

# Conspecific and congeneric interactions shape increasing rates of breeding dispersal of northern spotted owls

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**Citation:** Jenkins, J. M. A., D. B. Lesmeister, E. D. Forsman, K. M. Dugger, S. H. Ackers, L. S. Andrews, S. A. Gremel, B. Hollen, C. E. McCafferty, M. S. Pruett, J. A. Reid, S. G. Sovrn, and J. D. Wiens. 2021. Conspecific and congeneric interactions shape increasing rates of breeding dispersal of northern spotted owls. *Ecological Applications* 31(7):e02398. 10.1002/eap.2398

**Abstract.** Breeding dispersal, the movement from one breeding territory to another, is rare for philopatric species that evolved within relatively stable environments, such as the old-growth coniferous forests of the Pacific Northwest. Although dispersal is not inherently maladaptive, the consequences of increased dispersal on population dynamics in populations whose historical dispersal rates are low could be significant, particularly for a declining species. We examined rates and possible causes of breeding dispersal based on a sample of 4,118 northern spotted owls (*Strix occidentalis caurina*) monitored in seven study areas over 28 yr, 1990–2017, in Oregon and Washington, USA. Using a multistate mark–resight analysis, we investigated the potential impacts of an emergent congeneric competitor (barred owl *Strix varia*) and forest alteration (extrinsic factors), and social and individual conditions (intrinsic factors) on 408 successive and 1,372 unsuccessful dispersal events between years. The annual probability of breeding dispersal increased for individual owls that had also dispersed in the previous year and decreased for owls on territories with historically high levels of reproduction. Intrinsic factors including pair status, prior reproductive success, and experience at a site, were also associated with breeding dispersal movements. The percent of monitored owls dispersing each year increased from ~7% early in the study to ~25% at the end of the study, which coincided with a rapid increase in numbers of invasive and competitively dominant barred owls. We suggest that the results presented here can inform spotted owl conservation efforts as we identify factors contributing to changing rates of demographic parameters including site fidelity and breeding dispersal. Our study further shows that increasing rates of breeding dispersal associated with population declines contribute to population instability and vulnerability of northern spotted owls to extinction, and the prognosis is unlikely to change unless active management interventions are undertaken.

**Key words:** barred owl; competition; dispersal probability; philopatric species; population stressors; spotted owl; *Strix occidentalis occidentalis*; *Strix varia*.

## INTRODUCTION

Dispersal is a key demographic process in spatially and socially structured populations that evolves in association with other life history characteristics. Movements of individuals from one territory to another can affect individual fitness, promote gene flow, recolonize extinct patches, and, ultimately, influence species distributions

(Greenwood 1980, Switzer 1993, Bowler and Benton 2005). At the population level, increased movement from highly productive to declining populations can buffer, or even rescue, declining population segments from extinction (Levin 1974, Vance 1984). Some individuals that vacate territories may also become floaters (non-territory-holding adults), who can recolonize vacant territories when they become available (Penteriani et al. 2011). Yet increased dispersal rates can also intensify population declines or negatively influence productivity if individuals that move incur greater costs than site-faithful individuals, or if rates of emigration outpace

Manuscript received 11 August 2020; revised 11 January 2021; accepted 22 February 2021. Corresponding Editor: John M. Marzluff.

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immigration, local survival, and production (Levin 1974). There are two main types of dispersal recognized in philopatric breeding birds: natal and breeding dispersal. Natal dispersal, the movement from the natal site to the site of first breeding (Greenwood 1980), is more widely studied than breeding dispersal, the movement between subsequent breeding sites (Greenwood and Harvey 1982). Identifying breeding dispersal strategies is often limited by our ability to observe movements at a wide range of spatial and temporal scales in long-lived species, and further hampered by large arrays of possible factors that affect individual movement decisions of whether and how far to move (Nathan 2001, Bowler and Benton 2005).

In philopatric species that are territorial, the decision of whether to stay on a breeding territory (site fidelity) or move to a new one (breeding dispersal) is dependent upon multiple intrinsic and extrinsic conditions that may influence decisions at different stages of the dispersal process (Bowler and Benton 2005). A common precursor to breeding dispersal is past failure to produce young (Greenwood and Harvey 1982, Kim et al. 2007, Gutiérrez et al. 2011). In addition, intrinsic factors that influence the ability of an individual to defend a territory or attract a mate, such as an individual's age, sex, or previous breeding success at a site, also influence rates of breeding dispersal (Clarke et al. 1997, Forsman et al. 2002). Generally, the probability of breeding dispersal declines with increasing reproductive success and increasing age, and female-biased breeding dispersal is common in philopatric species with male-dominated territory defense systems (Greenwood and Harvey 1982, Clarke et al. 1997). Extrinsic factors, such as the presence and density of conspecifics or competitors, habitat quality, or disturbances, can also influence dispersal (Bowler and Benton 2005, Schuab and von Hirschheydt 2009, Bötsch et al. 2012, Marzluff et al. 2016). The multitude of interacting intrinsic and extrinsic factors that affect breeding dispersal make disentangling the proximate causes of dispersal difficult. Nonetheless, understanding the context-dependent nature of breeding dispersal and its importance to individual fitness and meta-population dynamics can increase an understanding of population dynamics and inform predictions of how individuals respond to changing environments or social conditions within populations (Walters 2000). In addition, because individuals should disperse to sites that maximize their fitness, studies of breeding dispersal can provide unique insight into gradients in habitat or territory quality (Betts et al. 2008). Furthermore, observing how rates of dispersal change through time can provide insight to population stability.

The northern spotted owl (*Strix occidentalis caurina*) is a long-lived, philopatric species that requires high canopy cover, large trees, and complex forest structure in core-use areas of their territories (see review by Lesmeister et al. [2018]). The population demography of this subspecies has been studied over a large geographic area

for the past three decades, revealing significant declines in populations and genetic diversity (Funk et al. 2010, Dugger et al. 2016) and increased inbreeding rates (Miller et al. 2018). Continued population declines have underscored the increasing vulnerability of spotted owls to extirpation. The cause of declines has been at least partially attributed to habitat loss through forest alteration, and, more recently, competition with barred owls (*Strix varia*), a congener that has rapidly expanded into the range of the northern spotted owl from its historical range in eastern North America (see reviews by Lesmeister et al. [2018], Long and Wolfe [2019]). Resource partitioning can alleviate congeneric interactions, but such behavioral adaptations may not keep pace with increased competitive pressure resulting from rapid increases in invader populations (Schoener 1974, Wiens et al. 2014, Lesmeister et al. 2015, Jenkins et al. 2019b). Spotted owls are an old forest obligate, and thus forest alteration, depending upon the extent and severity, is considered a primary threat to spotted owl persistence (reviewed in Lesmeister et al. [2018]) and may also affect owl dispersal. The estimated rate of breeding habitat loss on federal lands was slowed with the passage of the Northwest Forest Plan, but harvests on private timber lands have continued (U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior BLM 1994, Lesmeister et al. 2018).

Dispersal is a difficult process to study, particularly in long-lived, wide-ranging species that may be hard to detect or frequently disperse beyond finite study areas (Koenig et al. 1996, Nathan 2001). Nonetheless, quantifying changing rates of demographic parameters that may be vulnerable to population stressors, such as site fidelity, breeding dispersal, and emigration, can inform conservation and management of northern spotted owls. Long-term, mark-resight investigations of demographic traits and habitat associations of northern spotted owls have provided a unique opportunity to identify drivers of population change in this species (e.g., Dugger et al. 2016), including factors influencing breeding dispersal (e.g., Forsman et al. 2002). Northern spotted owls have generally high survival, and high fidelity to breeding territories and mates (Forsman et al. 2002, 2011, Anthony et al. 2006). Using banding and radio-telemetry data collected during 1985–1996, Forsman et al. (2002) found an average 7% annual rate of breeding dispersal over the 10-yr period. The intrinsic factors of reproductive success, site and mate experience, and sex best explained variation in breeding dispersal behavior (Forsman et al. 2002). More recently, breeding dispersal distances of northern spotted owls were found to be associated with forest disturbance and social status (Jenkins et al. 2019a). Territory quality, as defined by site-level occupancy and reproductive history, has also been found to play an important role in dispersal behavior of the California spotted owl (*Strix occidentalis occidentalis* [Seamans and Gutiérrez 2007, Gutiérrez et al. 2011]). Changes in forest stand characteristics through

disturbance events (e.g., wildfire, timber harvest) may also influence breeding dispersal rates in northern spotted owls. Barred owls can displace spotted owls from historical territories (Kelly et al. 2003, Pearson and Livezey 2007), which has contributed to an increase in breeding dispersal distances over time (Jenkins et al. 2019a). In addition to displacement, interspecific territoriality and competition for limited resources with barred owls at high-quality sites may decrease the realized quality of territories (Wiens et al. 2014) and lead to decreases in site occupancy by spotted owls (Yackulic et al. 2019). This evidence suggests that the frequency of breeding dispersal may also be increasing in populations of spotted owls.

Although dispersal is not inherently maladaptive, the consequences of increased dispersal rates on philopatric wildlife populations with historically low dispersal rates is uncertain. Moreover, increasing dispersal rates of spotted owls have methodological implications for how survival, and ultimately population trends, are estimated. We investigated the relationship of barred owls and forest disturbance (extrinsic factors), and social and individual conditions (intrinsic factors) on movement decisions of territorial northern spotted owls in Oregon and Washington, USA. Our specific objectives were to evaluate (1) rates of breeding dispersal in northern spotted owls over 28 yr (1990–2017) on seven demographic study areas spanning five ecophysiological provinces in Oregon and Washington; (2) whether rates and possible factors associated with the rate of breeding dispersal have changed over time; (3) if temporal changes could best be correlated with extrinsic (e.g., forest cover, forest disturbance, barred owl presence) vs. intrinsic factors (e.g., years of experience on a territory, prior breeding success); and (4) test whether there are changes in survival for dispersing owls.

## METHODS

Individual spotted owls were monitored in seven study areas within five ecophysiological provinces (hereafter, provinces) in Oregon and Washington, USA, between 1990 and 2017 (Fig. 1). Study areas were the Olympic Peninsula (OLY; 2,541 km<sup>2</sup>) and Cle Elum (CLE; 980 km<sup>2</sup>) areas in Washington and the Oregon Coast Range (OCR; 1,810 km<sup>2</sup>), Tyee (TYE; 810 km<sup>2</sup>), H. J. Andrews (HJA; 1,004 km<sup>2</sup>), South Cascades (CAS; 2,372 km<sup>2</sup>), and Klamath (KLA; 1,074 km<sup>2</sup>) areas in Oregon. All study areas were part of a long-term monitoring program for northern spotted owls established under the Northwest Forest Plan and were composed primarily of conifer or mixed conifer–hardwood forests and varied in climate, understory vegetation, and topography (Lint et al. 1999). Study areas that were primarily under federal forest management (Olympic Peninsula, H. J. Andrews, and South Cascades; Fig. 1) generally had >60% of the landscape covered by mature (80–200-yr-old) and old (>200-yr-old) conifer forest. Other study

areas (Cle Elum, Oregon Coast Range, Tyee, and Klamath; Fig. 1) contained a diverse mixture of seral stages resulting from timber harvests, wildfires, windstorms, insect infestations, and disease (Forsman et al. 2011). For more details on the environmental conditions of our study areas see Forsman et al. (2011).

We used a standardized survey protocol for locating and monitoring northern spotted owls each breeding season (March–August [Lint et al. 1999]). Methods included nighttime surveys of study areas extending 2.0–2.5 km out from historical activity centers (i.e., a nest tree, observations of fledged young, or a pair of resident owls [Forsman et al. 2011]), followed by daytime visits to relocate previously banded owls, band and determine the sex and age class of unmarked owls, and document owl reproduction. Detailed field protocols are provided in Franklin et al. (1996) and survey methods were consistent throughout the study period.

We defined a breeding dispersal event as any case in which a territorial owl moved to a different defended area between years, regardless of whether it actually bred or not (Forsman et al. 2002, Seamans and Gutiérrez 2007). We did not consider the use of alternate nests in the same territory as breeding dispersal (Forsman et al. 1984, 2002). At the end of each field season, we chose a single best location to represent the activity center for each territory based on nest status, presence of young, or phase of the breeding season for nonnesting owls (Forsman et al. 2011). An owl was assigned to a different territory if the best activity center for the year was clearly in a new territory based on local site knowledge of field biologists and territory occupancy histories of color-marked owls. We demarcated historical territories using Thiessen polygons generated from all annual activity center locations of northern spotted owls from 1990 to 2017. Polygons extended to a maximum of half of the median nearest-neighbor distance, or midway between the annual activity centers of owls occupying adjacent territories, whichever distance was shorter (Dugger et al. 2016). Because we generated these polygons using annual activity centers gathered across the study period, they did not fluctuate with annual variation of territory boundaries. Hereafter, we refer to the Thiessen polygons as territories for the purpose of discussion.

From annual survey data, we generated detection histories for all owls monitored between 1990 and 2017. Detection histories included time-varying individual covariates specific to each owl, including the owl's location (historical territory), age class (AGE), apparent experience at their current territory (number of years observed on the territory prior to a particular year; EXP), apparent pair status (PAIRSTAT), and apparent productivity (PROD; Table 1). We did not include observations of owls from outside study area boundaries. We classified owls into three non-juvenile age classes based on recovery of owls originally banded as juveniles, or by established differences in tail tip shape and color among first-year subadult, second-year subadult, and adult

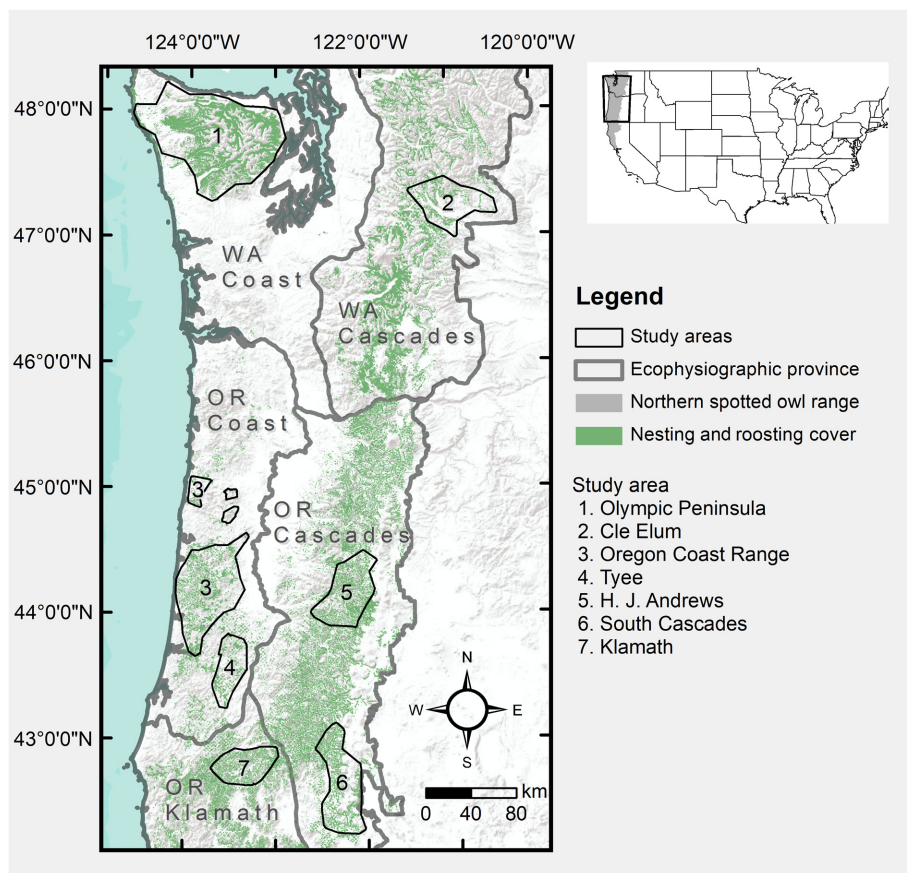


FIG. 1. Locations of the seven study areas within five ecophysiographic provinces within the northern spotted owl range in Oregon and Washington used to examine breeding dispersal trends, 1990–2017. Nesting and roosting cover map generated from Glenn et al. (2017).

owls (Forsman 1981, Forsman et al. 1984). Spotted owls are obligate natal dispersers and can establish a breeding territory and produce young as first-year subadults (Forsman et al. 2002). Thus, any first-year subadults found breeding were classified as natal dispersers rather than breeding dispersers and second-year subadults were only considered breeding dispersers if they had been observed as part of a territorial pair in the previous year. Hollenbeck et al. (2018) investigated natal dispersal from these data, so we focused only on breeding dispersal and omitted observations of first-year individuals from capture histories (508 records, 2.3%).

We calculated a naive estimate of the minimum proportion of monitored owls dispersing annually for comparisons with previous studies of spotted owl breeding dispersal. We estimated the proportion dispersing across the study period within each study area, province, and for the entire sample population by dividing the total number of color-marked owls for which we observed breeding dispersal by the total number of owls located in each interannual interval (Forsman et al. 2002, Blakesley et al. 2006). This naive dispersal rate does not

account for imperfect detection of individual owls so annual estimates are considered minimum estimates relative to the estimated probability of breeding dispersal we obtained via multistate models that accounted for resighting probabilities <1.0.

#### *Potential factors affecting breeding dispersal*

We generated year-specific environmental covariates applied at the territory scale to investigate how local conditions affected the decision to disperse or not. We used annual range-wide maps of northern spotted owl nesting and roosting forest cover types (Davis et al. 2011, 2016) to approximate these conditions within individual territories. For each survey year, we calculated the proportion of nesting and roosting forest type (NRFOREST) in each historical territory area (excluding any nonforest capable areas, such as open water). We used a 3-yr moving average to reduce variation due to location-specific inaccuracies of imputed forest condition from the selection of forest inventory and analysis plots used to generate cover type maps (10-yr rotation

TABLE 1. Variables considered for resighting probability ( $p$ ), apparent survival ( $\hat{S}$ ), and probability of breeding dispersal ( $\psi$ ) for territorial northern spotted owls during 1990–2017 in Oregon and Washington, USA.

| Variable                        | Description                                                                                                                          | Parameter |           |            |
|---------------------------------|--------------------------------------------------------------------------------------------------------------------------------------|-----------|-----------|------------|
|                                 |                                                                                                                                      | $p$       | $\hat{S}$ | $\psi$     |
| STATE <sub><i>j,t</i></sub>     | State F (fidelity: old site) or State D (dispersal: new site)                                                                        | *         | *         | *          |
| PROV <sub><i>j</i></sub>        | Ecophysiographic province                                                                                                            | *, †, ‡   | *, †, ‡   | *          |
| AREA <sub><i>j</i></sub>        | Study area                                                                                                                           | *, †, ‡   | *, †, ‡   | *          |
| SEX <sub><i>j</i></sub>         | Owl's sex                                                                                                                            | *, †, ‡   | *, †      | *, §, ¶, # |
| TIME                            | Year was tested as a linear trend, quadratic trend, or pseudo-threshold trend (ln [TIME])                                            | .         | *, †, ‡   | *          |
| Time                            | Annual variation                                                                                                                     | *, †, ‡   | *, †, ‡   | *          |
| PREVDET <sub><i>j,t</i></sub>   | Previous detection adjustment: 1 if seen last year, 0 if not seen last year                                                          | *         | .         | .          |
| EXP <sub><i>j,t</i></sub>       | Owl experience as the number of years owl has been observed occupying current territory: none, low (1–4 yr), or high ( $\geq 5$ yr)† | .         | .         | *, §       |
| AGE <sub><i>j</i></sub>         | Age class of owl: second-year sub-adult (SY) vs. adult (A)                                                                           | .         | .         | *, §       |
| PAIRSTAT <sub><i>j,t</i></sub>  | Apparent pair status: single/unknown, or paired‡                                                                                     | .         | .         | *, §       |
| PROD <sub><i>j,t</i></sub>      | Apparent productivity: fledged young or did not fledge young                                                                         | .         | .         | *, §       |
| EDGE <sub><i>i</i></sub>        | Territory on study area edge: within 1.5× the median nearest neighbor distance of study area boundary                                | *         | .         | *          |
| BO-T <sub><i>i,t</i></sub>      | Territory-specific barred owl index: barred owl observed in territory $i$ in or before year $t$ (binary)                             | *, ‡, #   | *, ‡,     | *          |
| BO-A <sub><i>s,t</i></sub>      | Percent of territories in study area $s$ with barred owl detections in or before year $t$ (temporal trend)                           | *, ‡, #   | *, ‡,     | *          |
| TQ <sub><i>i</i></sub>          | Territory quality based on historical productivity of territory                                                                      | .         | .         | *          |
| DISTURB <sub><i>i,t</i></sub>   | Proportion of territory $i$ disturbed in last 3 yr                                                                                   | .         | .         | *          |
| DISTURB_L <sub><i>i,t</i></sub> | Proportion of territory $i$ disturbed in last 3 yr with low severity disturbance                                                     | .         | .         | *          |
| DISTURB_H <sub><i>i,t</i></sub> | Proportion of territory $i$ disturbed in last 3 yr with medium-high severity disturbance                                             | .         | .         | *          |
| NRFOREST <sub><i>i,t</i></sub>  | Proportion of territory $i$ covered by nesting and roosting forest cover†† in year $t$                                               | .         | .         | *, ††      |

Notes: Variables were not included in all parameter model sets; included variables are designated with "\*" and omitted variables are designated with ".". For each variable we included sources for basis for inclusion if available. Unless otherwise specified, all variables were from originating territory (the observation prior to moving). Variables were calculated for each owl  $j$ , within historical territory  $i$ , study area  $s$ , and year  $t$ .

†Forsman et al. (2011).

‡Dugger et al. (2016).

§Forsman et al. (2002).

¶Blakesley et al. (2006).

#Olson et al. (2005).

||Anthony et al. (2006).

††Davis et al. (2011, 2016).

‡‡Tested and moved forward with one of three structures for territory experience based on stage 1 model rankings:  $n$  yr of territory tenure (EXP\_yrs; continuous variable), territory experience (EXP\_any; binary variable), and territory experience class (none, 1–4 yr [EXP\_low], or  $\geq 5$  yr [EXP\_high]).

§§Tested and moved forward with one of three structures for pair status based on stage 1 model rankings: a binary variable single/unknown vs. paired (PAIRSTAT), a categorical mate status covariate (MATESTAT; single/unknown, paired with a past mate, or paired with a new mate), and the number of years with the current mate if paired (PAIRSTAT:YCM).

among plots in annualized inventory) rather than true cover type change.

The impact of disturbance events on spotted owls can differ with the extent and/or the severity of disturbance (Comfort et al. 2016, Lesmeister et al. 2019). We used annual forest disturbance maps produced by the Laboratory for Applications of Remote Sensing in Ecology (LARSE) to produce annual estimates of forest disturbance occurring within each territory during the prior 3 yr (DISTURB; Table 1). Disturbance in our study areas was primarily associated with timber harvest and thinning operations, but also included wildfire and insect outbreaks. The annual disturbance maps were created using Landsat data and ensemble LandTrendr

methodology (Kennedy et al. 2010, 2018, Cohen et al. 2018). These maps capture the year, severity, duration (number of years), and extent of disturbance events at 30-m resolution. We used the relativized difference in the normalized burn ratio (RdNBR [Miller and Thode 2007]), which has been correlated with tree mortality (Reilly et al. 2017) as our index of disturbance severity. Following Reilly et al. (2017) we partitioned disturbance into two severity classifications based on estimated percent basal area removal: low (<25%) and moderate-to-high (>25%). We summarized the proportion of DISTURB in each territory as (1) "any severity" disturbance, (2) "low severity" disturbance, or (3) "moderate-to-high severity" disturbance, in the prior 3 yr. For

example, we calculated the 1990 DISTURB values using the sum of disturbance in 1988, 1989, and 1990. We used the proportion of territory rather than total area in our environmental metrics because the size of historical territories varied across the geographic range. To determine the degree to which forest conditions varied across space (i.e., territories as represented by the Thiessen polygons) vs. through time, we used generalized linear mixed models for our standardized environmental covariates, and estimated variation separately for each study area using territory and year as random effects (see Appendix S1).

We generated a territory specific index of territory quality (TQ) based on the productivity of territory  $i$  in province  $r$  across time (Blakesley et al. 2006):

$$TQ_i = \frac{\sum_t (NYF_{i,r,t} - \overline{NYF_{r,t}})}{n_i},$$

where NYF is the number of fledglings,  $t$  is the year with reproductive data available, and  $n$  is the number of years for which reproductive data were available. We calculated TQ for those historical territory areas for which we had at least 5 yr of productivity information available between 1985 and 2017. When territories did not have at least 5 yr of productivity information, the province mean was used (4% of observations). This variable does not account for temporal variation in habitat quality, but is a reasonable measure of the relative contribution of individual territories to population growth (Peery and Gutiérrez 2013) and was shown to be correlated with breeding dispersal in California spotted owls (Blakesley et al. 2006, Gutiérrez et al. 2011).

We detected over 22,500 incidental barred owl responses during annual spotted owl call-back surveys. Although a relatively coarse metric, these data can be a useful proxy representing annual changes in the presence of barred owls (Dugger et al. 2016, Yackulic et al. 2019). We generated two basic indices from the barred owl detection data. We defined barred owl presence within each historical territory core area each year as “present” if any barred owl was detected in territory  $i$  during or before year  $t$  (BO- $T_{i,t}$ ). For each study area and year, we also calculated the annual percentage of historical territory areas within study area  $s$  with  $\geq 1$  detection of barred owls during or before year  $t$  (BO- $A_{s,t}$ ). A subset of territories in the southern portion of the Olympic Peninsula study area were dropped from the demography study in 2006, thus for consistency, BO-A was generated across only the territories monitored throughout the study period. Both barred owl indices increased on all study areas over time (Fig. 2). In 2015, a barred owl removal experiment was initiated on the Cle Elum and Oregon Coast Range study areas, in which barred owls were removed from a subsection of sites (Wiens et al. 2020). We did not adjust our barred owl indices to account for removal activities.

### Multistate analysis of survival and breeding dispersal

We used a multistate mark–resight model (Hestbeck et al. 1991, Brownie et al. 1993, White et al. 2006) to estimate apparent survival ( $\hat{S}$ ), resighting rates ( $p$ ), and transition probabilities ( $\psi$ ; Fig. 3). For each interval between sampling occasions we defined two states that reflected whether an individual owl stayed on its previous nesting territory (site fidelity: state F) or moved to a different nesting territory (dispersed: state D). We assigned all initial observations of a territorial location to state F, which included both previously unmarked territorial owls and owls originally banded as juveniles in previous years. Although this decision affected the coding of the capture history, it did not alter the resulting parameter estimates (Schaub and Von Hirschheydt 2009). There were two potential transition probabilities representing breeding dispersal:  $\psi_{FD}$ , dispersal after being site faithful to a breeding site, and  $\psi_{DD}$ , dispersal after having dispersed the previous observation. Both site-fidelity transition probabilities are not estimated directly but can be derived via subtraction (e.g.,  $\psi_{FF} = 1 - \psi_{FD}$ ). Multistate mark–resight modeling permitted us to (1) use all available data (not just dispersal events of owls observed in successive years), (2) incorporate resighting probabilities, and (3) account for cases when owls dispersed more than once or when owls were not detected in every sampling occasion (year). Mortality and permanent emigration from monitored territories are confounded in multistate models and models assume that all annual mortality occurs prior to movement (White et al. 2006).

We used RMark (Laake 2013) in R v3.6.3 (R Development Core Team 2020) with program MARK (White and Burnham 1999) to generate model estimates and model selection results. We used program U-CARE to generate goodness-of-fit statistics for the general model including the grouping variables: province, sex, state, and time (Choquet et al. 2009). Goodness-of-fit tests suggested that our data violated the assumption of independence, which we associated with our study design and with the site-fidelity of northern spotted owls. We addressed this lack of independence conservatively by including both an individual covariate reflecting the previous detection history of individuals (PREVDET; seen in prior year or not) on  $p$  in all models and by including an overdispersion parameter ( $\hat{c} = 1.22$ ) which inflates standard errors (SE) and adjusts for overdispersed data. We used simulated annealing methods to check final models for optimal convergence.

Previous studies of apparent survival, resighting probabilities, and dispersal of spotted owls guided development of a priori variables to consider, especially for resighting and apparent survival parameters (Anthony et al. 2006, Forsman et al. 2011, Glenn et al. 2011, Dugger et al. 2016; Table 1). Because of the large number of parameters and covariates of interest, we used a multistage information-theoretic process to develop models from hypothesized covariates of interest for each

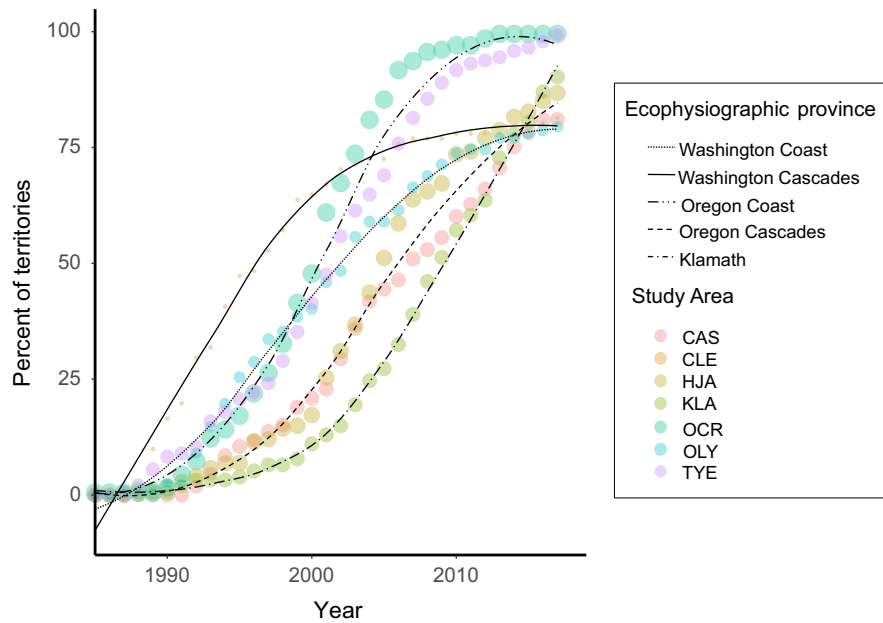


FIG. 2. Cumulative percentage of historical northern spotted owl territories with barred owl (barred owl index; BO-A) from 1990–2017 in seven study areas. Trend lines for ecophysiological provinces shown.

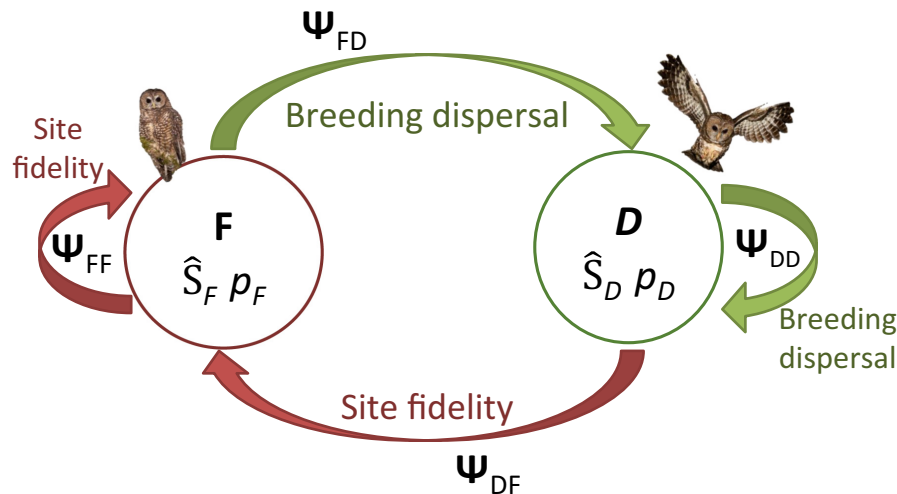


FIG. 3. Conceptual framework for our multistate mark–resight model of northern spotted owl apparent survival ( $\hat{S}$ ), resighting probability ( $p$ ), and transition probabilities ( $\psi$ ), between two potential states: a site faithful state (F) where owls remained on their previous territory and a breeding dispersal state (D), where owls moved from their most recent territory to another between observations.

parameter (Morin et al. 2020). For model selection, we used Akaike's information criterion adjusted for small sample size and overdispersion ( $QAIC_c$ ), differences between model  $QAIC_c$  and the model with the lowest  $QAIC_c$  ( $\Delta QAIC_c$ ), and Akaike weights (Burnham and Anderson 2002). We also used estimates of regression coefficients ( $\beta$ ) and their 95% confidence limits to provide additional strength of evidence for specific effects. Because our focus was modeling the dispersal

parameters ( $\psi_{DD}$ ,  $\psi_{FD}$ ), we limited our model sets for  $p$  and  $\hat{S}$  as much as possible based on findings from previous research (Table 1). Resighting probabilities were modeled first, then apparent survival, followed by dispersal probabilities. At each modeling stage we advanced all models within 5  $QAIC_c$  of the top model to ensure we did not omit relevant parameter combinations at later stages (Morin et al. 2020). We initially held a relatively general structure on  $\hat{S}$  (PROV + time) and  $\psi$

(STATE + SEX + PROV + time). At each stage, we crosschecked the best models against competitive models from a previous stage to ensure that we apportioned variation correctly among parameters and covariate effects.

For each parameter model set, we first ensured that each variable improved upon a base model for that parameter before combining any into additive models. The base  $p$  model included the intercept and the site fidelity adjustment (PREVDET). The base  $\hat{S}$  model was an intercept-only model, and the base  $\psi$  model included STATE only, permitting  $\psi_{FD}$  (nonsuccessive dispersal) to differ from  $\psi_{DD}$  (successive dispersal), an assumption that was supported in initial model tests. We also utilized the initial variable ranking to select among closely related covariates and covariate structures (where correlation or collinearity was likely) for consideration in additive models. We then generated and tested additive models in a stepwise fashion, where any variable from a previous stage that received all model weight was included as the base for subsequent steps. We did not allow any covariate combinations with a Spearman rank correlation  $|r| > 0.6$  and did not allow more than one temporal trend variable (e.g., time, TIME, BO-A) in any model. We also did not consider more than one territory-specific environmental covariate in any one model.

## RESULTS

Our study included resighting histories for 4,118 (2,146 M, 1,972 F) northern spotted owls on 1,135 historical territories in Oregon and Washington during 28 breeding seasons (Table 2). The average number of observations per owl was similar among regions (Table 2). The number of owls monitored decreased annually after 2005 because of population declines (Appendix S1: Supplemental Figures). Apparent survival rates varied annually, differed by study area, and were negatively associated with the territory-specific barred owl index (Appendix S1: Supplemental Results).

Twenty percent ( $n = 851$ ) of owls were observed only once. Of the 3,267 owls that we observed in at least 2 yr, 33% (582 M, 496 F) were observed to switch breeding

territories at least once between 1990 and 2017 (Table 2). Across all individuals, the naive (uncorrected for imperfect detection) annual breeding dispersal rate increased from a low of ~7% in 1990 to almost 25% of all monitored owls in 2017 (Fig. 4a). Of the 1,078 owls where breeding dispersal was observed at least once, 61% dispersed once (661 owls), 23% dispersed twice (248 owls), 9% dispersed three times (99 owls), and 6% dispersed 4–8 times (4 times: 40 owls, 5 times: 18 owls, 6 times: 10 owls, 8 times: 2 owls) during the 28-yr study period. The rates of naive dispersal increased over time and varied between provinces and study areas (Fig. 4). We observed the lowest increase in naive breeding dispersal events in Washington and the greatest in the Oregon Coast Range, where 48.3% of monitored owls dispersed between 2016 and 2017, which was approximately four times greater than the rate at the beginning of the study (Fig. 4).

We observed 408 successive dispersals ( $\psi_{DD}$ ) and 1,372 nonsuccessive dispersals ( $\psi_{FD}$ ). Pair status was the most supported factor affecting dispersal likelihood in initial models considering univariate covariate effects only (Table 3). Our top additive model garnered 100% of the total model weight and indicated that breeding dispersal probabilities ( $\psi_{DD}$  and  $\psi_{FD}$ ) differed depending on whether an individual had dispersed in the previous year ( $\psi_{DD}$ ;  $\beta = 1.04$ , 95% confidence interval [CI]: 0.86, 1.21), and varied additively by PAIRSTAT, AREA, PROD, EXP, BO-A, and TQ (Table 4). The probability of dispersing increased over time regardless of starting state when other covariates were held at study area annual means (Fig. 5). We observed the highest rates of dispersal in the Tyee study area within the Oregon Coast Range province and the lowest rates in the Olympic Peninsula study area in Washington (Table 5, Fig. 5, 6a).

Years spent on territory (EXP = 0, 1–4, or 5+) had more support for an effect on dispersal rates than AGE (Table 3). The likelihood of dispersal decreased as experience on a territory increased; birds with no experience were more likely to disperse than birds with 1–4 yr of experience ( $\beta = -0.35$ , 95% CI:  $-0.48$ ,  $-0.22$ ) and birds with >5 yr experience ( $\beta = -0.61$ , 95% CI:  $-0.77$ ,  $-0.45$ ; Fig. 6b). Thirty percent of observed nonsuccessive

TABLE 2. The number of monitored northern spotted owls, annual owl observations (Obs), and dispersal events (D) included from each ecophysiological province between 1990 and 2017 in Oregon and Washington, USA.

| Province            | Birds (males) | Observations | $D$ | Dispersals per bird† |      |     |     | Observations per bird‡ |      |     |     |
|---------------------|---------------|--------------|-----|----------------------|------|-----|-----|------------------------|------|-----|-----|
|                     |               |              |     | Mean                 | SD   | Min | Max | Mean                   | SD   | Min | Max |
| Klamath             | 689 (369)     | 3,675        | 279 | 0.40                 | 0.87 | 0   | 8   | 5.33                   | 3.84 | 1   | 19  |
| Oregon Cascades     | 1,342 (686)   | 6,803        | 464 | 0.35                 | 0.78 | 0   | 8   | 5.07                   | 3.91 | 1   | 20  |
| Oregon Coast Range  | 1,187 (623)   | 6,894        | 855 | 0.72                 | 1.16 | 0   | 6   | 5.81                   | 4.33 | 1   | 19  |
| Washington Cascades | 270 (144)     | 1,283        | 82  | 0.30                 | 0.67 | 0   | 4   | 4.75                   | 3.62 | 1   | 15  |
| Washington Coast    | 630 (324)     | 2,520        | 100 | 0.16                 | 0.46 | 0   | 4   | 4.00                   | 3.41 | 1   | 18  |

†Mean, standard deviation, and minimum and maximum number of dispersals per owl.

‡Mean, standard deviation, and minimum and maximum number of annual observations per individual owls.

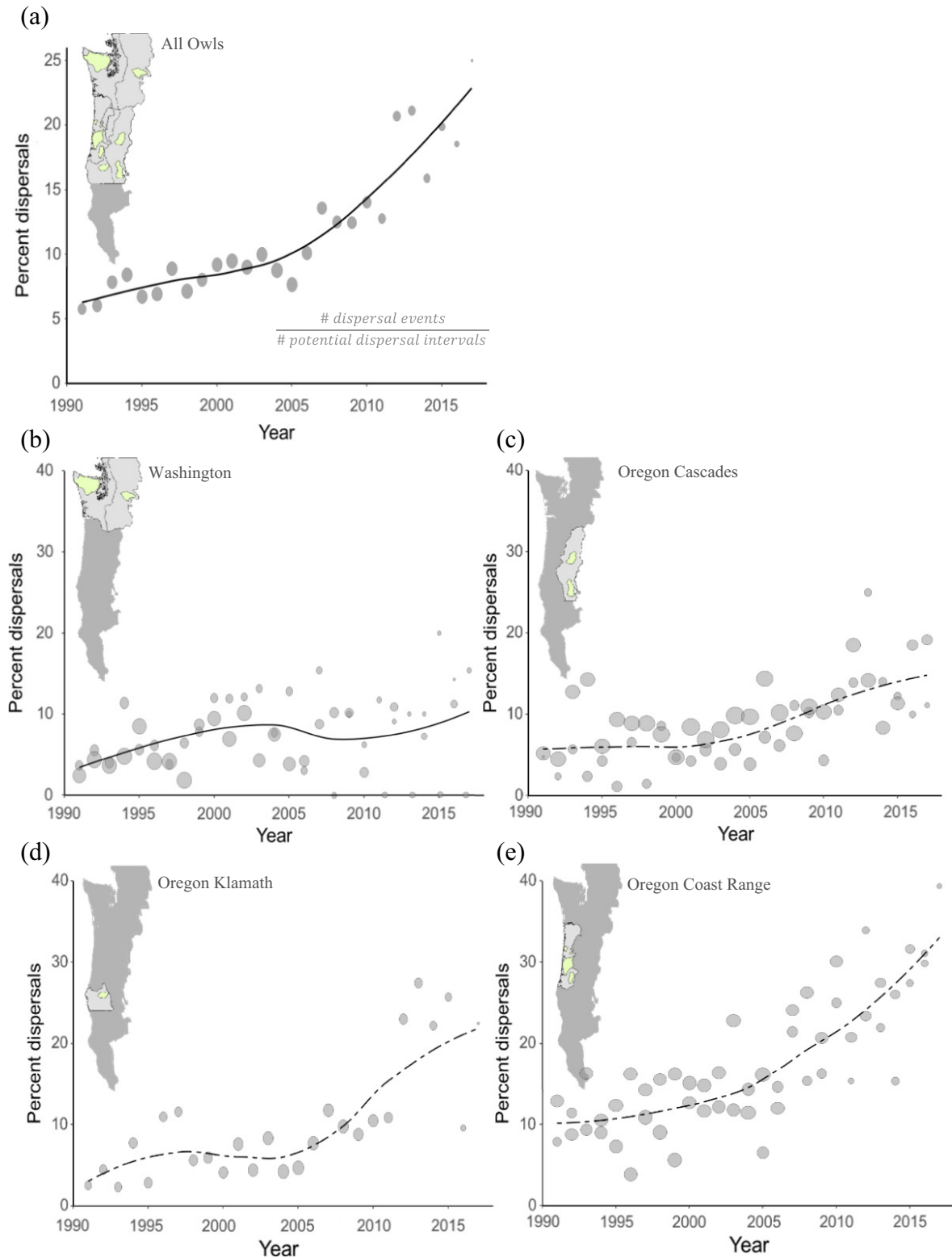


FIG. 4. The naive annual estimates of northern spotted owl breeding dispersal during 1990–2017 increased across our monitored population (a), within Washington ecophysiographic provinces (b), and within each Oregon ecophysiographic province (c)–(e). Point size increases with annual sample sizes across all sites in (a) ( $n = 216\text{--}857$  owls) and by study area in (b)–(e) ( $n = 7\text{--}210$  owls observed annually).

TABLE 3. Initial model ranking of dispersal transition probability ( $\psi$ ) models for breeding-age northern spotted owls during 1990–2017 in Oregon and Washington, USA.

| $\psi$                           | npar <sup>†</sup> | $\Delta\text{QAIC}_c^{\ddagger}$ | $w_i^{\S}$ | QDev <sup>¶</sup> |
|----------------------------------|-------------------|----------------------------------|------------|-------------------|
| STATE + PAIRSTAT*,#              | 73                | 0.00                             | 1.00       | 36,040.40         |
| STATE + PROD*                    | 73                | 490.35                           | 0.00       | 36,530.74         |
| STATE + BO-A*                    | 73                | 638.61                           | 0.00       | 36,679.00         |
| STATE + BO-T                     | 73                | 651.43                           | 0.00       | 36,691.83         |
| STATE + PAIRSTAT:YCM#            | 73                | 655.02                           | 0.00       | 36,695.41         |
| STATE + TIME + TIME <sup>2</sup> | 74                | 693.76                           | 0.00       | 36,732.14         |
| STATE + TIME                     | 73                | 697.13                           | 0.00       | 36,737.53         |
| STATE + time                     | 98                | 713.20                           | 0.00       | 36,703.19         |
| STATE + AREA*                    | 78                | 717.40                           | 0.00       | 36,747.72         |
| STATE + PROV                     | 76                | 726.28                           | 0.00       | 36,760.63         |
| STATE + ln(TIME)                 | 73                | 730.27                           | 0.00       | 36,770.67         |
| STATE + EXP_low + EXP_high*,     | 74                | 767.96                           | 0.00       | 36,806.34         |
| STATE + TQ*                      | 73                | 769.69                           | 0.00       | 36,810.09         |
| STATE + EXP_yrsl                 | 73                | 776.82                           | 0.00       | 36,817.21         |
| STATE + EXP_anyll                | 73                | 777.11                           | 0.00       | 36,817.50         |
| STATE + MATESTAT#                | 74                | 799.66                           | 0.00       | 36,838.04         |
| STATE + NRFOREST*                | 73                | 814.48                           | 0.00       | 36,854.87         |
| STATE + DISTURB_H*               | 73                | 829.66                           | 0.00       | 36,870.06         |
| STATE + DISTURB                  | 73                | 835.09                           | 0.00       | 36,875.48         |
| STATE + AGE                      | 73                | 835.54                           | 0.00       | 36,875.93         |
| STATE + SEX*                     | 73                | 837.49                           | 0.00       | 36,877.88         |
| STATE + EDGE*                    | 73                | 837.50                           | 0.00       | 36,877.90         |
| STATE (base model)               | 72                | 838.88                           | 0.00       | 36,881.29         |
| STATE + DISTURB_L                | 73                | 840.43                           | 0.00       | 36,880.82         |

Notes: We only moved forward with one structure for related variables; variables with asterisks “\*” were considered in additive models. All models included the best resighting probability structure [ $p$  (PREVDET + AREA + time + EDGE + SEX)] and apparent survival structure [ $S$ (AREA + time + BO-T)] from initial modeling stages.

<sup>†</sup>Number of variables in model.

<sup>‡</sup>Change in Akaike’s information criteria adjusted for small sample size and overdispersion compared to the  $\text{QAIC}_c$  of top model, which was 36,275.12.

<sup>§</sup>Model weight.

<sup>¶</sup>Deviance.

#Tested and moved forward with one of three structures for pair status based on stage 1 model rankings: a binary variable single/unknown vs. paired (PAIRSTAT), a categorical mate status covariate (MATESTAT; single/unknown, paired with a past mate, or paired with a new mate), and the number of years with the current mate if paired (PAIRSTAT:YCM).

||Tested and moved forward with one of three structures for territory experience based on stage 1 model rankings:  $n$  yr of territory tenure (EXP\_yrs; continuous variable), territory experience (EXP\_any; binary variable), and territory experience class (none, 1–4 yr [EXP\_low], or  $\geq 5$  yr [EXP\_high]).

dispersers had no experience on their prior territory, 48% had low experience (1–4 yr), and 22% had spent  $\geq 5$  yr on their previous territory (compared to 15%, 53%, and 32%, respectively for observations of successive dispersing birds).

Single birds were more likely to disperse than owls who had a mate ( $\beta = -1.67$ , 95% CI:  $-1.79$ ,  $-1.55$ ; Fig. 6c). Birds who successfully produced young were also less likely to undertake dispersal compared to non-reproductive birds ( $\beta = -0.60$ , 95% CI:  $-0.76$ ,  $-0.44$ ; Fig. 6c). Prior to moving, 77% of observed dispersers were paired (38% new mate, 39% with a repeat mate), compared to 93% of apparently site-faithful owls. Forty percent of site-faithful birds that produced at least one offspring remained on their territory compared to only 18.7% for birds that dispersed. The proportion of owls apparently gaining or maintaining a mate after a

transition was generally higher for site-faithful individuals, compared to dispersers, but that proportion decreased for all transition groups over time, suggesting a decline in overall mate availability in the last 28 yr (Appendix S1: Fig. S3a). Seventy-five percent of all dispersers had equal or improved productivity after dispersing and the annual proportions of site faithful or dispersing birds that were observed to be productive following a transition were similar and relatively stable over the course of the study period (Appendix S1: Fig. S3b). Nineteen percent of unsuccessful and 12% of successful dispersers that were unproductive in the year prior to dispersal were observed productive in the observation following dispersal.

The study area specific barred owl variable (BO-A), performed better than any other temporal structure (e.g., time, TIME, TIME + TIME<sup>2</sup>, ln(TIME); Table 3).

TABLE 4. Top 10 ranked multistate models of dispersal transition probability ( $\psi$ ) for breeding-age northern spotted owls during 1990–2017 in Oregon and Washington, USA.

| Rank | $\psi$                                                  | npar <sup>†</sup> | $\Delta\text{QAICc}$ <sup>‡</sup> | w <sub>§</sub> | QDev <sup>¶</sup> |
|------|---------------------------------------------------------|-------------------|-----------------------------------|----------------|-------------------|
| 1    | STATE + PAIRSTAT + AREA + PROD + BO-A + EXP + TQ        | 84                | 0.00                              | 1.00           | 35,569.09         |
| 2    | STATE + PAIRSTAT + AREA + PROD + BO-A + EXP + EDGE      | 84                | 20.25                             | 0.00           | 35,589.33         |
| 3    | STATE + PAIRSTAT + AREA + PROD + BO-A + EXP             | 83                | 27.34                             | 0.00           | 35,598.44         |
| 4    | STATE + PAIRSTAT + AREA + PROD + BO-A + EXP + DISTURB_H | 84                | 27.58                             | 0.00           | 35,596.67         |
| 5    | STATE + PAIRSTAT + AREA + PROD + BO-A + TQ              | 82                | 43.29                             | 0.00           | 35,616.41         |
| 6    | STATE + PAIRSTAT + AREA + PROD + BO-A + EDGE            | 82                | 67.20                             | 0.00           | 35,640.31         |
| 7    | STATE + PAIRSTAT + AREA + PROD + BO-A + DISTURB_H       | 82                | 73.40                             | 0.00           | 35,646.52         |
| 8    | STATE + PAIRSTAT + AREA + PROD + BO-A                   | 81                | 73.66                             | 0.00           | 35,648.79         |
| 9    | STATE + PAIRSTAT + AREA + BO-A + TQ                     | 81                | 90.28                             | 0.00           | 35,665.42         |
| 10   | STATE + PAIRSTAT + AREA + BO-A + EXP                    | 82                | 91.24                             | 0.00           | 35,664.35         |
| 71   | STATE (base model)                                      | 72                | 1,288.02                          | 0.00           | 36,881.29         |

Notes: We included the base  $\psi$  model (STATE:  $\psi_{DD} \neq \psi_{FD}$ ) for comparison. See Table 1 for parameter definitions. All models included the best resighting probability structure [ $p$  (PREVDET + AREA + time + EDGE + SEX)] and apparent survival structure [ $S$ (AREA + time + BO-T)] from initial modeling stages.

<sup>†</sup>Number of variables in model.

<sup>‡</sup>Change in Akaike's information criteria adjusted for small sample size and overdispersion compared to the QAIC<sub>c</sub> of top model, which was 35,737.77.

<sup>§</sup>Model weight.

<sup>¶</sup>Deviance.

As the annual percentage of territories with barred owl detections increased, so did breeding dispersal rates (Fig. 6d,  $\beta = 0.99$ , 95% CI: 0.81, 1.18). Proportions of spotted owls observed transitioning into territories unoccupied by barred owls decreased over time for both site-faithful and dispersing owls (Appendix S1: Fig. S4). Dispersing birds were rarely able to reduce their contact with barred owls; of owls leaving territories occupied by barred owls (BO-T: 953 owls), 27% moved onto territories where barred owls had not yet been detected.

Territory quality performed better than the environmental extrinsic variables (NRFOREST and DISTURB) in initial univariate model rankings and additive models (Tables 3 and 4). Territory quality was negatively related to dispersal probability ( $\beta = -0.87$ , 95% CI:  $-1.15$ ,  $-0.58$ ), so birds were less likely to leave territories that had historically been productive (Fig. 6e). Only 42% of birds that were observed dispersing (571 of nonsuccessive dispersers and 171 of successive dispersers) moved to a territory with a higher territory quality value than their originating territory. Fifty-three percent of dispersing birds (724 nonsuccessive and 216 successive) increased the percent of NRFOREST in their territory post dispersal by  $12.5 \pm 10.3\%$  for nonsuccessive and  $11.5 \pm 9.4\%$  for successive dispersers (mean  $\pm$  SD). In site-faithful territories, NRFOREST increased slightly in 70% of cases (via forest succession) by an average of  $0.4 \pm 0.6\%$  ( $\pm$ SD). Similarly, 54% of dispersers (740 nonsuccessive and 220 successive) moved to a territory with less recent disturbance, reducing their territory disturbance  $3.3 \pm 5.1\%$  on average (maximum of 69% disturbance reduction). Generally, the proportion of owls transitioning to a territory with an improved environmental metric (e.g., higher TQ, higher NRFOREST, lower DISTURB) fluctuated from year to year but

remained relatively stable over time (see Appendix S1: Fig. S4).

## DISCUSSION

Widespread changes in landscape structure, disturbance regimes, and climate are considered primary factors causing wildlife population declines (e.g., Rosenberg et al. 2019). Such changes are also closely tied to the colonization of native communities by invasive species (Hobbs and Huenneke 1992, Hellmann et al. 2008, Rodewald and Arcese 2016), which can produce widespread cascading effects in ecosystems (Dukes and Mooney 2004, Walsh et al. 2016). In the Pacific Northwest, population declines and range contractions for several wildlife species have been attributed to loss of old growth forests (Yezerinac and Moola 2006, Forsman et al. 2016, Betts et al. 2018, 2019) and these same communities are increasingly experiencing altered competitive environments due to invasive species. The dynamics governing territory fidelity in northern spotted owls changed during our long-term study, as shown by the increased annual rate of breeding dispersal over a 27-yr period. The increase in dispersal was substantial; historically ~7% of individual owls on an annual basis moved to a new territory (Forsman et al. 2002), but that rate increased to ~25% in the last years of our study. Breeding dispersal affects individual fitness by influencing survival, mating success, and, ultimately, reproductive success (Forero et al. 1999, Bowler and Benton 2005, Terraube et al. 2015), so increasing rates of dispersal could exacerbate existing population declines, particularly in a k-selected species with historically high site fidelity. The increasing rate of northern spotted owl breeding dispersal coincided with the range-wide

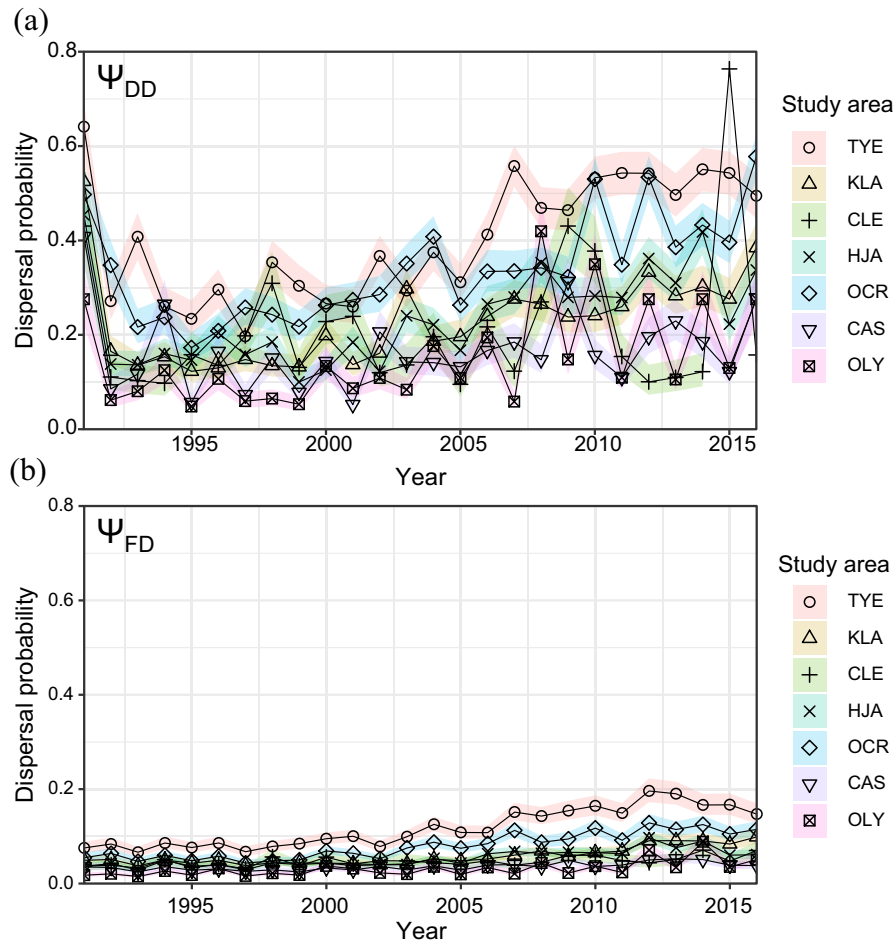


FIG. 5. Estimated (a) successive ( $\Psi_{DD}$ ) and (b) nonsuccessful ( $\Psi_{FD}$ ) annual breeding dispersal transition probabilities with 95% confidence bands for northern spotted owls observed within 7 study areas from 1991 to 2016. Estimates were generated using the top model in Table 4 holding other variables at their study area annual mean values. Study area abbreviations: CAS, South Cascades; CLE, Cle Elum; HJA, H. J. Andrews; KLA, Klamath; OCR, Oregon Coast Range; OLY, Olympic Peninsula; TYE, Tyee.

invasion by the competitively dominant barred owl, a generalist apex predator at high densities that has the potential to trigger trophic cascades in the Pacific Northwest (Holm et al. 2016). Our findings provide new insight as how invasive species may interact with population dynamics of impacted native wildlife via altered dispersal patterns.

Over the last 30 yr, the rapid expansion of barred owls into the Pacific Northwest has greatly altered the competitive landscape, as this generalist predator displaces and excludes spotted owls from their preferred historical territories. There is limited evidence beyond anecdotal observations of barred owls directly killing spotted owls (e.g., Leskiw and Gutiérrez [1998]). Barred owls not only limit the amount and distribution of available resources for spotted owls within shared foraging areas, but also exclude spotted owls from historical nesting areas via interspecific territoriality (Wiens et al. 2014). Our study indicated that this combination of exploitation and

interference competition from barred owls also results in increased breeding dispersal of spotted owls, as shown by an increasing annual probability of breeding dispersal in regions with an increasing occurrence of barred owls. Previous work has documented a negative effect of barred owl presence on spotted owl territory occupancy and detection probability (Olson et al. 2005, Pearson and Livezey 2007, Yackulic et al. 2019, Duchac et al. 2020), which could represent increased mortality or emigration. Additionally, Yackulic et al. (2014) found evidence that spotted owls were less likely to colonize areas already occupied by barred owls, supporting the hypothesis that barred owls reduce territory availability and/or quality for dispersing spotted owls. Increased occupancy of study areas by barred owls was associated with greater breeding dispersal distances for spotted owls in our study areas, suggesting that it has become more difficult for spotted owls to locate favorable habitat conditions (Jenkins et al. 2019a). In addition to direct displacement

TABLE 5. Estimates of model coefficients ( $\beta$ ), standard errors (SE), and upper and lower 95% confidence limits (UCL, LCL) from the breeding dispersal transition model with the strongest support [ $\psi$  (STATE + PAIRSTAT + AREA + PROD + BO-A + EXP + TQ)].

|                                                                  | $\beta$ | SE   | LCL   | UCL   |
|------------------------------------------------------------------|---------|------|-------|-------|
| Intercept ( $\psi_{FD}$ , single owl, Area: Cascades, EXP: none) | -1.41   | 0.11 | -1.62 | -1.20 |
| State transition: $\psi_{DD}$                                    | 1.04    | 0.09 | 0.86  | 1.21  |
| Area: Cle Elum                                                   | 0.09    | 0.15 | -0.20 | 0.38  |
| Area: H. J. Andrews                                              | 0.19    | 0.11 | -0.02 | 0.40  |
| Area: Klamath                                                    | 0.47    | 0.11 | 0.26  | 0.69  |
| Area: Oregon Coast Range                                         | 0.36    | 0.10 | 0.16  | 0.57  |
| Area: Olympic Peninsula                                          | -0.60   | 0.13 | -0.86 | -0.33 |
| Area: Tyee                                                       | 0.95    | 0.11 | 0.74  | 1.16  |
| PAIRSTAT                                                         | -1.67   | 0.06 | -1.79 | -1.55 |
| PROD                                                             | -0.60   | 0.08 | -0.76 | -0.44 |
| BO-A                                                             | 0.99    | 0.10 | 0.81  | 1.18  |
| EXP: 1-4 yr                                                      | -0.35   | 0.07 | -0.48 | -0.22 |
| EXP: $\geq 5$ yr                                                 | -0.61   | 0.08 | -0.77 | -0.45 |
| TQ                                                               | -0.87   | 0.15 | -1.15 | -0.58 |

Notes: Results were of an analysis of breeding-age northern spotted owls during 1990–2017 in Oregon and Washington, USA. See Table 1 for parameter definitions.

of territorial spotted owls, barred owls may also affect breeding dispersal by negatively influencing the reproductive rates or courtship activities of spotted owls (Wiens et al. 2014), thereby providing an indirect trigger to dispersal via reduced productivity.

Individual decisions regarding breeding dispersal are highly dynamic and regulated by a series of trade-offs between possible costs and benefits of dispersal. By studying a large, marked population of individuals and analyzing dispersal within a mark–recapture context, we were able to distinguish among a multitude of intrinsic and extrinsic factors known to influence individual dispersal decisions, not only in spotted owls, but territorial species in general. A frequent finding from mammal and avian species, for example, is that individuals tend to change territories or alter home ranges following an unsuccessful reproductive attempt, mate loss, or after occupying a poor-quality territory (e.g., Wauters et al. [1995], Forero et al. [1999], Jerina et al. [2014], Terraube et al. [2015]). Intrinsic factors, including loss of mate, prior reproductive success, and experience at a site, were the largest contributing factors to northern spotted owl breeding dispersal across the 27 yr, consistent with Forsman et al. (2002). We also found that rates of dispersal were lower for individuals that held historically productive territories. These territories were presumably more stable and contained high-quality environmental conditions, likely resulting in benefits to fitness. However, less than half of our dispersing owls moved to territories with higher territory quality index values. In separate studies of California spotted owl breeding dispersal, Blakesley et al. (2006) and Gutiérrez et al. (2011) found that owls

occupying higher-quality territories—also measured via historical productivity rather than forest cover—were less likely to disperse and in most cases breeding dispersal resulted in improved territory quality. These findings suggest that territory quality (as determined by reproductive history) is a strong driver in decisions to either remain site faithful or disperse to a new territory, but that owls are not guaranteed to find improved conditions on new sites, particularly in recent years, as barred owls spread and continue to increase in density across the northern spotted owl range.

The degree of breeding philopatry is generally highest for territorial species that occupy stable environments with predictable fitness requirements (Greenwood and Harvey 1982, Switzer 1993, Bowler and Benton 2005). Other birds of prey (e.g., snowy owl *Nyctea scandiaca*, rough-legged hawk *Buteo lagopus*) live somewhat nomadic lifestyles because they feed on cyclic prey populations, and thus have high breeding dispersal rates resulting from movements to sites where prey abundance is higher. For nomadic species, large-scale dispersal events are presumably advantageous for individual fitness via emigration following a depletion of prey abundance (Greenwood and Harvey 1982). For these species, high dispersal rates are typically characteristic of adults and juveniles of both sexes. Spotted owls, on the other hand, are philopatric, having evolved with relatively stable prey populations and environmental conditions. Historically, the mature coniferous forest environments inhabited by spotted owls in Oregon and Washington experienced low to moderate frequencies of disturbances, and where disturbances were more common, severity of disturbance was low (Kennedy and Spies 2004, Spies et al. 2018). However, with anthropogenic forest disturbance and the expansion of barred owls throughout the spotted owl's geographic range, the quality of forests for nesting and roosting has become more variable over space and time (Kennedy and Spies 2004, Wilson and Forsman 2013). Intensive timber harvests, which sparked initial conservation efforts for the northern spotted owl in the early 1990s, significantly slowed on federal lands after the Northwest Forest Plan's enactment in 1994 (Lesmeister et al. 2018, Spies et al. 2018). Since that time, forest alteration within the region has tended to vary more spatially, rather than temporally (unlike barred owls), with a few regional exceptions in the last decade caused by wildfire or disease/insect outbreaks (Spies et al. 2018; Appendix S1: Supplemental Results). Our study areas were almost entirely within federally managed late-successional reserves, and consequently, our study did not fully capture the severity or extent of forest disturbances that occurred throughout the spotted owl's range, particularly the levels of forest harvest on state-owned and private lands. As such, our study was not able to quantify the effect of disturbance or proportion of nesting and roosting forest on dispersal probabilities fully. Although nesting and roosting forest cover or amount of disturbance were not within the

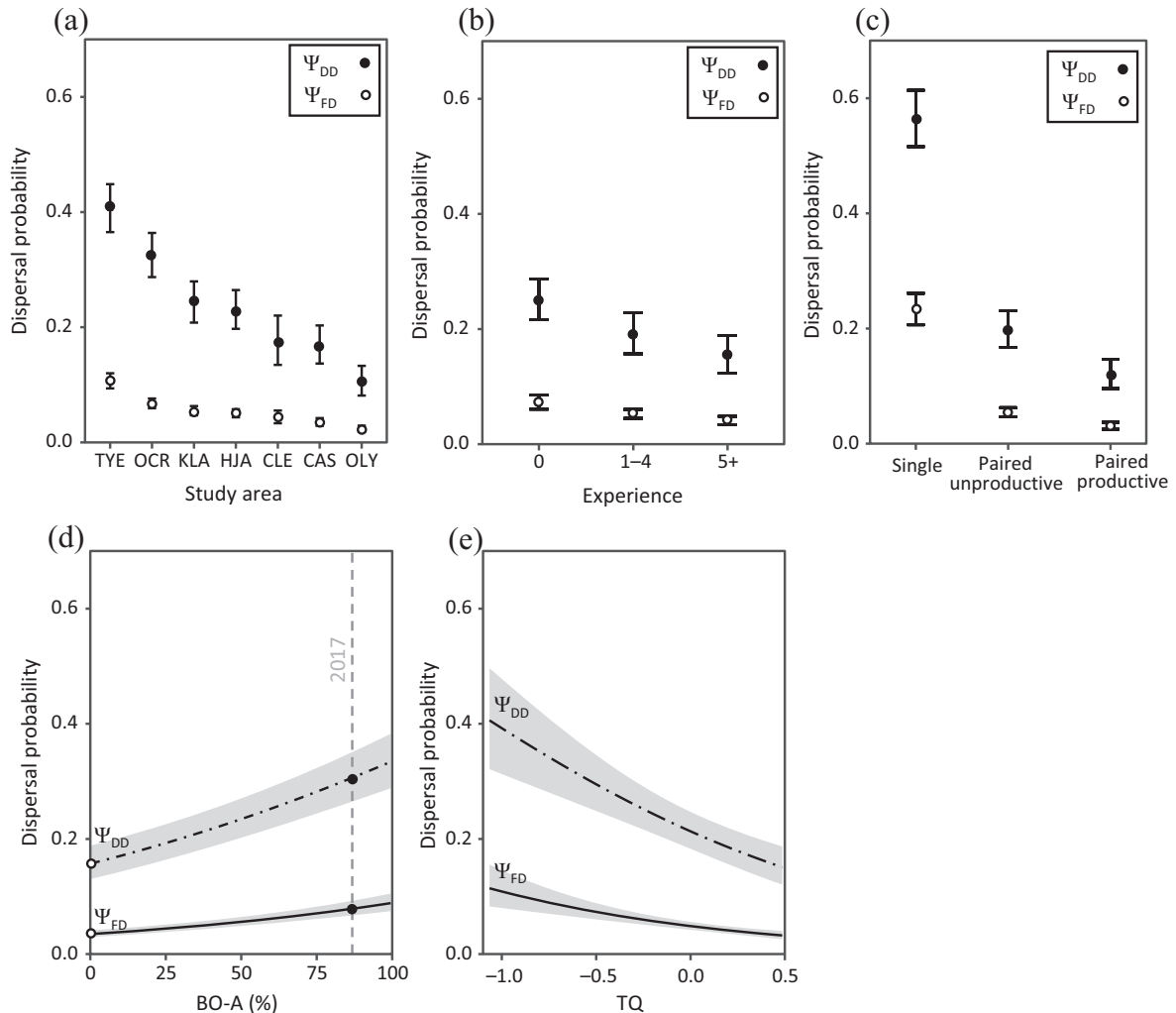


FIG. 6. The probability of successive ( $\Psi_{DD}$ ) and nonsuccessive ( $\Psi_{FD}$ ) breeding dispersal transitions for northern spotted owls (during 1990–2017) varied with (a) study area, (b) amount of territory experience, (c) pair and productivity of individuals, (d) the proportion of territories with barred owl detections, and (e) the territory quality index. Estimates were generated using the top ranked model in Table 4 while holding all other variables at study area means; (b)–(e) were generated using study area means for H. J. Andrews. The open and solid points in (d) represent the value of BO-A at H. J. Andrews in 1990 and 2017, respectively. Study area abbreviations: CAS, South Cascades; CLE, Cle Elum; HJA, H. J. Andrews; KLA, Klamath; OCR, Oregon Coast Range; OLY, Olympic Peninsula; TYE, Tyee.

most-supported dispersal model, extreme disturbance events of clear-cut timber harvesting and high-severity wildfire significantly degrade forest (Lesmeister et al. 2018, 2019) and negatively affect spotted owl populations (Jones et al. 2016, 2020, Rockweit et al. 2017). Additionally, fitness costs associated with dispersal also typically increase with increasing habitat fragmentation (Travis and Dytham 1999).

The increased rate of breeding dispersal was likely due in part to reduced mate availability from declining spotted owl populations (Dugger et al. 2016). We found that the loss of a mate was a stronger catalyst to breeding dispersal than not fledging young. The ability to produce young is dependent upon access to a quality mate and

spotted owls generally do not breed every year (Anthony et al. 2006), making a single unproductive year less likely to induce movement compared to the lack of a mate. We also observed that spotted owls with more experience at a site were less likely to make a breeding dispersal movement compared to individuals with less time invested on a territory (these were also younger individuals, on average). For territorial animals, more experienced individuals are typically able to displace conspecific competitors and hold territories with a positive effect on fitness (Murray 1967, Payne and Payne 1993, Daniels and Walters 2000). Dispersal rates often vary between the sexes in philopatric birds, typically with females more likely to disperse than males (Greenwood and Harvey 1982). We

did not find strong support for an effect of sex on dispersal rates, although Jenkins et al. (2019a) reported that females had slightly longer breeding dispersal distances compared to males. Forsman et al. (2002) did not include site-faithful individuals in their analyses, but they reported higher rates of dispersal by females in the same study areas. The apparent shift to roughly equal breeding dispersal rates among males and females may be further indication that significant perturbations have occurred in the ecosystem to alter spotted owl dispersal patterns from their evolved dynamics.

Unbiased estimates of animal survival rely on low rates of permanent emigration from surveyed areas (Zimmerman et al. 2007). We found a negative association of barred owls at the territory level with northern spotted owl apparent survival, a finding also supported in previous demographic analyses (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016). Prior to our study, it was unclear whether this negative association reflected increased spotted owl mortality through competition with barred owls (e.g., decreased food resources, or increased predation risk) or an increase in the displacement of spotted owls by barred owls and subsequent emigration from study areas. If spotted owl breeding dispersal rates are increasing, emigration rates are also likely increasing and there could be an observed decrease in apparent survival estimates in long-term demography analyses attributable to emigration rather than true mortality (Dugger et al. 2016). However, estimates of site occupancy, tied to historic spotted owl territories, not individual birds, have also exhibited strong declining trends over time (e.g., Yackulic et al. [2019]), supporting steep declines of northern spotted owl populations. Additionally, if increased dispersal rates are leading to increased movement through young industrial forests or other low-quality roosting cover, higher rates of mortality associated with dispersal are possible. Ongoing efforts to monitor individual owls to estimate apparent survival and rates of population change may need to consider conducting mark-recapture studies on larger study areas in order to encompass increased movements and movement distances (Jenkins et al. 2019a), and thereby decrease potential bias (Zimmerman et al. 2007).

Our findings highlight that the underlying factors influencing breeding dispersal rates are complex and multidimensional. Although our study is observational, our results support the hypothesis that barred owls have displaced spotted owls from their preferred territories, resulting in increased rates of breeding dispersal. The emergent factors causing increased rates of dispersal in northern spotted owls (e.g., barred owls) are likely to have compounding effects on individual fitness as well as negative impacts on population dynamics and play a role in the continued population decline of northern spotted owls. Approximately half of dispersing birds in our study were able to increase the amount of nesting and roosting cover or decrease the amount of recent disturbance on

their new territories; however, less than a third were able to move to territories with no barred owls. Historically, we believe the primary reason spotted owls dispersed was to improve fitness, but now, spotted owls likely also disperse to avoid competition with barred owls. Unlike our study, dispersal studies of California spotted owls (Gutiérrez et al. 2011) and Mexican spotted owls (Ganey et al. 2014) in areas without barred owls found that dispersing owls were generally able to increase territory quality or social and reproductive status. Thus, the presence of barred owls may have degraded habitat quality at a landscape level, driving northern spotted owls to disperse but not allowing them to improve fitness in doing so. Barred owl management that includes removals to reduce competitive pressures on spotted owls may improve territory stability and reduce northern spotted owl breeding dispersal (Wiens et al. 2020). Implementation of the Northwest Forest Plan also remains necessary to promote forest conditions to support population recovery on federally managed lands (Lesmeister et al. 2018). Conservation approaches that address these broad environmental stressors (e.g., habitat fragmentation, reduction and encroachment, resource competition) may prove successful in improving the long-term prognosis for spotted owl persistence.

#### ACKNOWLEDGMENTS

The USDA, U.S. Department of Interior BLM, and the National Park Service provided primary funding for this project. This study would not have been possible without the tireless dedication of many field biologists who collected the data over the 28 yr. We would also like to thank Raymond Davis, U.S. Forest Service spotted owl monitoring lead and Zhiqiang Yang for help with environmental covariates. The findings and conclusions in this publication should not be construed to represent any official USDA determination or policy. This publication has been peer reviewed and approved for publication consistent with U.S. Geological Survey Fundamental Science Practices (<http://pubs.usgs.gov/circ/1367/>). Oregon State University's Institutional Animal Care and Use Committee approved all data collection protocols. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Author contributions: DBL, EDF, KMD, and JDW conceived the research, design, sourced funding, and substantially edited the manuscript. MJM developed and performed the analysis and wrote the manuscript. DBL, EDF, KMD, SHA, LSA, CEM, MSP, JAR, SGS, BH, and SAG conducted the research and reviewed the manuscript.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2398/full>

## OPEN RESEARCH

Data (Jenkins et al. 2021) are available from Dryad: <https://doi.org/10.5061/dryad.0k6djhb0c>