] More complex model structures for CLE, COA, KLA, and RAI exhibited signs of overfitting, so we chose to use simpler model structures for these study areas.

[c] Rates of observed occupancy were extremely low or 0 for the final years on these areas; we set the final 3 years as equal for CLE and final 2 years as equal for COA to fit the YEAR models.

and model weights for each study area (Table 2). Similar statistics for the entire model set for each study area are available from ScholarsArchive (Rockweit et al., 2022; see *Data availability statement*). Although the top models were not identical for the 11 study areas, they did show many similarities, supporting some general conclusions.

Detection probabilities

We retained state-specific detection probabilities for all modeling and, as predicted, the probability of detecting a pair on sites where successful reproduction did not occur was lower than on sites where pairs successfully reproduced $\left(\widehat{p}^{[1]}_{i,t,j} < \widehat{p}^{[2]}_{i,t,j}\right)$ for all study areas (Table 2; Appendix S1: Table S2). There was strong evidence of an additive trap response for all study areas as well, with greater detection probabilities following the initial detection of a pair at a site (Table 2; Appendix S1: Table S2). Strong evidence ($\sum w_k > 0.99$) for a negative effect of barred owls on detection probability was present on all but the HJA study area (Table 2; Appendix S1: Table S2). Evidence of year-to-year variation in pair detection probabilities was present for only the HJA study area (Table 2). Point estimates of detection probabilities for secondary survey periods varied widely across study areas and covariates and ranged from <0.10 for initial detection probabilities for sites in state 1 with barred owls present, to >0.90 for detection probabilities following an initial detection for sites in state 2 with no barred owls present.

Classification probabilities

There was strong evidence ($\sum w_k \sim 1$) for differences in the probability of detecting successful reproduction between early- and late-season surveys, with estimated model coefficients ($\widehat{\beta}$) all positive and precise (Table 2; Appendix S1: Table S3). Estimated probabilities of detecting successful reproduction were near zero for early-season surveys ($j < 7$) and much greater for late-season surveys ($j \geq 7$). Evidence for the importance of barred owls on classification probability varied across the study areas with strong support ($\sum w_k > 0.90$) for a negative barred owl effect on four study areas: CLE, CAS, COA, and KLA (Table 2; Appendix S1: Table S3). Therefore, the probability of detecting successful reproduction was more difficult in these study areas when barred owls also occupied the site. There was weak evidence ($\sum w_k > 0.20$) for barred owl effects on classification probability for RAI, HJA, GDR, NWC, and HUP, no evidence of a barred owl effect ($\sum w_k < 0.01$) on classification probability for the TYE study area (Table 2), and strong support ($\sum w_k \sim 0.85$) for a positive barred owl effect for the OLY study area.

Occupancy transition probabilities

We found strong evidence that the probability of a site being occupied by a pair in the current year was dependent on the occupancy status of the site in the previous year such that $\widehat{\Psi}^{[0]}_{i,t+1} \ll \widehat{\Psi}^{[1]}_{i,t+1} < \widehat{\Psi}^{[2]}_{i,t+1}$ (Table 3). All study areas showed strong evidence of a negative time trend, with less frequent transitions to occupied states in recent years (Table 3). Study areas were also markedly consistent in showing strong evidence of barred owl effects on occupancy transitions. Barred owl effects were negative and additive (i.e., the same for all occupancy states) for nine of the study areas: CLE, OLY, RAI, COA, HJA, KLA, GDR, HUP, NWC. Models with barred owl effects that varied by state were supported for two areas: CAS and TYE, and were all negative for CAS, and mixed for TYE. Barred owl effects on sites previously occupied by a nonnesting pair (state 1) in TYE were positive, whereas barred owl effects for states 0 and 2 were negative (Table 3).

Successful reproduction transition probabilities

The probability that a site transitioned to the successful reproduction state (state 2), $R^{[m]}_{i,t+1}$, was a primary focus of our analyses and included some of the more complicated model structures. Strong year-to-year variation in reproductive success required the estimation of many parameters, which led to reduced precision of model coefficients (Table 4). Site transitions from unoccupied by a pair in one year to successfully producing young in the next were rare, leading to sparse data for estimating $R^{[0]}_{i,t+1}$. Reduced sample sizes near the final years of our study led to additional losses in precision and the need to combine multiple years for some study areas.

Despite these difficulties, some of our inferences were quite strong. The effect of previous year's status on current year's reproduction was consistent across all study areas. Sites not occupied by an owl pair in year t, but occupied in year $t+1$, had low chances of successful reproduction in $t+1$. Reproductive success in year $t+1$ was similar for occupied sites that did, and did not, experience successful reproduction in the previous year, t, but the former sites usually had slightly higher estimated probabilities of success (Table 4).

Models with barred owl effects on reproductive success transitions received substantial support on all study areas (Table 2) and barred owl effects on these transitions

TABLE 3 Estimates of β coefficients (standard errors) from the top-ranked model for each study area describing relationships between occupancy transition probabilities), previous reproductive state (0, 1 or 2), BO, PNR, and TIME.

Study area		$\mathrm{STATE}_{i,t}$[a]	$\mathrm{BO}_{i,t}$	TIME_t
		$\hat{\beta}\left(\widehat{\mathrm{SE}}\left(\hat{\beta}\right)\right)$	$\hat{\beta}\left(\widehat{\mathrm{SE}}\left(\hat{\beta}\right)\right)$	$\hat{\beta}\left(\widehat{\mathrm{SE}}\left(\hat{\beta}\right)\right)$
CLE	0	−3.06 (0.357)	−0.92 (0.189)	−0.05 (0.018)
	1	4.26 (0.416)		
	2	6.52 (0.534)		
OLY	0	−1.54 (0.339)	−0.53 (0.106)	−0.10 (0.015)
	1	4.52 (0.426)		
	2	5.04 (0.538)		
RAI	0	−1.81 (0.372)	−0.44 (0.123)	−0.09 (0.013)
	1	4.53 (0.450)		
	2	5.06 (0.745)		
CAS	0	−1.65 (0.230)	−0.05 (0.200)	−0.09 (0.013)
	1	4.76 (0.427)	−0.46 (0.425)	
	2	6.38 (0.393)	−1.25 (0.271)	
COA	0	−1.10 (0.155)	−0.41 (0.066)	−0.09 (0.009)
	1	3.55 (0.205)		
	2	5.14 (0.386)		
HJA	0	−1.31 (0.185)	−0.45 (0.060)	−0.07 (0.010)
	1	4.07 (0.214)		
	2	6.05 (0.577)		
KLA	0	−0.59 (0.235)	−0.58 (0.089)	−0.17 (0.017)
	1	4.45 (0.379)		
	2	6.25 (0.366)		
TYE	0	−2.46 (0.441)	−2.76 (0.667)	−0.18 (0.032)
	1	7.34 (0.988)	3.44 (0.888)	
	2	8.73 (0.870)	1.83 (0.617)	
GDR	0	−1.08 (0.204)	−0.19 (0.046)	−0.05 (0.010)
	1	3.33 (0.231)		
	2	6.01 (1.059)		
HUP	0	−0.87 (0.293)	−0.26 (0.103)	−0.06 (0.019)
	1	3.39 (0.320)		
	2	40.75 (–[b])		
NWC	0	−0.96 (0.235)	−0.25 (0.094)	−0.06 (0.013)
	1	3.33 (0.289)		
	2	4.82 (0.491)		

Note: Models with state interactions include β coefficients for all three previous states, whereas additive models only include a single β coefficient. Covariates are described in Appendix S1: Table S1. CAS, South Cascades; CLE, Cle Elum; COA, Coast Range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.

[a] Models were run with state 0 as the common intercept.

[b] Standard error not estimable.

were additive and negative on seven study areas (OLY, RAI, COA, HJA, GDR, HUP, and NWC; Table 4). Contrary to our predictions, barred owl effects were additive and positive on the remaining four study areas (CLE, CAS, KLA, and TYE; Table 4).

Model selection results suggested strong support for the importance of PNR to reproductive success transitions in three of the 11 study areas ($\sum w_k < 0.80$), with one of these also including an interaction between PNR and barred owls (OLY; Table 2). However, the effect of PNR was mixed with positive effects on CAS and KLA, and mixed effects that were imprecise on OLY, in which the top model included an interaction between the previous year's state and PNR (Table 4).

We found little evidence that either of the climate covariates was responsible for the strong year-to-year variation in reproductive transitions (Table 2). Instead, our models retained full, year-specific variation in these transitions.

Derived estimates of system state and reproductive success

We combined estimates of initial occupancy and reproduction with estimates of occupancy and reproduction transitions to derive model-averaged estimates of the proportion of sites in each of the three states $\left(\hat{\phi}_{i,t}^{[m]}\right)$ for each year of the analysis. Estimates of $\phi_{i,t}^{[0]}$ (sites unoccupied by a pair) showed a steep increase over the years on all study areas (Figure 2). For Washington study areas, estimated proportions of sites not occupied by northern spotted owl pairs $\left(\hat{\phi}_{i,t}^{[0]}\right)$ was 0.00–0.23 in 1993 but increased to nearly 0.90 in 2018 (Figure 2a). The proportion of sites not occupied by northern spotted owl pairs on Oregon study areas increased from ~0.10–0.27 in 1993 to ~0.75–0.90 in 2018 (Figure 2b). On California study areas, estimated proportions of sites not occupied by northern spotted owl pairs were all <0.20 for the early years of study but increased to >0.60 by 2018 (Figure 2c). Model-averaged estimates of the proportion of sites in states 1 $\left(\hat{\phi}_{i,t}^{[1]}\right)$ or 2 $\left(\hat{\phi}_{i,t}^{[2]}\right)$ fluctuated from year to year and generally decreased between 1993–2018 on all study areas (Figure 3).

Derived estimates of reproductive rate generally fluctuated from year to year as expected. Strong even–odd-year effects (oscillating years of high/low reproduction) were evident across nearly all years for two study areas in Washington (OLY, RAI), for some years in one study area in Washington (CLE), three

TABLE 4 Estimates of β coefficients (standard errors) from the top-ranked model for each study area describing relationships between probability of successful reproduction $\left(R_{i,t+1}^{[m]}\right)$, previous reproductive state (0, 1 or 2), BO$_{i,t+1}$, PNR$_{i,t}$, and a BO$_{i,t+1}$ × PNR$_{i,t}$ interaction.

		STATE$_{i,t}$[a]	**BO$_{i,t+1}$**	**PNR$_{i,t}$**	**PNR$_{i,t}$ × BO$_{i,t+1}$**
Study area		$\hat{\beta}$	$\hat{\beta}$	$\hat{\beta}$	$\hat{\beta}$
CLE	0	−20.89 (1.310)	10.39 (0.769)	...	...
	1	26.22 (1.462)			
	2	27.61 (1.457)			
OLY	0	−0.83 (1.839)	−0.27 (0.135)	2.81 (1.997)	...
	1	1.17 (1.821)		−2.70 (2.016)	
	2	3.16 (1.817)		−3.46 (2.020)	
RAI	0	−0.98 (1.572)	−0.67 (0.173)	...	...
	1	1.08 (1.364)			
	2	0.84 (1.456)			
CAS	0	−89.86 (0.381)	15.86 (0.890)	0.32 (0.093)	...
	1	94.76 (0.358)			
	2	96.22 (0.381)			
COA	0	−21.45 (0.583)	−0.71 (0.095)	...	...
	1	21.25 (0.589)			
	2	22.93 (0.618)			
HJA	0	−23.70 (0.461)	−0.31 (0.071)	...	...
	1	22.65 (0.476)			
	2	23.45 (0.519)			
KLA	0	1.89 (1.084)	29.02 (2.301)	0.19 (0.099)	...
	1	2.46 (1.076)			
	2	3.68 (1.057)			
TYE	0	2.52 (1.341)	25.06 (2.193)	...	...
	1	0.55 (1.387)			
	2	2.95 (1.350)			
GDR	0	−1.93 (1.262)	−0.29 (0.091)	0.03 (0.069)	−0.18 (0.093)
	1	2.35 (1.248)			
	2	3.04 (1.238)			
HUP	0	−5.98 (3.282)	−0.35 (0.136)	...	...
	1	5.08 (3.286)			
	2	6.63 (3.304)			
NWC	0	−75.18 (0.306)	−0.49 (0.120)	...	...
	1	75.411 (0.342)			
	2	75.825 (0.393)			

Note: Models with state interactions include β coefficients for all three previous states, whereas additive models only include a single β coefficient. Covariates are described in Appendix S1: Table S1. CAS, South Cascades; CLE, Cle Elum; COA, Coast Range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.

[a] Models were run with state 0 as the common intercept.

study areas in Oregon (CAS, COA, HJA), and two study areas in California (HUP, GDR), but were generally not evident in the other study areas (HJA, KLA, TYE, NWC). Annual estimates of the probability of successful reproduction ranged from 0.00 to >0.90, with the majority of estimates in Washington and Oregon, on average, greater than estimates in California (Figure 4).

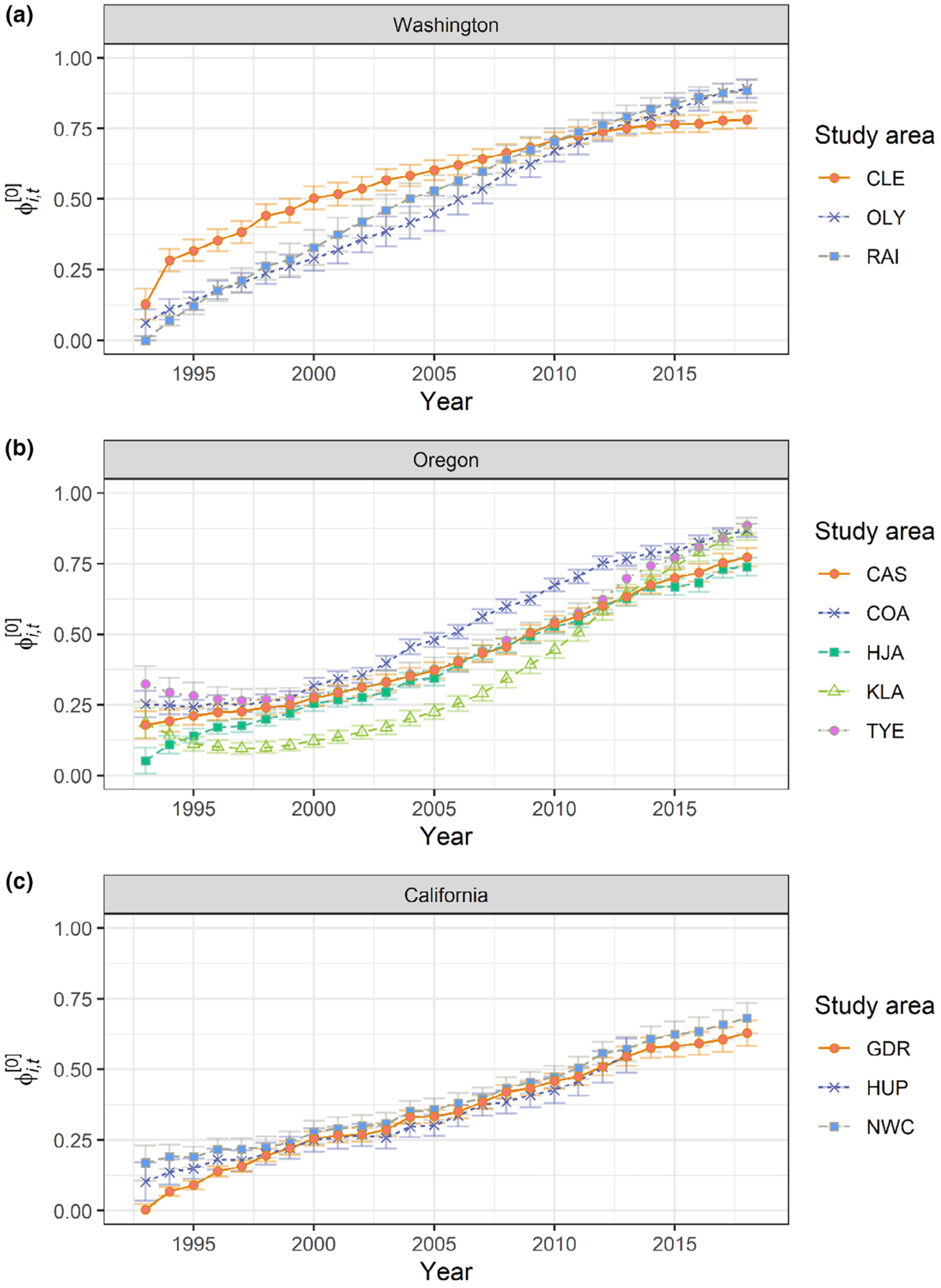

FIGURE 2 The probability of a site being unoccupied by a pair of northern spotted owls $\left(\phi^{[0]}_{i,t}\right)$ on 11 study areas in Washington (a), Oregon (b), and California (c), USA, 1993–2018. Error bars are one standard error. CAS, South Cascades; CLE, Cle Elum; COA, Coast Range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.

DISCUSSION

This analysis focused on northern spotted owl reproductive rate dynamics, in which reproductive rate is defined as the probability that a site occupied by a pair of northern spotted owls in a breeding season produces at least one young bird. We had two primary motivations for this analysis: (1) examining environmental factors thought to be responsible for driving range-wide trends in northern spotted owl reproduction dynamics, and (2) establishing a framework for future analyses that incorporates imperfect detection and misclassification of sites.

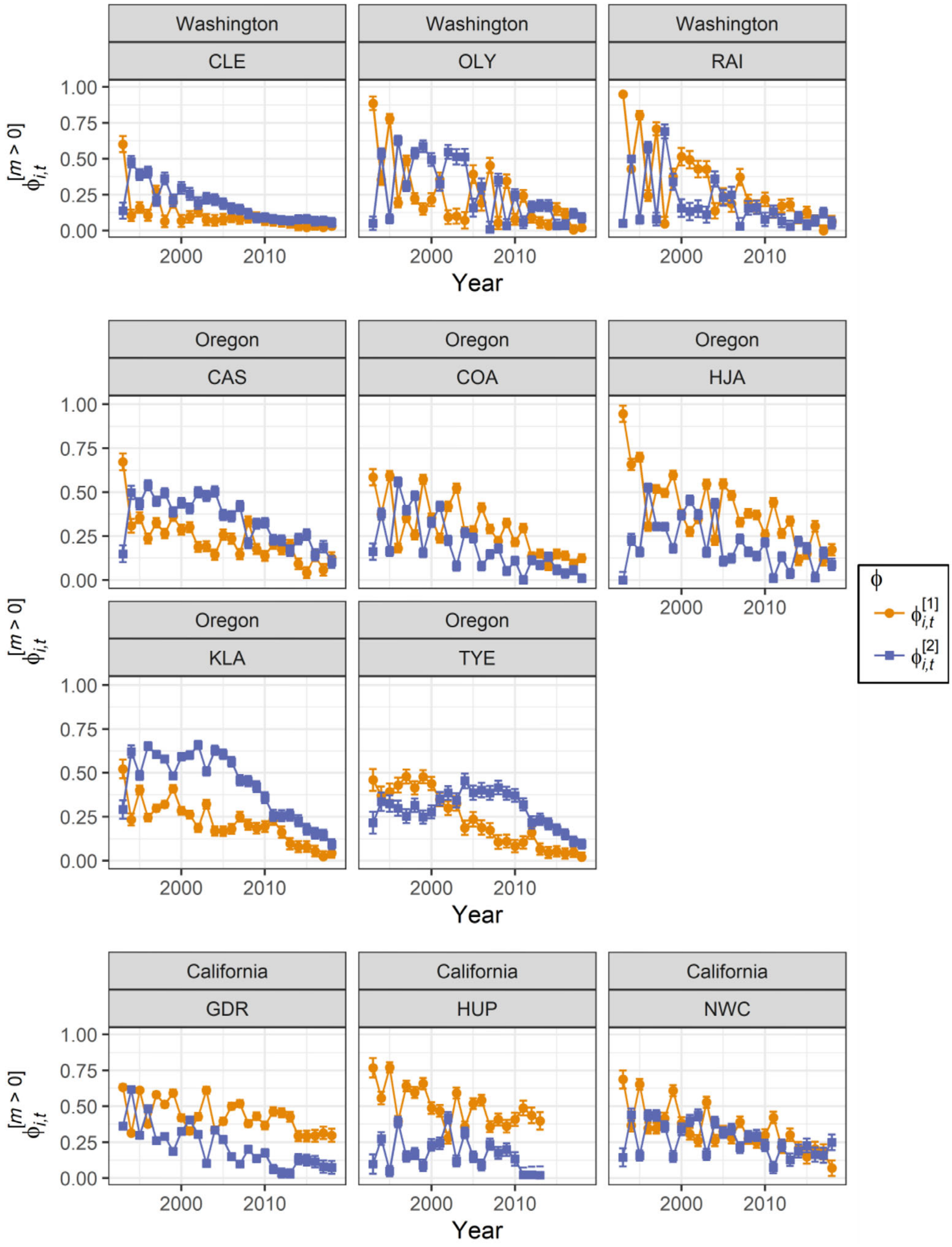

FIGURE 3 The probability of a site being occupied by either an unproductive pair $\left(\text{orange}, \phi_{i,t}^{[1]}\right)$ or productive pair $\left(\text{blue}, \phi_{i,t}^{[2]}\right)$ of northern spotted owls over time in 11 study areas in Washington, Oregon, and California, USA, 1993–2018. Error bars are one standard error. CAS, South Cascades; CLE, Cle Elum; COA, coast range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.

Occupancy state transitions and derived occupancy estimates

Our estimates of state-specific occupancy transition probabilities strongly supported our prediction that sites not occupied by pairs the previous year were much less likely to be occupied by pairs in the current year, and sites at which successful reproduction occurred in the previous year were more likely to be occupied than previously occupied sites without successful reproduction. These findings are consistent with previous research on spotted owls (Lee & Bond, 2015; MacKenzie et al., 2009; Mangan et al., 2019) and other territorial raptor species (León-Ortega et al., 2017; Martínez et al., 2006; Wiens et al., 2018).

Our predictions about the influence of environmental variables on occupancy transition probabilities were supported on some study areas but not others. Barred

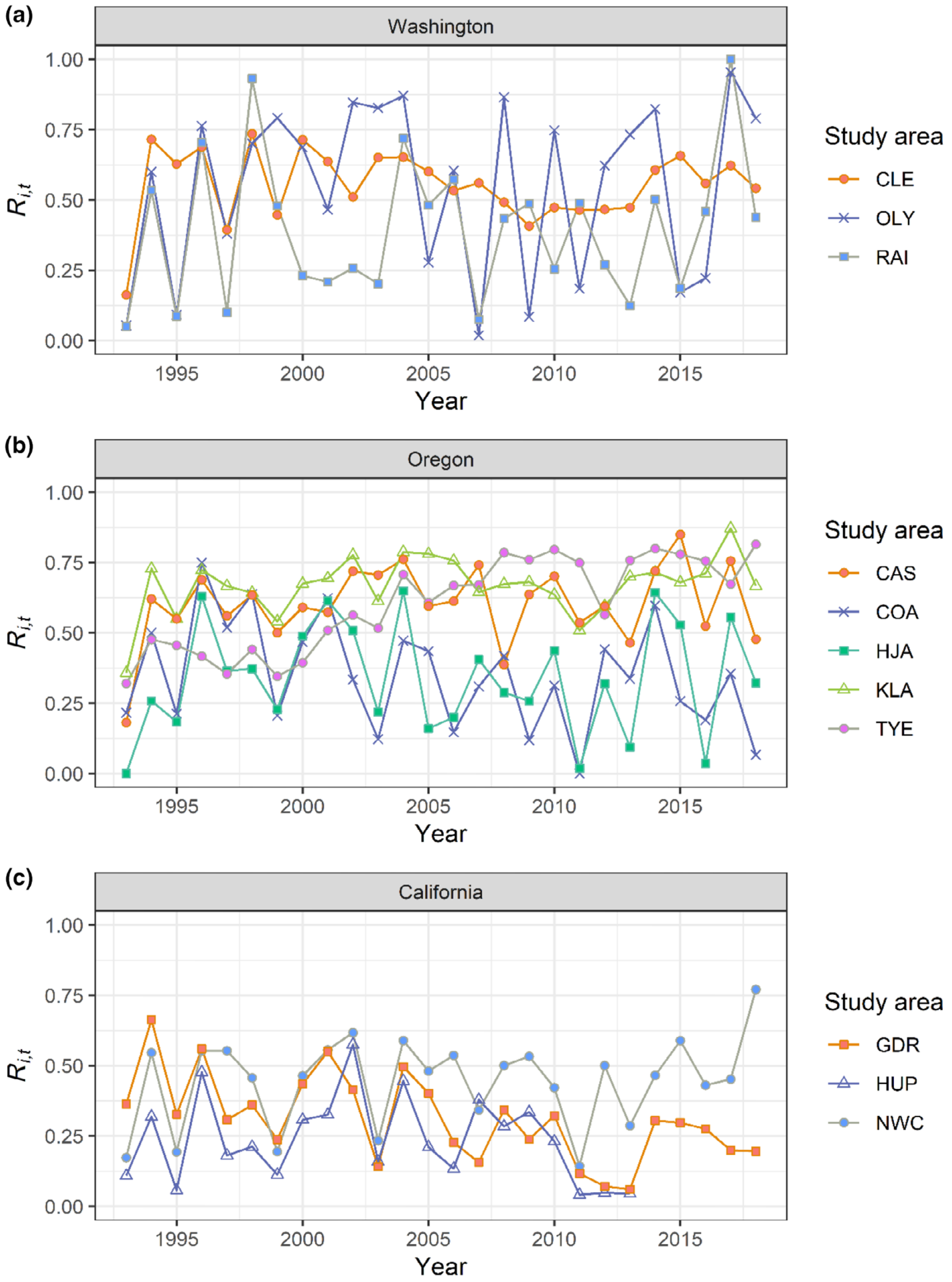

FIGURE 4 Probability that a pair of northern spotted owls successfully reproduced $\left(R_{i,t} = \phi^{[2]}_{i,t} / \left(\phi^{[1]}_{i,t} || + \phi^{[2]}_{i,t}\right)\right)$ in 11 study areas in Washington (a), Oregon (b), and California (c), USA, 1993–2018. CAS, South Cascades; CLE, Cle Elum; COA, Coast Range; GDR, Green Diamond; HJA, HJ Andrews; HUP, Hoopa; KLA, Klamath; NWC, NW California; OLY, Olympic; RAI, Rainier; TYE, Tyee.

owl effects on occupancy transitions were consistent, strong, and negative on 10 of 11 study areas, as expected, yielding further evidence of the negative effect of barred owls on northern spotted owl site occupancy dynamics (Dugger et al., 2016; Franklin et al., 2021; Yackulic et al., 2014, 2019). In contrast, we did not find an effect of the proportion of NR cover on occupancy transitions. The lack of an effect of habitat components on northern spotted owl site occupancy might partially be explained by the nonrandom selection of owl sites used in this analysis. Most sites in this analysis represent locations on the landscape that have been defended by owls at one time or another, and therefore are locations that owls have occupied. As such, these sites are likely to represent locations with relatively higher proportions of suitable NR cover. We note, however, that a comparison of forest conditions on federally managed public lands within and outside of these study areas found similar amounts of suitable forest cover in both landscapes (Anthony et al., 2006, appendix F). Finally, we predicted negative time trends for all occupancy transition probabilities based on the strong evidence of declining population sizes and site occupancy provided by past studies (e.g., Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021). Support for this prediction was strong and consistent, with all study areas showing a sharp, negative decline in occupancy transition probabilities over time resulting in small populations, especially in Washington study areas. These declines warrant serious concern.

Our derived estimates of the proportions of sites in each of the three occupancy states for all study areas showed steep, monotonic decreases in the proportion of sites occupied by northern spotted owl pairs over the 1993–2018 period (Figures 2 and 3). The proportion of sites occupied but unproductive (state 1) and occupied and productive (state 2) fluctuated over the years, but the overall decline in northern spotted owl site occupancy was substantial, with dangerously low occupancy levels estimated for Washington study areas. The declines that we observed are clear, dramatic, and consistent with the complementary meta-analysis of northern spotted owl population change (Franklin et al., 2021). The current trend in northern spotted owl site pair occupancy (this study), combined with declining rates of overall site occupancy, apparent survival, and population change (Franklin et al., 2021), suggest that, without intervention, the long-term persistence of northern spotted owl populations is unlikely (e.g., Yackulic et al., 2019).

As vertebrate populations decline to only a few individuals an extinction vortex can occur in which positive feedbacks occur among environmental and demographic stochasticity, inbreeding, and disrupted behaviors (Gilpin & Soulé, 1986), resulting in rapid progression to extinction in just a few years (Fagan & Holmes, 2006). Several recent papers have documented factors characteristic of an extinction vortex in northern spotted owl populations, including small population size (Franklin et al., 2021), increased rates of inbreeding (Miller et al., 2018), and destabilized dispersal dynamics (Jenkins et al., 2021). If these trends continue, it is conceivable the northern spotted owl will become extirpated throughout large portions of its range in the next decade. Similar results and conclusions were reported in a recent range-wide meta-analysis on the long-term population trends of northern spotted owls which found dramatic, long-term declines in northern spotted owl site occupancy, apparent survival, and realized population change (Franklin et al., 2021).

Reproductive success transitions and derived reproductive rate estimates

A primary motivation of our modeling efforts focused on the probability of a site transitioning into a site with successful reproduction in year $t+1$ $\left(R_{i,t+1}^{[m]}\right)$. Inferences about these parameters were made difficult by the need for models with year-specific variation, sparse data for informing $\widehat{R}_{i,t+1}^{[0]}$, and very low occupancy for the final few years on some study areas. Therefore, uncertainty was greater for inferences about reproductive transitions than for other model parameters. Nonetheless, we found strong evidence that a site's previous reproductive status was an important determinant of the current year's reproductive status. In 10 of 11 study areas, estimates of $R_{i,t+1}^{[0]}$ were substantially smaller than estimates of $R_{i,t+1}^{[1]}$ and $R_{i,t+1}^{[2]}$. A Markov process for which $R_{i,t+1}^{[1]} > R_{i,t+1}^{[2]}$, in conjunction with a synchronizing environmental effect (e.g., a year of especially high or low prey availability), would be capable of generating annual fluctuations in reproductive success similar to those seen in previous fecundity analyses (Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021). In contrast, a process for which $R_{i,t+1}^{[1]} < R_{i,t+1}^{[2]}$ would tend to dampen year-to-year fluctuations. In 10 of the 11 study areas, sites that experienced successful reproduction in the previous year had greater estimated reproduction transition probabilities than sites not experiencing successful reproduction the previous year $\left(\widehat{R}_{i,t+1}^{[1]} < \widehat{R}_{i,t+1}^{[2]}\right)$. However, transition probability differences between these states were small and, in most cases, the estimates were statistically indistinguishable. Therefore, our results did not provide strong support for an a priori hypothesis about how the previous year's reproductive state influenced current year's reproduction.

One plausible mechanism for the patterns in reproductive success we observed (strong annual fluctuations and a possible pair/territory quality effect) might be a combination of a strong, periodic, synchronizing event and a site/pair effect. For example, years with high resource availability might synchronize all sites to a high reproductive state, but in subsequent years with lower resource availability only sites and/or pairs of higher quality may reproduce, leading to a disruption of the even–odd-year effect found in previous meta-analyses. If this pattern of synchronizing event followed by a site/pair effect recurs at a somewhat regular interval, we might expect to find the same type of pattern as we observed in this analysis. Indeed, a post hoc examination of reproductive success transitions $\left(\widehat{R}_{i,t+1}^{[1]} \text{ and } \widehat{R}_{i,t+1}^{[2]}\right)$ and derived estimates of reproductive rate showed that during years of overall low reproductive rate (e.g., 1995, 1999, 2003, 2011, 2012 for all CA study areas), sites that successfully reproduced the previous year were disproportionately more likely to reproduce than sites that did not reproduce the previous year. $\left(\text{i.e.}, \widehat{R}_{i,t+1}^{[1]} \ll \widehat{R}_{i,t+1}^{[2]}\right)$. This effect was not consistent across all study areas, but provided additional evidence for a site/pair effect on reproductive success on at least some study areas and warrants future research focusing on possible drivers (e.g., fluctuations in prey availability, variation in habitat quality, sensu Franklin et al., 2000).

As with the occupancy transition probabilities, our predictions about the influence of environmental variables on reproductive success were supported for some study areas, but not for others. Our prediction of a negative effect of barred owls on reproductive success of northern spotted owls was supported for seven study areas, but the remaining four study areas had results supporting positive barred owl effects. These findings are counterintuitive, but they may reflect site-specific habitat components not included in our models that were selected by barred owls and that also led to higher reproductive success for northern spotted owls. Another possible explanation is that some spotted owl pairs may actively defend their territories from barred owls (Duchac et al., 2020) and successfully compete with barred owls in shared territories of higher quality. Indeed, anecdotal evidence seems to indicate that as barred owls invade an area they quickly displace most spotted owls, but some spotted owls appear to hold on to their territory for some years before eventually being displaced. This observation suggests that certain site/pair characteristics unknown to us are partly responsible for this unexpected result. Finally, as barred owl presence increases and northern spotted owl site occupancy declines to just a few occupied sites, it is likely the only spotted owl sites that successfully produce young will also contain barred owls, thereby establishing a positive statistical relationship between barred owl presence and successful reproduction in northern spotted owls.

It is also possible that model results from these four study areas are questionable. Our modeled barred owl effects for these four study areas included large beta coefficients with very small standard errors (Table 4). We checked these models for evidence of poor model fit (please refer to *Model set development*) and simplified model structures for CLE and KLA during the model fitting process because models including interactions exhibited signs of overfitting. However, in each case the magnitude and direction of beta coefficients and standard errors was similar to the more complicated model structures.

Lastly, given the overwhelming consistent, range-wide evidence of a negative effect of barred owls on northern spotted owl vital rates in previous studies (Dugger et al., 2016; Franklin et al., 2021; Wiens et al., 2021; Yackulic et al., 2014, 2019), we urge caution when drawing conclusions from this single, contrary finding.

In general, our prediction of a positive effect of NR cover on reproductive success transitions was not supported, as this covariate was only associated with reproductive transitions in three of 11 study areas, leading to no overall conclusion about the effect of NR cover on reproductive success transitions. In addition, interaction effects between barred owls and the proportion of NR cover were potentially important for one study area (GDR) where increasing proportions of NR cover appeared to buffer northern spotted owls from the negative effects of barred owls (Table 4). The lack of a consist effect of NR cover on spotted owl reproductive rates is not a new finding, as previous analyses of territory-specific fecundity in northern spotted owls (Dugger et al., 2005; Franklin et al., 2000; Olson et al., 2004) found mixed results when associating amounts of interior mid–late seral stage forests and fecundity. This finding could be partly explained by a changing prey base across the range of the species. For example, in the southern parts of their range, spotted owls prefer larger bodied woodrats (*Neotoma* spp.; Ward et al., 1998) that occur predominately in early seral stands (Hamm & Diller, 2009; Sakai & Noon, 1993), whereas in the more northern parts of their range spotted owls prey on Humboldt's flying squirrels (*Glaucomys oregonensis*) which occur predominately in late successional stands (Carey et al., 1992). Therefore, perhaps it is not surprising we did not find a pattern of habitat effects on northern spotted owl reproduction that was consistent across study areas.

Finally, previous meta-analyses of northern spotted owls found certain climate-related variables important for explaining some of the annual variation in fecundity (Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021), and for this reason we included two climate covariates in our analysis. However, neither of the climate variables we examined were well supported in our analysis. This was somewhat surprising given the support that climate-related variables have received in previous meta-analyses, but the lack of an effect in our study may be tied to our choice of climate variables. Previous site-specific analyses of spotted owl reproduction found that the timing of relatively short-term weather effects, such as the amount of precipitation during a specific breeding stage, was important for explaining reproductive output (Dugger et al., 2005; Franklin et al., 2000; Glenn et al., 2011; Olson et al., 2004). Therefore, our use of annual, region-wide climate covariates may represent a mismatch between the scale at which climate or weather affects spotted owl reproduction and our use of SOI and PDO (Bütikofer et al., 2020; Potter et al., 2013).

Our derived estimates of reproductive rate, $\widehat{R}_{i,t}$, showed substantial year-to-year fluctuations (Figure 4), as expected based on the even–odd-year patterns found consistently in northern spotted owl meta-analyses of fecundity (Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021). None of the time-varying variables we examined were informative in explaining this strong temporal trend. Instead, the strong year-to-year variation required full, time-specific modeling of successful reproduction transitions. Therefore, we can conclude that these fluctuations are not primarily driven by a Markov process reflecting reproductive costs. Instead, we propose our results suggest that a combination of a periodic synchronizing event, such as extreme weather or resource availability, along with a site/owl pair effect, may be responsible for driving northern spotted owl reproductive dynamics, and we suggest additional modeling that may provide insights into this hypothesis. For example, our post hoc finding provides evidence of a site/pair effect that could be formally tested by parameterizing a model with $R_{i,t+1}^{[1]}$ and b, where $R_{i,t+1}^{[2]} = b \times R_{i,t+1}^{[1]}$ to determine whether b varies with respect to reproductive rate. If some sites/pairs are reproductively superior to others, we would predict those sites to produce disproportionately more young in years of low reproductive output. The spatially explicit nature of these models also creates a linkage between site occupancy and reproductive dynamics and landscape conditions, and while this was beyond the scope of this analysis, future analyses might consider examining spatial patterns in reproductive output and site quality.

Despite devoting the majority of our effort to modeling state-specific reproductive success transitions, our overall model set was of course not exhaustive, and several options remain for the modeling this parameter in future meta-analyses. For example, we did not include models that constrained reproductive success probabilities for states 1 and 2 to be equal $\left(R_{i,t+1}^{[1]} = R_{i,t+1}^{[2]}\right)$, but our results suggest that these values were similar across most study areas. Similarly, given the low reproductive success transition probabilities for sites in state 0 in year t, subsequent modeling efforts might consider fixing these transition probabilities to 0. In addition, we did not include models that permitted an interaction between state and time effects, such that Markovian effects could vary by year. We also did not explore the possibility of higher order Markov processes (e.g., effects of state in years $t-2$ or $t-3$), which might be relevant under a site/pair quality hypotheses. Such models were beyond the scope of our objectives and may challenge the inferential limits of our data, but seem worthy of consideration in future analyses.

Incorporating imperfect detection and misclassification

Our second motivation for this analysis was to base inferences about northern spotted owl reproductive rates on analytical methods that incorporated imperfect detection and misclassification. These issues were potentially important, as prior to initial detection, estimated pair detection probabilities per visit were sometimes <0.10 and frequently <0.50, with detection probabilities decreasing over time. Additionally, correct classification probabilities did not approach 1 even for late-season sampling periods, further highlighting the importance of accounting for misclassification. As such, we believe that the analytic methods presented here will be especially useful in (1) permitting use of information from sites with varying levels of survey effort, including sites that may not meet a project-defined sampling protocol, and (2) guarding against the possibility that these latter sites may differ from those at which protocol is met.

As expected, pair detection probabilities were greater for sites at which reproduction was successful than for sites without successful reproduction, presumably because of the greater territoriality and site fidelity of reproductively active owls. There was also strong evidence of a within-season trap response across all study areas, with estimated detection probabilities greater for secondary sampling periods after the initial detection of the pair. This result was also consistent with our predictions, as subsequent visits to a site typically begin where the birds were last found. Finally, we predicted that pair detection probability would decrease on sites where the probability of barred owl presence was high (Bailey et al., 2009; Dugger et al., 2016; Yackulic et al., 2014). Evidence for a barred owl effect was consistent with the strong evidence of a negative effect of barred owls on pair detection for 10 of 11 study areas. This was similar to previous analyses that found consistent, strong, and negative effects of barred owls across all study areas (Dugger et al., 2016; Yackulic et al., 2019). These results argue for the importance of collecting barred owl data during northern spotted owl surveys, as barred owl presence often produces decreased detection probabilities of northern spotted owls and further highlights the importance of incorporating methods that account for nondetection.

As we expected, the probability of correctly classifying a site with successful reproduction was greater for secondary sampling occasions that occurred later in the season across all study areas, as classification depends on the presence of young. However, we found mixed support for our prediction of a negative effect of barred owl presence on correct classification with strong support for a negative barred owl effect for four study areas, weak support for five study areas, no support for one study area, and strong support for a positive barred owl effect on one study area. Therefore, although barred owls had a negative effect on correct classification probability for some study areas, the effect was not consistent across all study areas.

Summary

We found strong evidence that northern spotted owl site occupancy is declining range-wide and that the species is at immediate risk of extirpation from large portions of its geographic range. This finding is not unique to this study (Dugger et al., 2016; Franklin et al., 2021; Yackulic et al., 2019), and other research has pointed to evidence of an extinction vortex (Gilpin & Soulé, 1986) for northern spotted owls (Franklin et al., 2021; Jenkins et al., 2021; Miller et al., 2018).

We recommend that our approach to estimating the probability of successful pair reproduction be incorporated into subsequent meta-analyses for northern spotted owls. Inferences about both pair detection probabilities and state classification parameters provide strong evidence for the utility of modeling this sampling process when attempting to make general ecological inferences. Including the sampling process explicitly in parameter modeling is especially important in cases such as ours in which key factors affecting ecological processes (e.g., barred owl presence) also have important influences on sampling processes.

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ACKNOWLEDGMENTS

We thank the small army of crew members responsible for collecting all of the field data over the past three decades. None of these studies could have persevered for as long as they have without their contributions. We also thank the funding agencies for their continued support. Funding for study areas on public lands was provided by the USDA Forest Service, US Bureau of Land Management, and US National Park Service. Funding for study areas on private and sovereign lands was provided by Green Diamond Resource Company, Plum Creek Timber Company, Weyerhaeuser, and the Hoopa Valley Tribe. Data from CAS, CLE, COA, HJA, KLA, NWC, and TYE was collected under Oregon State University's and Colorado State University's Institutional Animal

Care and Use Committees, and under the terms and conditions provided for by all relevant state and federal scientific collecting permits. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official US Department of Agriculture, or US Fish and Wildlife Service policy. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Rockweit et al., 2022) are available from Oregon State University ScholarsArchive at https://doi.org/10.7267/7w62fh122_v3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Rockweit, Jeremy T., Julianna M. Jenkins, James E. Hines, James D. Nichols, Katie M. Dugger, Alan B. Franklin, Peter C. Carlson, et al. 2023. "Range-Wide Sources of Variation in Reproductive Rates of Northern Spotted Owls." *Ecological Applications* 33(1): e2726. https://doi.org/10.1002/eap.2726