



RESEARCH ARTICLE

Social status, forest disturbance, and Barred Owls shape long-term trends in breeding dispersal distance of Northern Spotted Owls

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ABSTRACT

Dispersal among breeding sites in territorial animals (i.e. breeding dispersal) is driven by numerous selection pressures, including competition and spatiotemporal variation in habitat quality. The scale and trend of dispersal movements over time may signal changing conditions within the population or on the landscape. We examined 2,158 breeding dispersal events from 694 male and 608 female individually marked Northern Spotted Owls (*Strix occidentalis caurina*) monitored over 28 yr on 7 study areas to assess the relative importance of individual (sex, experience), reproductive (annual productivity, mate availability), and environmental (forest alteration, presence of competitor) sources of variation in breeding dispersal distance. Median breeding dispersal distance was 3.17 km, with 99% of all breeding dispersal events <37 km. Mean annual dispersal distances increased by 2.43 km in Oregon and 9.40 km in Washington between 1990 and 2017, which coincided with increases in annual detections of nonnative Barred Owl (*S. varia*). Frequency of breeding dispersal events, both among and within individuals, also increased over time. Female owls moved farther than males (median of 3.26 and 3.10 km, respectively), and birds with less experience (territory tenure) moved farther than those with more experience. Owls that were single in the year prior to dispersal moved 13–31% farther than those paired prior to dispersal. The greatest environmental change occurring over the course of our study was the expansion of Barred Owl populations. Breeding dispersal distance was positively related to Barred Owls in the study area and disturbance within the originating territory. While it appears that social factors continue to be important drivers of breeding dispersal distance in Spotted Owls, increased competition from Barred Owls and habitat alteration have a contributing effect. Increased breeding dispersal distances should be of concern for conservation efforts and considered in population monitoring because changing dispersal behavior may lead to higher rates of mortality and/or emigration from historical study areas.

Keywords: Barred Owl, breeding dispersal, forest disturbance, Northern Spotted Owl, *Strix occidentalis caurina*, *Strix varia*

El estatus social, los disturbios del bosque y la presencia de *Strix varia* determinan las tendencias de largo plazo de la distancia de dispersión reproductiva de *Strix occidentalis caurina*

RESUMEN

La dispersión entre los sitios reproductivos en los animales territoriales (i.e. dispersión reproductiva) está determinada por numerosas presiones de selección, incluyendo competencia y variación espacio-temporal en la calidad del hábitat. La escala y la tendencia de los movimientos de dispersión a lo largo del tiempo pueden indicar las condiciones cambiantes al interior de la población o en el paisaje. Examinamos 2,158 eventos de dispersión reproductiva provenientes de 694 machos y 608 hembras de *Strix occidentalis caurina* marcados individualmente, monitoreados a lo largo de 28 años en siete áreas de estudio, para evaluar la importancia relativa de las fuentes de variación individual (sexo, experiencia), reproductiva (productividad anual, disponibilidad de pareja) y ambiental (disturbio del bosque, presencia de competidores) en la distancia de dispersión reproductiva. La distancia media de dispersión reproductiva fue 3.17 km, con el 99% de todos los eventos de dispersión reproductiva menores a 37 km. Las distancias de dispersión media anual aumentaron 2.43 km en Oregon y 9.40 km en Washington entre 1990 y 2017, lo que coincidió con aumentos en las

detecciones anuales de la especie no nativa *S. varia*. La frecuencia de los eventos de dispersión reproductiva, tanto entre individuos como para un mismo individuo, también aumentaron a lo largo del tiempo. Las hembras de los búhos se movieron más que los machos (mediana de 3.26 y 3.10 km, respectivamente), y las aves con menos experiencia (tenencia territorial) se movieron más lejos que aquellas con más experiencia. Los búhos solteros durante el año anterior a la dispersión se movieron 13–31% más lejos que aquellos en pareja antes de la dispersión. El cambio ambiental más grande ocurrido a lo largo del tiempo de nuestro estudio fue la expansión de las poblaciones de *S. varia*. La distancia de dispersión reproductiva estuvo positivamente relacionada con *S. varia* en el área de estudio y los disturbios dentro del territorio de origen. Si bien parece que los factores sociales continúan siendo condicionantes importantes de la distancia de dispersión reproductiva en *Strix occidentalis caurina*, el aumento de la competencia por parte de *S. varia* y la alteración del hábitat tienen un efecto adicional. El aumento de las distancias de dispersión reproductiva debería ser motivo de preocupación para los esfuerzos de conservación y considerados en el monitoreo poblacional debido a que los cambios de comportamiento en la dispersión pueden llevar a mayores tasas de mortalidad y/o de emigración de las áreas de estudio históricas.

Palabras clave: dispersión reproductiva, disturbio del bosque, *Strix occidentalis caurina*, *Strix varia*

INTRODUCTION

Dispersal in territorial animals is driven by numerous selection pressures including inbreeding avoidance, competition, and spatiotemporal variation in habitat quality (Bowler and Benton 2005, Roze and Rousset 2005). There are 2 general categories of dispersal movements recognized in birds: natal dispersal, which is the movement between territories prior to the first breeding attempt, and breeding dispersal, defined as the movement of individuals between successive breeding places (Greenwood and Harvey 1982, Morrison and Wood 2009). Breeding dispersal is likely adaptive because switching breeding territories may increase access to mates or to higher-quality habitats with fewer threats or competitors. Alternatively, dispersers may also incur costs from movement to unfamiliar breeding territories, such as increased predation, resource limitation, or intra- or inter-specific aggression (Daniels and Walters 2000, Morrison and Wood 2009). Often, one sex disperses farther than the other; in mammals, male-biased dispersal is common, whereas in birds, female-biased dispersal is the norm (Greenwood 1980). Moreover, breeding dispersal movements may be short, perhaps representing a shift to an adjacent territory, or relatively far, potentially signifying emigration to another metapopulation. As a consequence, breeding dispersal involves a series of strategic decisions concerning whether or not to move, and if so, how far.

Breeding dispersal distances tend to be lower for abundant species with generalist habits, and greater for species that specialize on patchily distributed habitats (Paradis et al. 1998, Martin and Fahrig 2018). Dispersal movements may also be longer from poor-quality territories since those territories are often spatially larger (Bowman 2003). The magnitude and trend in breeding dispersal movements over time may signal population or environmental alterations. Changes within a territory such as a disturbance event (e.g., fire), the introduction of a predator (Bried and Jouventin 2007, Forero et al. 2008), or an increase in

intra- or inter-specific competition may increase dispersal distances by decreasing the realized quality of a territory in terms of resource abundance, availability, and distribution (Kim et al. 2009). The abundance, availability, and distribution of resources and competitors across the landscape likely also influence the amount of time and distance required to locate a suitable territory.

The Northern Spotted Owl (*Strix occidentalis caurina*; hereafter Spotted Owl) is a long-lived territorial species with strong site and mate fidelity in both sexes (Forsman et al. 1984). Spotted Owls specialize on areas with mature coniferous forest and require old forest for nesting and roosting (Forsman et al. 2015, Davis et al. 2016, Sovern et al. 2019). The subspecies was listed as threatened under the Endangered Species Act in 1990 because of extensive loss of these forest conditions to timber harvest (USFWS 1990). Despite extensive efforts to protect old forest on federal lands under the Northwest Forest Plan (USDA and USDI 1994), Spotted Owl populations continue to decline. These declines have been linked with interspecific competition and territorial displacement by a novel invader, the Barred Owl (*S. varia*) (Dugger et al. 2016, Lesmeister et al. 2018). Forsman et al. (2002) reported a mean breeding dispersal rate of ~7% annually by color-marked Spotted Owls monitored in Oregon and Washington, USA, during 1985–1996. Investigations prior to the widespread Barred Owl expansion found that breeding dispersal in the Northern Spotted Owl and California Spotted Owl (*S. o. occidentalis*) was primarily affected by an individual's age, sex, social status (e.g., non-return of mate), and amount of habitat disturbance or alteration within their territory (Forsman et al. 2002, Blakesley et al. 2006, Gutiérrez et al. 2011).

An increased understanding of what environmental and social factors affect breeding dispersal distance in declining populations, and how these factors may change over time, can help inform conservation planning. Our primary objective was to document trends in Spotted Owl breeding dispersal distance, particularly in relation to forest disturbance and the range expansion of Barred Owls. We expected

dispersal distance to increase with increasing forest disturbance or the increasing occurrence of Barred Owls on historical territories of Spotted Owls. We also examined the effects of sex, prior reproductive status (productivity and pair status), and territory quality (historical productivity) on Spotted Owl breeding dispersal distances. We predicted that dispersal distance would be longer for females compared to males (Clarke et al. 1997, Forsman et al. 2002, Blakesley et al. 2006, Ganey et al. 2014), inexperienced (e.g., younger) compared to more experienced birds (Forsman et al. 2002, Kim et al. 2007), single compared to paired owls (Forsman et al. 2002, Andreu and Barba 2006), birds paired with a new mate compared to those paired with a previous mate (Forsman et al. 2002, Kim et al. 2007), and unproductive owls compared to owls that successfully fledged young prior to dispersal, or were on historically productive territories (Forsman et al. 2002, Calabuig et al. 2008, Jiménez-Franco et al. 2013).

METHODS

Spotted Owl Monitoring

We analyzed all documented breeding dispersal events of marked adult Spotted Owls from 7 study areas within 5 ecophysiological provinces in Oregon and Washington during 1990 to 2017 (Figure 1). Study areas were the Olympic Peninsula (OLY; 2,541 km²) and Cle Elum (CLE; 980 km²) areas in Washington and the Oregon Coast Range (OCR; 1,810 km²), Tyee (TYE; 810 km²), H.J. Andrews (HJA; 1,004 km²), South Cascades (CAS; 2,372 km²), and Klamath (KLA; 1,074 km²) areas in Oregon (Figure 1). Study areas and ecophysiological provinces varied in climate, vegetation, and amount of topographic relief, but all areas were dominated by conifers or mixed conifer–hardwood forests. For more details on the environmental conditions of our study areas see Forsman et al. (2011) and Dugger et al. (2016).

We studied breeding dispersal as part of a long-term monitoring program for Spotted Owls that used a standardized survey protocol for locating and monitoring individually color-marked owls (Lint et al. 1999). Surveys were conducted during the breeding season (March through August) using night call-back methods to elicit territorial responses followed by daytime visits to locate owls, resight previously banded owls, band and determine the sex and age class of unmarked owls, and document owl social status and productivity. Specific protocols have been extensively described in prior publications (e.g., Lint et al. 1999, Dugger et al. 2016) and were consistent throughout the study period with the exception of the OLY study area where monitoring was discontinued on a portion of southern historical territories in 2006 because of budgetary limitations. We generated Thiessen polygons to represent historically

occupied owl territories and to calculate territory-specific metrics (Dugger et al. 2016). Polygons were created using annual activity center locations (e.g., a used nest tree) of owls during 1990–2017. Because these polygons were generated using activity centers gathered across the study period, they are representative of historical Spotted Owl annual activity centers and do not capture annual variation in territory boundaries. Thiessen polygons extended from activity center locations 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).

We defined a breeding dispersal event as the movement of a territorial owl between years to a different territory where it had the opportunity to breed, regardless of whether it actually bred previously, which included both paired or single residents (Daniels and Walters 2000, Forsman et al. 2002, Seamans and Gutierrez 2007). Spotted Owls often use different nest sites within a territory (Forsman et al. 1984), so we excluded cases where movements involved use of alternate nests in the same historical territory in different years. Movements by sub-adults (age 1–2) were only included if birds were observed as territorial with a mate prior to moving (i.e. the natal dispersal had been confirmed).

For each time interval between annual observations we recorded whether or not an individual owl dispersed to a new territory and the linear distance between activity centers. We compiled a database of breeding dispersal movements that included characteristics of the owl and territory before and after the movement. For this analysis, we only looked at dispersal events, including movements that occurred to areas outside study area boundaries. We did this to reduce potential bias toward shorter dispersal distances that can occur when study area boundaries are finite (Koenig et al. 1996). However, because our annual search effort was primarily focused within study area bounds, the frequency of long-distance breeding dispersal events are still likely underrepresented.

We considered age class and number of years at a territory prior to dispersal as measures of experience. We characterized owls into 3 age classes based on known age at banding and plumage differences between birds at year 1 (S1; rectrices with white, slightly pointed tips), year 2 (S2; rectrices with white, slightly rounded tips), and >2 years (adult; rectrices with white and brown blotches, rounded tips) (Forsman et al. 1984). We generated 3 measures of experience at a territory (i.e. territory tenure pre-dispersal): (1) number of years spent on the territory prior to moving; (2) a binary variable describing if a bird was new to a territory ($n = 0$ yr) or had previously occupied the territory ($n \geq 1$ yr); and (3) a categorical variable assigned as no prior experience ($n = 0$ yr), low experience ($0 \text{ yr} < n < 3 \text{ yr}$), or high

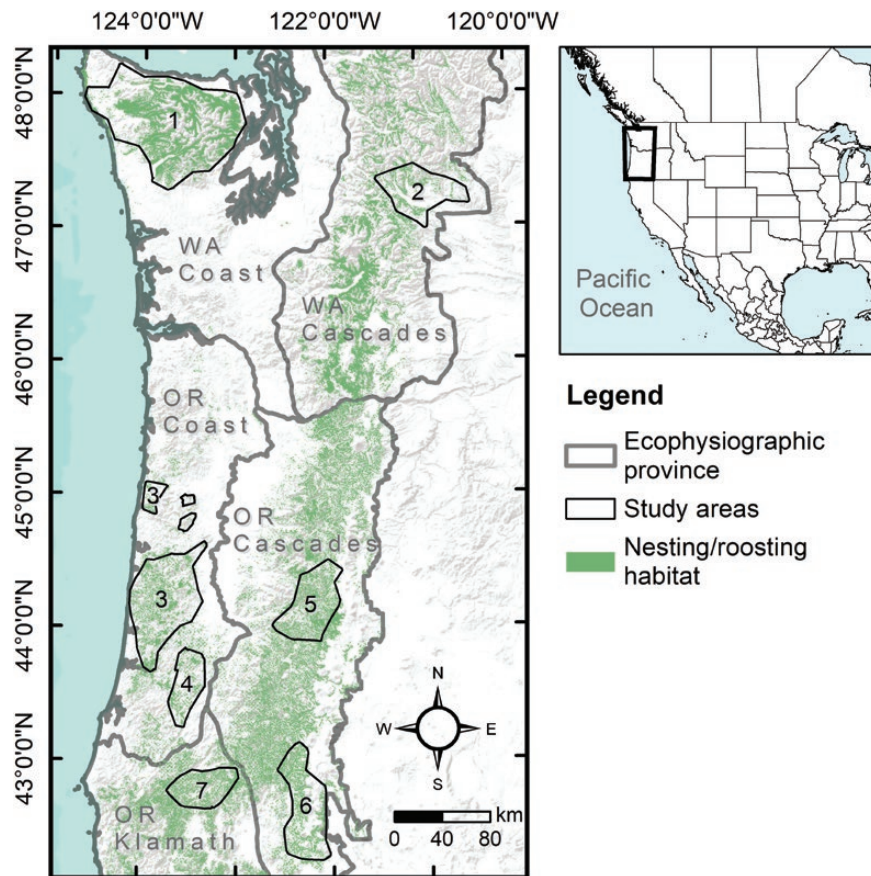


FIGURE 1. Locations of the 7 study areas (Olympic Peninsula [1], Cle Elum [2], Oregon Coast Range [3], Tyee [4], H.J. Andrews [5], South Cascades [6], and Klamath [7]) in 5 ecophysiographic provinces of Oregon and Washington used to examine trends in breeding dispersal distance in Northern Spotted Owls, 1990–2017. Also shown is the landscape distribution of suitable nesting and roosting habitat for Northern Spotted Owls as of 2012, based on a habitat suitability map developed by Glenn et al. (2017).

experience ($n \geq 3$ yr). The categorization between “low” and “high” territory experience was arbitrarily made based on category sample sizes. Because S1 and S2 birds could only have 0–1 yr of experience at a prior territory, all “experience” variables were somewhat confounded with age, thus we tested age and experience separately in models. We also generated and considered 3 potential measures of owl reproductive status prior to and after movement based on capture histories of color-marked individuals. These measures were also interrelated and considered separately in models. We recorded pair status as single, paired, or unknown, and mate status as single, paired with a new or unknown mate, paired with a mate from a previous year, or unknown. Productivity was categorized as no young fledged, successfully fledged ≥ 1 young, or unknown. We tested for differences in proportions of male vs. female dispersers, and in rates of productivity and pair status before and after dispersal with simple chi-square tests and report P values.

To address our hypothesis that dispersal distance would be shorter when individuals occupied historically

productive territories, we generated an index of territory quality (TQ) based on the number of young produced from territory i within ecophysiographic province p during the study period (Blakesley et al. 2006):

$$TQ_i = \frac{\sum_j (NYF_{ipj} - \overline{NYF_{pj}})}{n_i}$$

where NYF is the number of young fledged, j is the year with reproductive data available for each p , and n is the number of years for which reproductive data were available for a territory i . We only calculated TQ for territories for which we had at least 5 yr of productivity information available and acknowledge that this variable does not account for temporal variation in habitat quality.

Forest Disturbance

Old forest is a primary component of Spotted Owl habitat, which is susceptible to loss from timber harvest, wildfires, windstorms, insect infestations, and disease (Davis et al. 2016, Lesmeister et al. 2018). The impact of these

disturbance events on Spotted Owls can vary with the extent and severity of the disturbance (Comfort et al. 2016, Lesmeister et al. 2018, 2019). Following Reilly et al. (2017) we partitioned disturbances into 3 severity classifications based on estimated percent basal area removal: low (<25% removal), moderate (25–75% removal), and high (>75% removal). We predicted that low-severity disturbance (e.g., primarily timber stand thinning and insect-related loss) would have less effect on dispersal distance compared to moderate- or high-severity disturbance (e.g., clear-cut harvest, stand-replacing wildfire). Low-severity wildfires have little effect on nesting habitats of Spotted Owls, which may be more resistant to high-severity wildfire compared to younger or less-structurally complex forests (Lesmeister et al. 2019). While we acknowledge that wildfire and timber harvest are not equivalent disturbances, we combined them for our disturbance metrics because of the scarcity of fire in our dataset (Appendix Figure 6). We used Google Earth Engine (Gorelick et al. 2017) and annual Landsat disturbance data in *LandTrendr* (Kennedy et al. 2010, Cohen et al. 2017) to estimate 3 annual measures of forest disturbance for each territory (i.e. Thiessen polygon) within the prior 3 yr: (1) proportion of territory with “any severity” disturbance, (2) proportion of territory with “low severity” disturbance, and (3) proportion of territory with “moderate-to-high severity” disturbance (e.g., 1990 habitat alteration proportion was generated using the sum of disturbance in 1988, 1989, and 1990).

Occurrence of Barred Owls

Although Barred Owls were not specifically surveyed, we documented over 22,500 incidental detections of Barred Owls during surveys of Spotted Owls, and detections of Barred Owls were an effective proxy for increases in the presence of Barred Owls in each study area (Dugger et al. 2016, Yackulic et al. 2019). For each year and study area, we calculated the annual percentage of historical Spotted Owl territories (Thiessen polygons) with ≥ 1 detection of Barred Owls at any year previous to, and including, the current monitoring year (BO; Figure 2). A subset of territories in the OLY study area were dropped from the demography study in 2006. Thus, for consistency, the Barred Owl covariate was generated across only the OLY territories monitored throughout the study.

Dispersal Distance Modeling

We used generalized linear mixed models within an information-theoretic framework to evaluate relationships between breeding dispersal distance and individual and environmental sources of variation (Table 1; Burnham and Anderson 2002, Bolker et al. 2009). We did not include movements from non-dispersers in analyses. Prior to generating models with additive covariate effects, we

ranked and selected the best performing a priori univariate model structure (linear, quadratic, pseudo-threshold vs. categorical) for related groups of covariates, using Akaike's information criterion (AIC; Table 1). Our final additive model set was generated as combinations of covariates from univariate models with $\Delta\text{AIC} \leq 2$ in each covariate group. Only univariate models that scored above the null model were considered in additive models. Covariates with a Spearman's rank correlation coefficient >0.6 were not included in the same model. We observed no linear trend in disturbance variables over time within our sampled territories (Spearman's rank correlation coefficients with year $<|0.01|$) but the Barred Owl covariate was considered a temporal covariate (Spearman's rank correlation with year = 0.86) because the proportions of territories with detections increased over time in all study areas (Figure 2).

We fit all models using the *lme4* package in program R using a gamma distribution with a log link (Bates et al. 2015, R Core Team 2018). We included random effects of ecophysiographic province and year on the intercept in all models, including the “intercept-only” model with no fixed effects. The random effect of ecophysiographic province was included to account for regional variation in landscape and sample sizes. Year was included as a random effect to account for temporal process variance not associated with Barred Owl occurrence. Our dataset contained multiple dispersals from some individuals; however, models failed to converge when we included a random effect of individual. When we used only the data for individuals with more than one movement, the interclass correlation coefficient for distance was 0.27 (95% CI: 0.22–0.34), indicating low measurement repeatability (Wolak et al. 2012), so we retained all movements in our analyses. We considered effects in top-ranked models to be strongly supported if the 95% confidence interval (CI) for the parameter coefficient did not include zero. We report means $\pm$ standard error unless otherwise noted. Model assumptions were verified by plotting residuals vs. fitted values. To assess model fit, we report Nakagawa's R^2 for mixed effect models for the top model (Johnson 2014, Nakagawa et al. 2017).

RESULTS

We documented 2,158 breeding dispersal events during 1990–2017 from 1,302 owls (694 male, 608 female) with median breeding dispersal distance of 3.17 km. Ninety-nine percent of all documented breeding dispersal movements were ≤ 37 km (range: 0.04–94.55 km; Figure 3A). Sample sizes were uneven between provinces and birds in Oregon accounted for 90% of all dispersal events (Appendix Table 4). Washington birds moved farther on average than Oregon birds; mean annual dispersal distances in Washington increased by 9.40 km between

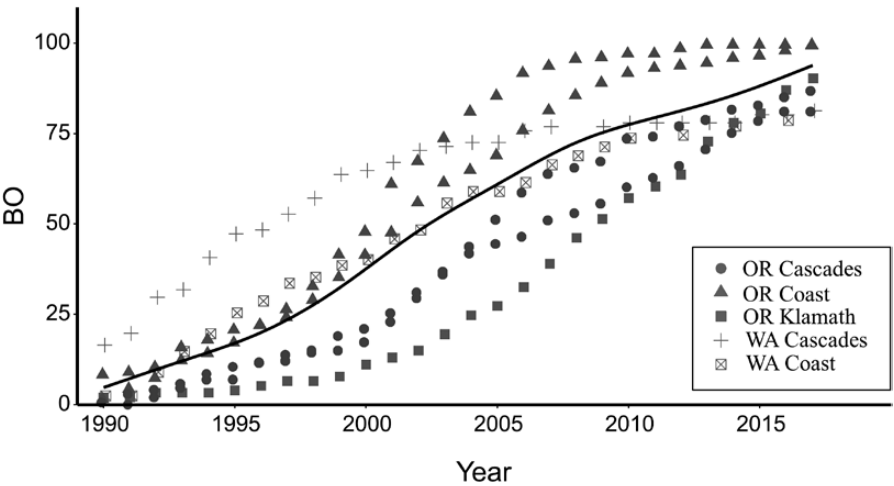


FIGURE 2. Annual trend in the percentage of cumulative Northern Spotted Owl territories with ≥ 1 Barred Owl (BO) detection for different ecophysiological provinces in Oregon and Washington, USA. Spearman’s rank correlation of 0.86 between year and BO (all areas combined). The solid line indicates the smoothed annual mean across provinces.

TABLE 1. Descriptions of variables and model structures considered in analyses of breeding dispersal distance for Northern Spotted Owls in Oregon and Washington, USA, 1990–2017.

Group	Variable	Structures tested against null model ^a	Used in additive model set
Sex Experience	SEX, female or male	Categorical	SEX EAS (3 groups)
	EAS, experience at territory in observation prior to dispersal (years)	Linear Quadratic Pseudo-threshold ^b Categorical 2 groups Categorical 3 groups	
Reproductive status	AGE, age class in observation prior to dispersal (S1, S2, Adult)	Categorical 2 groups Categorical 3 groups	MS
	PS, pair status in observation prior to dispersal (single, paired, unknown)	Categorical 2 groups Categorical 3 groups	
	MS, mate status in observation prior to dispersal (single, paired with new mate, paired with old mate, unknown)	Categorical 4 groups	
Barred Owl	P, productivity in observation prior to dispersal	Categorical 3 groups	BO
	BO, annual proportion of study area territories with Barred Owl detections	Linear Pseudo-threshold	
Territory quality Habitat	TQ, index of territory quality of prior location (–1 to 1)	Linear	Not used Ln(D)
	D, proportion of prior territory with any severity forest disturbance in prior 3 years	Linear Quadratic Pseudo-threshold	
	D_MH, proportion of prior territory with moderate-to-high severity forest disturbance in prior 3 years	Linear Quadratic Pseudo-threshold	
	D_L, proportion of prior territory with low severity forest disturbance in prior 3 years	Linear Quadratic Pseudo-threshold	

^a See Appendix Table 5 for model-selection results of initial tests of variable structures and related groups of variables.
^b Pseudo-threshold structure was approximated using $\ln(x)$.

1990 and 2017 (Figure 3B); while in Oregon, mean annual dispersal distances increased by 2.43 km between 1990 and 2017 (Figure 3C). Sixty-one percent of owls in our dataset ($n = 793$) moved once. However, the proportion of repeat dispersers each year (>1 previous dispersals on record) increased over time (Figure 4), with 23% of birds ($n = 300$) moving 2 times, 10% ($n = 131$) moving 3 times, 3% ($n = 40$) moving 4 times, and 3% moving 5–8 times (23 moved 5 times, 10 moved 6 times, 3 moved 7 times, 2 moved 8 times).

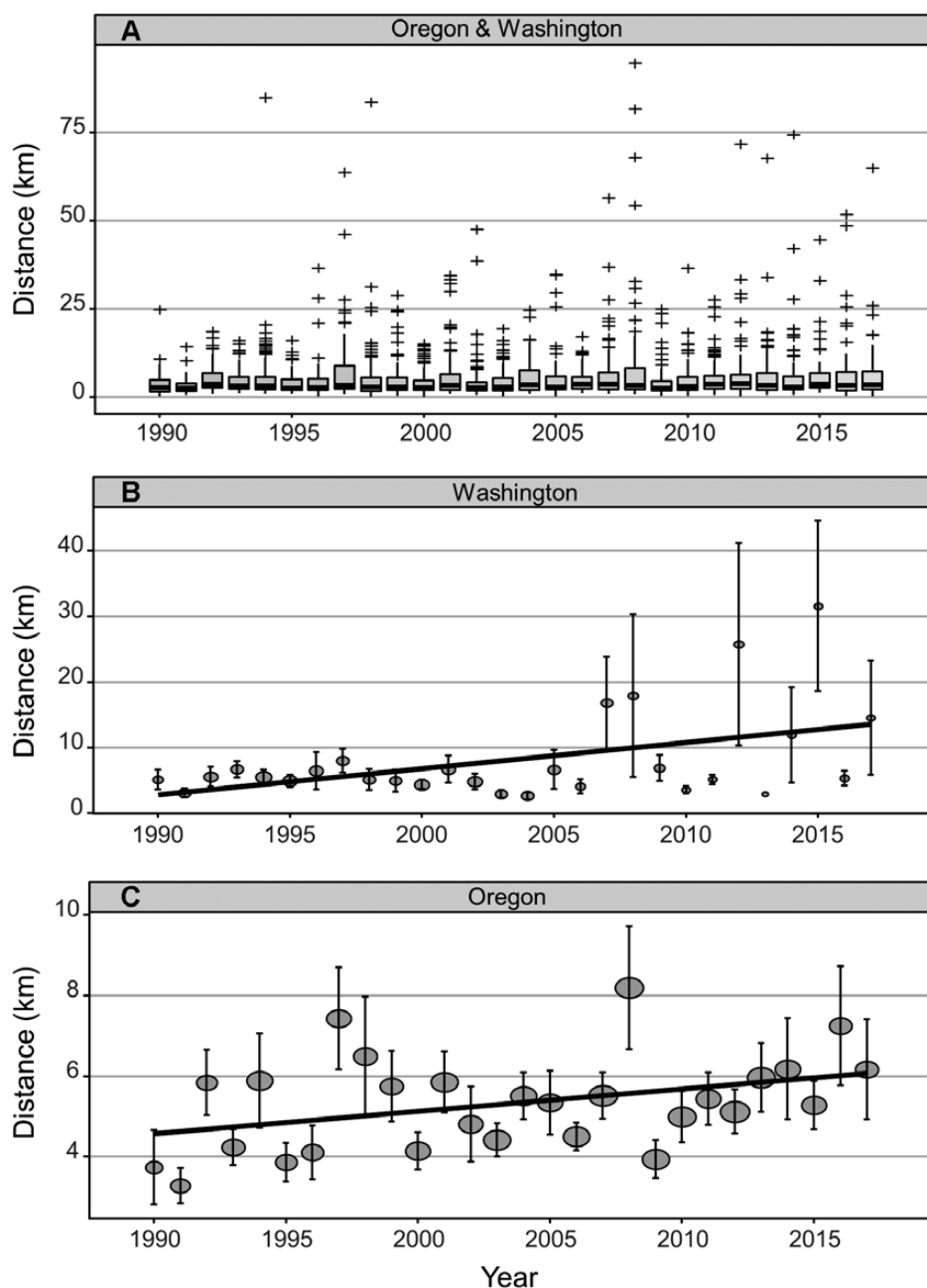


FIGURE 3. Boxplot and mean annual trend in observed breeding dispersal events in Northern Spotted Owls in Oregon and Washington from 1990 to 2017. The majority of breeding dispersal observations were <10 km from prior territories, but outliers extended as far as 95 km (A). Mean ($\pm$ SE) breeding dispersal distances fluctuated over time with an overall positive trend, which was greater in Washington (B) ($n = 210$) compared to Oregon (C) ($n = 1,948$). The point size in panels (B) and (C) vary with annual sample size.

Ninety-two percent of all breeding dispersals were made by birds ≥ 3 yr old ($n = 1,993$; Appendix Table 4). More breeding dispersal events were observed from male Spotted Owls (54% of observed breeding dispersal events; $\chi^2 = 16.91$, $P < 0.001$; Appendix Table 4). The average owl experience at the territory prior to moving was 2.06 ± 0.06 yr (range: 0–17; Appendix Figure 7). Based on the total number of territorial birds that dispersed, the percentage

of birds paired and successfully producing young increased post-dispersal ($\chi^2 = 27.77$, $P < 0.001$). In the year before dispersing, 18% of individuals produced young. After dispersal, 24% of dispersers produced young. The percentage of birds paired also increased post-dispersal ($\chi^2 = 18.45$, $P < 0.001$). Prior to dispersal, 77% of dispersers were paired (18% single, 36% paired with prior mate, 41% paired with new/unknown mate, 5% pair status unknown).

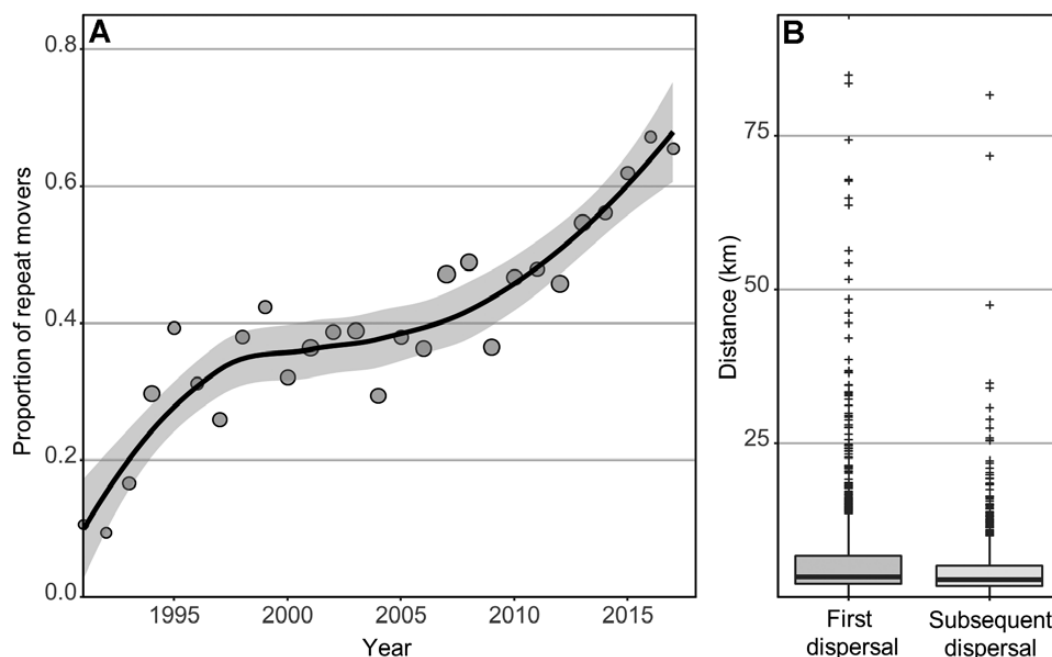


FIGURE 4. The annual proportion of individual Northern Spotted Owls dispersing more than once increased over time in our sample of 1,258 breeding dispersal events (A). Subsequent dispersal distances were indistinguishable from initial dispersal events (B). In panel (A), point size reflects annual sample size with the smoothed mean and standard error shown.

After dispersal, 83% of dispersers were paired (13% single, 20% paired with prior mate, 62% paired with new/unknown mate, 4% unknown paired status). Of the owls that were paired prior to dispersing, the mean experience with that mate was 1.37 ± 0.08 yr (range: 0–15 yr; Appendix Figure 7). Overall, forest disturbance was low across territories within our dispersal dataset; 75% of breeding dispersal movements originated from territories with <2% of their area disturbed at any severity in the prior 3 yr and 99% of movements originated from territories with <23% of their area disturbed at any severity in the prior 3 yr (Appendix Figure 6). Eleven movements originated from territories with >30% of the area disturbed within the prior 3 yr (max = 96.4%).

The best-supported model of breeding dispersal distance included the additive effects of sex, experience at a site prior to dispersal, the pseudo-threshold effect of disturbance at a site, Barred Owl occurrence, and mate status (SEX + EAS + $\ln[D]$ + BO + MS) with random effects of ecophysiological province and year on the intercept (Table 2; Appendix Figure 8). Ecophysiological province accounted for 1.2% of the overall variance and year accounted for 3.3% of the overall variance. The 95% CIs of coefficients of all covariates in the top model did not overlap zero, except for mate status “unknown” (Table 3), which was not different from mate status “single.” Holding other covariates constant at their median or mode, male breeding dispersals were 20% shorter than females ($\exp[\beta] = 0.80$, 95% CI: 0.75–0.86; Table 3, Figure 5). Similarly, breeding

dispersals were 31% shorter when experience at territory prior to dispersal was high ($\exp[\beta] = 0.69$, 95% CI: 0.62–0.76; Figure 5) compared to no prior experience at a territory, and 14% shorter when experience at territory prior to dispersal was low ($\exp[\beta] = 0.86$, 95% CI: 0.77–0.95; Figure 5) compared to no prior experience at a territory. Dispersal distance was positively associated with Barred Owl occurrence ($\exp[\beta] = 1.50$, 95% CI: 1.20–1.86; Figure 5) and with proportion of disturbance on the originating territory ($\exp[\beta] = 1.04$, 95% CI: 1.02–1.06; Figure 5). Models with additive effects of disturbance and Barred Owl occurrence outperformed models that considered these effects independently (Table 2). We tested for an interaction between forest disturbance and our Barred Owl covariate within the top model; however, the interaction term was not supported based on AIC ranking.

DISCUSSION

We found that sex, territory tenure, pair status prior to moving, Barred Owl occurrence, and the degree of territory disturbance were all predictors of breeding dispersal distance in Spotted Owls. Our data fit the general pattern observed in birds of females dispersing farther than males, often attributed to intrasexual competition and inbreeding avoidance (Greenwood and Harvey 1982, Pusey 1987, Forsman et al. 2002). We also found that younger birds or those with less experience with mates or territories dispersed farther than older or more

TABLE 2. Model-selection results used to characterize sources of variation in breeding dispersal distances of Northern Spotted Owls in Oregon and Washington, USA, 1990–2017. Model covariates include sex, experience at prior territory (EAS), mate status prior to move (MS), Barred Owl (BO), and territory disturbance prior to move (D). All models also included random effects of ecophysiographic province and time on the intercept. k is number of parameters. w_i is Akaike's weight. Dev is the residual deviance.

Model	ΔAIC^a	k	w_i	Dev
EAS + SEX + ln(D) + BO + MS ^b	0	12	0.9936	1698.6
EAS + SEX + ln(D) + BO	10.1	9	0.0063	1708.6
EAS + SEX + ln(D)	19.2	8	<0.001	1706.5
EAS + SEX + MS	25.9	10	<0.001	1711.3
EAS + SEX + BO	29.8	8	<0.001	1724.3
EAS + SEX	37.3	7	<0.001	1721.9
EAS + ln(D)	42	7	<0.001	1725.2
EAS + BO	49.5	7	<0.001	1740.9
EAS + MS	55.4	9	<0.001	1734.2
EAS	57.3	6	<0.001	1738.6
MS	99.5	7	<0.001	1770.2
ln(D)	124.8	5	<0.001	1791.3
SEX	125.5	5	<0.001	1791.8
BO	137.8	5	<0.001	1807.9
Intercept only	141.8	4	<0.001	1806.1
EAS + SEX + ln(D) + MS ^c	.	11	.	.

^a Akaike's information criterion (AIC) of top model was 41266.2.

^b Nakagawa's marginal R^2 value was 0.48; see Appendix Figure 8 for residual plot.

^c Model did not converge.

TABLE 3. Estimated coefficients (β), standard error (SE), and confidence intervals (CI) from the top candidate model of breeding dispersal distance for Northern Spotted Owls in Oregon and Washington, USA, 1990–2017.

Variable	β^a	SE	95% CI	
			lower	upper
Intercept ^b	8.984	0.109	8.770	9.197
MALE	−0.220	0.038	−0.294	−0.146
EAS, 1–2 years	−0.147	0.054	−0.252	−0.042
EAS, ≥ 3 years	−0.373	0.053	−0.477	−0.269
MS, paired new mate	−0.131	0.055	−0.238	−0.024
MS, paired previous mate	−0.213	0.059	−0.329	−0.097
MS, unknown	0.019	0.093	−0.164	0.202
ln(D)	0.043	0.009	0.025	0.062
BO	0.402	0.111	0.184	0.621

^a All coefficient statistics are presented untransformed on log-link scale.

^b Intercept: adult female, single prior to dispersing, first year at prior territory.

Abbreviations: EAS = experience at prior territory; MS = mate status in prior year; D = proportion of prior territory disturbed (any severity) within 3 years; BO = cumulative proportion of study area with Barred Owl detection.

experienced individuals, which may reflect a competitive advantage of strong site and mate fidelity (Andreu and Barba 2006, Calabuig et al. 2008, Forero et al. 2008). In contrast to our findings, Blakesley et al. (2006) did not find differences in dispersal distance between sexes or age classes in California Spotted Owls. However, they utilized a much smaller sample size ($n = 54$). Generally, in territorial animals, adults (or territory holders) are able to displace younger individuals (or nonresidents) from established areas (Murray 1967). Spotted Owls do not vacate territories annually (nonmigratory). Thus,

the ability of a nonresident to displace a resident individual is likely further reduced. Furthermore, since dispersal comes with inherent risk, we expected dispersing individuals to settle on the first uncontested suitable site they found (Murray 1967). Collectively, dispersal distances were negatively skewed toward short-distance dispersal events and the median dispersal distance (3.17 km) was similar to what was observed in our region previously (3.5 km; Forsman et al. 2002), which is shorter than observations of California Spotted Owls (7 km; Blakesley et al. 2006).

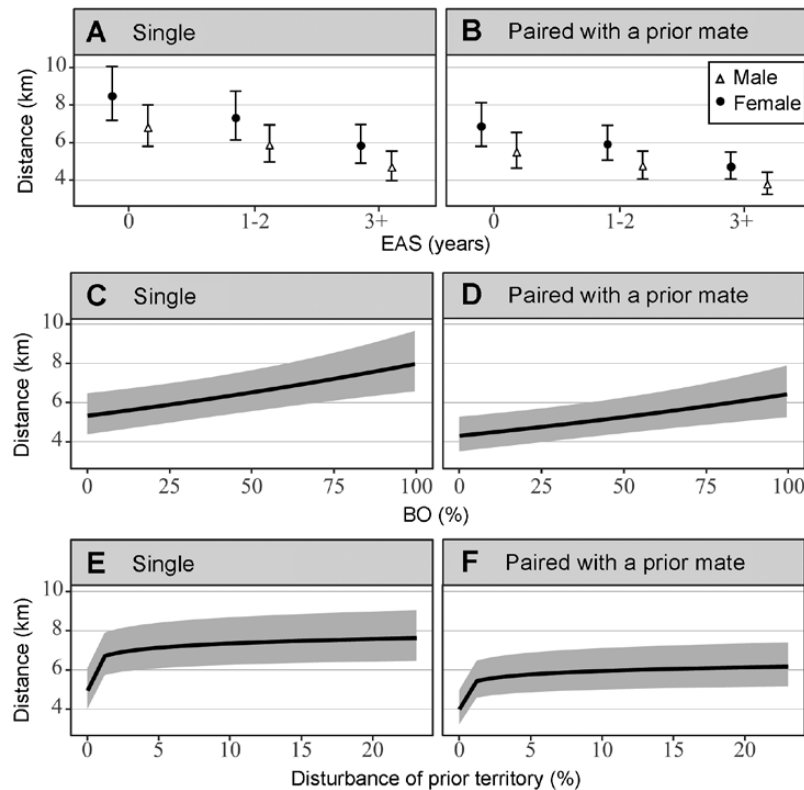


FIGURE 5. Predicted dispersal distance of Northern Spotted Owls with 95% confidence intervals for sex, prior territory experience (EAS) (**A** and **B**), Barred Owl coverage within study areas (BO) (**C** and **D**), and disturbance (**E** and **F**). Predictions were generated for Spotted Owls that were single or paired with a previous mate before dispersing, while holding other covariates at the covariate median or mode.

Animals occupying habitats with stable conditions typically show site fidelity or restricted movements between alternate breeding sites (Greenwood and Harvey 1982). Historically, this was true of Spotted Owls (Forsman et al. 2002). We found some support for increased breeding dispersal distances over time as well as an increase in the number of dispersal events by individual Spotted Owls, which could indicate a potential reduction in stability of habitat conditions for Spotted Owls in the last 20 yr. Early increases in frequency of repeat movers (1990–1995) were likely representative of study initiation effects (i.e. our ability to detect a second dispersal improved as the length of the study increased), rather than true biological increase. However, this was also a period of consistent old-forest harvest on federal lands, which may have contributed to greater dispersal movements during this time. We did not detect time trends in forest disturbance within our sampled territories, but since 1990 there was a positive trend in the proportion of Spotted Owl territories with Barred Owl detections and a correspondingly negative trend in survival and recruitment of Spotted Owl populations in our study areas (Dugger et al. 2016). Our data and analyses suggested that additive effects of habitat disturbance

and competition with Barred Owls increased distances moved by Spotted Owls. We also observed higher rates of long-distance dispersal and an increased frequency of repeat dispersal events in the later years of our study, which coincided with increasing occurrence of Barred Owls.

Interspecific interactions have important implications for spatial ecology of sympatric predator communities. Interspecific competition with brown bears (*Ursus arctos*), for example, affects movement patterns of American black bears (*U. americanus*) but only when high-quality resources are spatially restricted (Belant et al. 2010). Similarly, interference competition among gray wolves (*Canis lupus*) can influence the distribution of coyotes (Berger and Gese 2007). Because of antagonistic interactions and high overlap in resource selection, Barred Owls may increase Spotted Owl breeding dispersal distance directly through conspecific territorial displacement and resource competition (Jenkins et al. 2019b, Wiens et al. 2014). Hybridization (direct competition for mates) occurs but is uncommon in our study areas (Kelly and Forsman 2004). Competition with Barred Owls has been linked to reductions in territory occupancy (Kelly et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011, 2016; Yackulic et al. 2012,

Sovern et al. 2014, Forsman et al. 2015) and apparent survival (Anthony et al. 2003, Forsman et al. 2011, Glenn et al. 2011, Diller et al. 2016, Dugger et al. 2016), both of which represent a combination of increased emigration (dispersal outside of a study area) and/or increased mortality of territory-holding adults. Barred Owls have also been associated with reduced reproduction by Spotted Owls (Olson et al. 2005, Wiens et al. 2014, Dugger et al. 2016). In contrast, Barred Owl presence was not supported as affecting natal dispersal distance in the same study populations of Spotted Owls during 1985–2013 (Hollenbeck et al. 2018). However, Hollenbeck et al. (2018) modeled annual Barred Owl presence at the individual-territory scale, which includes temporal and spatial variability associated with the lack of focused Barred Owl surveys (i.e. Barred Owl detection rates <1.0). In contrast, for this study we developed an annual index of cumulative Barred Owl presence across each study area. This cumulative index is likely a better representation of overall increases in density of Barred Owls at the study area scale, but precludes direct comparisons between these 2 studies. Elsewhere, experimentally augmented nest predation risk increased the likelihood and distance of breeding dispersal in Boreal Owls (*Aegolius funereus*; Hakkarainen et al. 2001). We do not consider Barred Owls a primary nest predator of Spotted Owls, but interspecific territoriality may disrupt Spotted Owl pair bonding and limit the availability of breeding territories for Spotted Owls, thereby leading to reductions in breeding propensity (Mangan et al. 2019), mate retention, and nesting success, and subsequent increases in breeding dispersal distances. Barred Owls may also reduce prey availability for Spotted Owls, either indirectly through changes to predator avoidance strategies used by prey (e.g., Schmidt 2006), or directly by excluding Spotted Owls from productive foraging habitats or via reductions in prey populations (Hamer et al. 2001, Wiens et al. 2014).

The decline in populations of Spotted Owls throughout the region (Dugger et al. 2016) is also likely a factor contributing to increased breeding dispersal patterns in recent years. In a review of 75 bird species, Paradis et al. (1998) found that breeding dispersal distances were longer for less abundant species than among abundant species, and dispersal distances of male Merlin (*Falco columbarius*) decreased with increased population density (Wiklund 1996). Spotted owl populations have declined on all of our study areas, and Washington study areas experienced declines earlier in the study period and more precipitously than study areas in Oregon provinces (Dugger et al. 2016), which may help explain the greater increase in mean dispersal distances in those areas. Spotted Owls occur at low densities because of their large home ranges and small populations. Spotted Owl territory size also increases with latitude (Dugger et al. 2016), which likely contributes

to the reduced density and correspondingly higher mean breeding dispersal distances observed in Washington birds. Concomitant with declines in population density, it stands to reason that mate availability also declined across our study, thus increasing the distances that single birds must travel to find an available mate. As in previous studies of Spotted Owls (Forsman et al. 2002, Gutiérrez et al. 2011), the greatest proportion of dispersal movements were made by birds that failed to successfully produce young in the year prior (Appendix Table 4). However, our model with mate status was more supported than the model of productivity for predictions of dispersal distance (Appendix Table 5). Our model predicted that single Spotted Owls moved farther than formerly paired individuals, which indicates that mate availability is a primary social driver of breeding dispersal distance. Spotted Owls are a K-selected species that do not often breed every year (Stoelting et al. 2015). Thus one unsuccessful year with a mate may have less importance to a long-lived animal than the loss or lack of a mate.

We found that dispersal distance increased with increasing proportions of forest disturbance within the original territory prior to dispersal. We predicted that moderate- to high-severity disturbances would have a greater effect on distance than low-severity disturbances. However, our tests of disturbance variables, ranked “any” disturbance severity higher than “low” or “moderate-to-high” severity in predicting dispersal distances. This lack of distinction could have been because the extent of disturbances within occupied territories was small as the majority (90%) of dispersing birds had ≤7% of their territory disturbed in the 3 yr prior to movement (Appendix Figures 6 and 7). Our study areas were mostly within the late-successional reserve network under the Northwest Forest Plan (Lint et al. 1999), which has been largely successful in protecting late-successional forest on federal lands (Davis et al. 2016). When considering broadly all federal lands, most losses of Spotted Owl nesting habitat have been due to wildfire (Davis et al. 2016), but we observed relatively little loss of forest due to wildfire within our 28-yr sample of breeding dispersals. Further targeted study of breeding owl movements and survival following fire in our region are needed. Timber harvest or wildfire is unlikely to be contained within a single territory, thus it makes sense that birds that lost a proportion of their territory may need to travel farther to find an unoccupied or unaffected territory. Additionally, given dispersal distances are increasing due to Barred Owls, dispersing Spotted Owls may increasingly encounter non-habitat on lands managed outside the standards and guidelines of the Northwest Forest Plan. These areas include non-forest and intensively managed industrial forests that commonly surround late-successional reserves.

There are multiple factors influencing Spotted Owl breeding dispersal, and while it appears that social factors such as mate availability continue to be the important drivers in movement decisions, increased competition from Barred Owls and forest disturbance also have an effect. Increases in dispersal distance, when paired with increased rates of adult dispersal observed in recent years (D. B. Lesmeister and K. M. Dugger personal observations), may have important implications for studies estimating apparent survival from long-term Spotted Owl demographic data. Given Spotted Owls are moving farther and more frequently, permanent emigration from study areas is likely also increasing over time. Apparent survival models cannot differentiate between emigration and mortality, so dispersal movements that result in permanent emigration from study area boundaries can lead to underestimates of apparent survival (Zimmerman et al. 2007). Conversely, if increased dispersal distances are leading to increased movement through young industrial forests or other non-suitable roosting cover, higher rates of mortality are also possible. Given the changing dispersal patterns we have observed, it is increasingly important to consider the impact of these behavioral changes on conservation efforts as well as long-term monitoring programs designed to detect trends in Spotted Owl populations.

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edited the manuscript. J.M.J. developed and performed analysis and wrote the manuscript. J.M.J., D.B.L., E.D.F., K.M.D., S.H.A., L.S.A., C.E.M., M.S.P., J.A.R., S.G.S., R.B.H., and S.A.G. conducted the research. Z.Y. developed environmental metrics and reviewed the manuscript.

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LITERATURE CITED

- Andreu, J., and E. Barba (2006). Breeding dispersal of Great Tits *Parus major* in a homogeneous habitat: Effects of sex, age, and mating status. *Ardea* 94:45–58.
- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, et al. (2003). Status and trends in demography of Northern Spotted Owls, 1985–2003. *Wildlife Monographs* 163:1–48.
- Bates, D., M. Maechler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Belant, J. L., B. Griffith, Y. Zhang, E. H. Follmann, and L. G. Adams (2010). Population-level resource selection by sympatric brown and American black bears in Alaska. *Polar Biology* 33:31–40.
- Berger, K. M., and E. M. Gese (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *The Journal of Animal Ecology* 76:1075–1085.
- Blakesley, J. A., D. R. Anderson, and B. R. Noon (2006). Breeding dispersal in the California Spotted Owl. *The Condor* 108:71–81.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. Stevens, and J. S. White (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Bowler, D. E., and T. G. Benton (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society* 80:205–225.
- Bowman, J. (2003). Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology* 81:195–202.
- Bried, J., and P. Jouventin (2007). Influence of breeding success on fidelity in long-lived birds: An experimental study. *Journal of Avian Biology* 30:392–398.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second edition. Springer-Verlag, New York, NY, USA.
- Calabuig, G., J. Ortego, P. J. Cordero, and J. M. Aparicio (2008). Causes, consequences and mechanisms of breeding dispersal in the colonial Lesser Kestrel, *Falco naumanni*. *Animal Behaviour* 76:1989–1996.
- Clarke, A. L., B.-E. Sæther, and E. Røskft (1997). Sex biases in avian dispersal: A reappraisal. *Oikos* 79:429–438.
- Cohen, W. B., Z. Yang, S. P. Healey, R. E. Kennedy, and N. Gorelick (2017). A LandTrendr multispectral ensemble for forest disturbance detection. *Remote Sensing of Environment* 205:131–140.
- Comfort, E. J., D. A. Clark, R. G. Anthony, J. Bailey, and M. G. Betts (2016). Quantifying edges as gradients at multiple scales improves habitat selection models for Northern Spotted Owl. *Landscape Ecology* 31:1227–1240.

- Daniels, S. J., and J. R. Walters (2000). Between-year breeding dispersal in Red-cockaded Woodpeckers: Multiple causes and estimated cost. *Ecology* 81:2473–2484.
- Davis, R. J., B. Hollen, J. Hobson, J. E. Gower, and D. Keenum (2016). Status and trends of Northern Spotted Owl habitats. USDA Forest Service General Technical Report PNW-GTR-929. Pacific Northwest Research Station, Portland, OR, USA.
- Diller, L. V., K. A. Hamm, D. A. Early, D. W. Lamphear, K. M. Dugger, C. B. Yackulic, C. J. Schwarz, P. C. Carlson, and T. L. McDonald (2016). Demographic response of Northern Spotted Owls to Barred Owl removal. *Journal of Wildlife Management* 80:691–707.
- Dugger, K. M., R. G. Anthony, and L. S. Andrews (2011). Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present. *Ecological Applications* 21:2459–2468.
- Dugger, K. M., E. D. Forsman, A. B. Franklin, R. J. Davis, G. C. White, C. J. Schwarz, K. P. Burnham, J. D. Nichols, J. E. Hines, C. B. Yackulic, et al. (2016). The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. *The Condor: Ornithological Applications* 118:57–116.
- Forero, M. G., J. A. Donazar, J. Blas, and F. Hiraldo (2008). Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80:1298–1310.
- Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, et al. (2011). Population demography of Northern Spotted Owls. *Studies in Avian Biology*, no. 40.
- Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, B. L. Biswell, E. A. Ellingson, C. Meslow, G. S. Miller, et al. (2002). Natal and breeding dispersal of Northern Spotted Owls. *Wildlife Monographs* 149:1–35.
- Forsman, E. D., E. C. Meslow, and H. M. Wight (1984). Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monographs* 122:1–64.
- Forsman, E. D., S. G. Sovern, M. Taylor, and B. L. Biswell (2015). Home range and habitat selection by Northern Spotted Owls on the eastern slope of the Cascade Mountains, Washington. *Journal of Raptor Research* 49:109–128.
- Ganey, J. L., D. L. Apprill, T. A. Rawlinson, S. C. Kyle, R. S. Jonnes, and J. P. Ward (2014). Breeding dispersal of Mexican Spotted Owls in the Sacramento Mountains, New Mexico. *The Wilson Journal of Ornithology* 126:516–524.
- Glenn, E. M., R. G. Anthony, E. D. Forsman, and G. S. Olson (2011). Local weather, regional climate, and annual survival of the Northern Spotted Owl. *The Condor* 113:150–158.
- Glenn, E. M., D. B. Lesmeister, R. J. Davis, B. Hollen, and A. Poopatanapong (2017). Estimating density of a territorial species in a dynamic landscape. *Landscape Ecology* 32:563–579.
- Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202:18–27.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Greenwood, P. J., and P. H. Harvey (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- Gutiérrez, R. J., W. S. LaHaye, and G. S. Zimmerman (2011). Breeding dispersal in an isolated population of Spotted Owls *Strix occidentalis*: Evidence for improved reproductive output. *Ibis* 153:592–600.
- Hakkaraianen, H., P. Ilmonen, V. Koivunen, and E. Korpimäki (2001). Experimental increase of predation risk induces breeding dispersal of Tengmalm's Owl. *Oecologia* 126:355–359.
- Hamer, T. E., D. W. Hays, C. M. Senger, and E. D. Forsman (2001). Diets of Northern Barred Owls and Northern Spotted Owls in an area of sympatry. *Journal of Raptor Research* 35:221–227.
- Hollenbeck, J. P., S. M. Haig, E. D. Forsman, and J. D. Wiens (2018). Geographic variation in natal dispersal of Northern Spotted Owls over 28 years. *The Condor: Ornithological Applications* 120:530–542.
- Jenkins, J. M. A., D. B. Lesmeister, E. D. Forsman, K. M. Dugger, S. H. Ackers, L. S. Andrews, C. E. McCafferty, M. S. Pruett, J. A. Reid, S. G. Sovern, et al. (2019a). Data from: Social status, forest disturbance, and Barred Owls shape long-term trends in breeding dispersal distance of Northern Spotted Owls. *The Condor: Ornithological Applications* 121:1–17. doi:10.5061/dryad.931zcrjfr.
- Jenkins, J. M. A., D. B. Lesmeister, J. D. Wiens, J. T. Kane, V. R. Kane, and J. Verschuyt (2019b). Three-dimensional partitioning of resources by congeneric forest predators with recent sympatry. *Scientific Reports* 9:6036.
- Jiménez-Franco, M. V., J. E. Martínez, I. Pagán, and J. F. Calvo (2013). Factors determining territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraaetus pennatus*. *Journal of Ornithology* 154:311–318.
- Johnson, P. C. (2014). Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods in Ecology and Evolution* 5:944–946.
- Kelly, E. G., and E. D. Forsman (2004). Recent records of hybridization between Barred Owls (*Strix varia*) and Northern Spotted Owls (*S. occidentalis caurina*). *The Auk* 121:806–810.
- Kelly, E. G., E. D. Forsman, and R. G. Anthony (2003). Are Barred Owls displacing Spotted Owls? *The Condor* 105:45–53.
- Kennedy, R. E., Z. Yang, and W. B. Cohen (2010). Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr – Temporal segmentation algorithms. *Remote Sensing of Environment* 114:2897–2910.
- Kim, S. Y., R. Torres, and H. Drummond (2009). Simultaneous positive and negative density-dependent dispersal in a colonial bird species. *Ecology* 90:230–239.
- Kim, S. Y., R. Torres, C. Rodríguez, and H. Drummond (2007). Effects of breeding success, mate fidelity and senescence on breeding dispersal of male and female Blue-footed Boobies. *The Journal of Animal Ecology* 76:471–479.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution* 11:514–517.
- Kroll, A. J., T. L. Fleming, and L. L. Irwin (2010). Site occupancy dynamics of Northern Spotted Owls in the Eastern Cascades, Washington, USA, 1990–2003. *Journal of Wildlife Management* 74:1264–1274.
- Lesmeister, D. B., R. J. Davis, P. H. Singleton, and J. D. Wiens (2018). Northern Spotted Owl habitat and populations: Status and threats. In *Synthesis of science to inform land management within the Northwest Forest Plan area* (T. A. Spies, P. A. Stine, R. A. Gravenmier, J. W. Long, and M. J. Reilly, Editors). USDA

- Forest Service General Technical Report PNW-GTR-966. Pacific Northwest Research Station, Portland, OR, USA. pp. 245–299.
- Lesmeister, D. B., S. G. Sovern, R. J. Davis, D. M. Bell, M. J. Gregory, and J. C. Vogeler (2019). Mixed-severity wildfire and habitat of an old-forest obligate. *Ecosphere* 10:e02696.
- Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey (1999). Northern Spotted Owl effectiveness monitoring plan for the Northwest Forest Plan. USDA Forest Service General Technical Report PNW-GTR-440:43. Pacific Northwest Research Station, Portland, OR, USA.
- Mangan A. O., T. Chestnut, J. C. Vogeler, I. K. Breckheimer, W. M. King, K. E. Bagnall, and K. M. Dugger (2019). Barred Owls reduce occupancy and breeding propensity of Northern Spotted Owl in a Washington old-growth forest. *The Condor: Ornithological Applications* 121:1–20.
- Martin, A. E., and L. Fahrig (2018). Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. *Ecology* 99:2058–2066.
- Morrison, J. L., and P. B. Wood (2009). Broadening our approaches to studying dispersal in raptors. *Journal of Raptor Research* 43:81–89.
- Murray, B. G. (1967). Dispersal in vertebrates. *Ecology* 48:975–978.
- Nakagawa, S., P. C. D. Johnson, and H. Schielzeth (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface* 14:20170213.
- Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple (2005). Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. *Journal of Wildlife Management* 69:918–932.
- Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution* 2:295–299.
- R Core Team (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs (2017). Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* 8:e01695.
- Roze, D., and F. Rousset (2005). Inbreeding depression and the evolution of dispersal rates: A multilocus model. *The American Naturalist* 166:708–721.
- Schmidt, K. A. (2006). Non-additivity among multiple cues of predation risk: A behaviorally-driven trophic cascade between owls and songbirds. *Oikos* 133:82–90.
- Seamans, M. E., and R. J. Gutierrez (2007). Habitat selection in a changing environment: The relationship between habitat alteration and Spotted Owl territory occupancy and breeding dispersal. *The Condor* 109:566–576.
- Sovern, S. G., E. D. Forsman, G. S. Olson, B. L. Biswell, M. Taylor, and R. G. Anthony (2014). Barred Owls and landscape attributes influence territory occupancy of Northern Spotted Owls. *The Journal of Wildlife Management* 78:1436–1443.
- Sovern, S. G., D. B. Lesmeister, K. M. Dugger, M. S. Pruett, R. J. Davis, and J. M. Jenkins (2019). Activity center selection by Northern Spotted Owls. *Journal of Wildlife Management* 83:714–727.
- Stoelting, R. E., R. J. Gutiérrez, W. L. Kendall, and M. Z. Peery (2015). Life-history tradeoffs and reproductive cycles in Spotted Owls. *The Auk: Ornithological Advances* 132:46–64.
- USDA and USDI (1994). Final Supplemental Environmental Impact Statement on Management of Habitat for Late-Successional and Old-Growth Forest Related Species within the Range of the Northern Spotted Owl. USDA Forest Service and USDI Bureau of Land Management, Portland, OR, USA.
- USFWS (1990). Endangered and threatened wildlife and plants: Determination of threatened status for the Northern Spotted Owl. *Federal Register* 55:26114–26194.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman (2014). Competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls in western Oregon. *Wildlife Monographs* 185:1–50.
- Wiklund, C. G. (1996). Determinants of dispersal in breeding Merlins (*Falco columbarius*). *Ecology* 77:1920–1927.
- Wolak, M. E., D. J. Fairbairn, and Y. R. Paulsen (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution* 3:129–137.
- Yackulic, C. B., L. L. Bailey, K. M. Dugger, R. J. Davis, A. B. Franklin, E. D. Forsman, S. H. Ackers, L. S. Andrews, L. V. Diller, S. A. Gremel, et al. (2019). The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls. *Ecological Applications* 29:e01861.
- Yackulic, C. B., J. Reid, R. Davis, J. E. Hines, J. D. Nichols, and E. Forsman (2012). Neighborhood and habitat effects on vital rates: Expansion of the Barred Owl in the Oregon coast ranges. *Ecology* 93:1953–1966.
- Zimmerman, G. S., R. J. Gutiérrez, and W. S. Lahaye (2007). Finite study areas and vital rates: Sampling effects on estimates of Spotted Owl survival and population trends. *Journal of Applied Ecology* 44:963–971.

APPENDIX TABLE 4. Summary statistics for breeding dispersal distance moved by different groups of Northern Spotted Owls, 1990–2017.

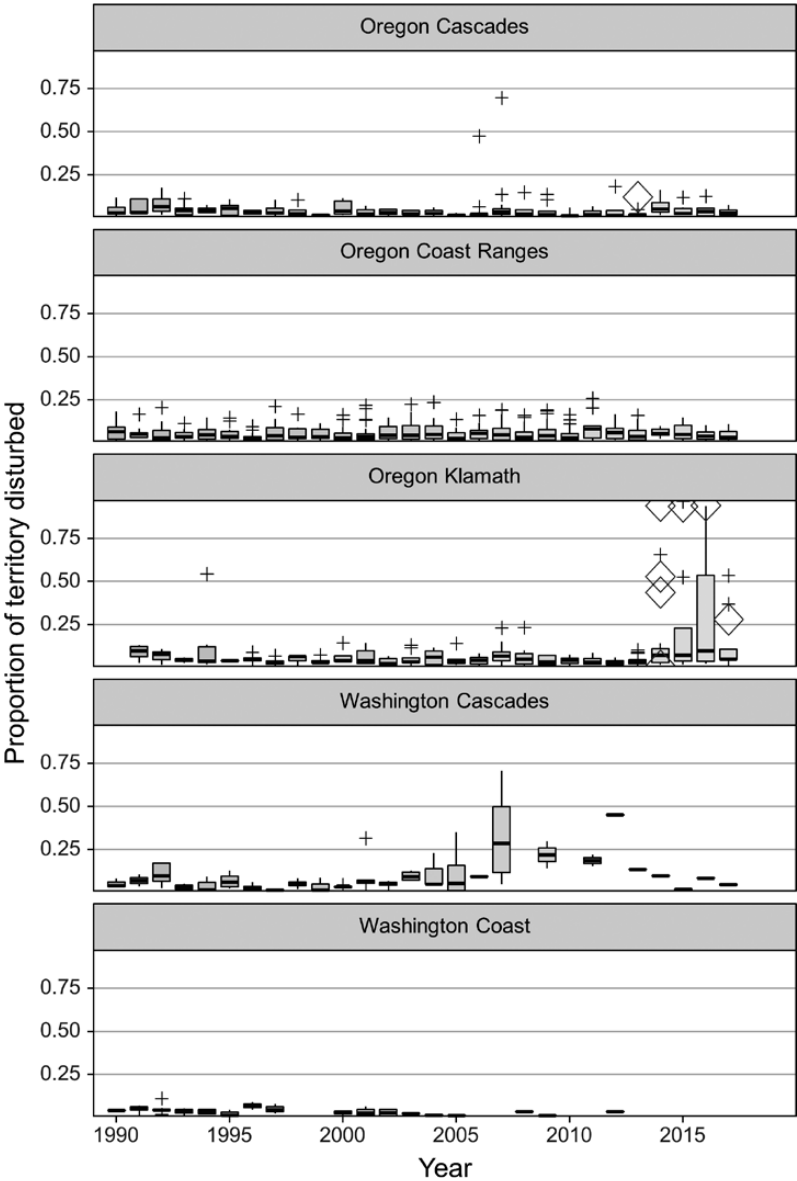
	<i>n</i>	Breeding dispersal distance (km)			
		Mean	SE	min	max
Sex, female	983	5.98	0.27	0.04	94.55
Sex, male	1,175	5.17	0.20	0.09	84.86
Oregon Cascades	520	5.48	0.33	0.51	84.86
Oregon Coast Range	1,086	5.57	0.24	0.04	94.55
Oregon Klamath	342	4.84	0.33	0.24	67.66
Washington Cascades	99	6.75	0.83	0.88	56.37
Washington Coast	111	6.61	0.90	0.18	71.69
P0, unproductive	1,540	5.65	0.20	0.04	94.55
P1, fledged young	382	4.82	0.34	0.25	64.89
P2, unknown productivity	236	6.02	0.51	0.28	67.66
MS1, single	376	6.30	0.43	0.39	94.55
MS2, paired with new mate	895	5.84	0.28	0.04	84.86
MS3, paired with previous mate	773	4.64	0.21	0.17	67.66
MS4, unknown status	114	6.86	0.86	0.55	63.70
Age, adult (age 3+)	1,993	5.43	0.17	0.04	94.55
Age, sub-adult (age 1)	50	6.25	0.74	0.09	22.79
Age, sub-adult (age 2)	115	7.18	0.74	0.91	67.92
EAS, 0 years	971	6.47	0.30	0.04	94.55
EAS, 1–2 years	544	5.31	0.28	0.23	54.34
EAS, 3–17 years	643	4.33	0.20	0.24	67.66

Abbreviations: P = prior productivity, MS = prior mate status, EAS = experience at prior territory, *n* = number of breeding dispersals.

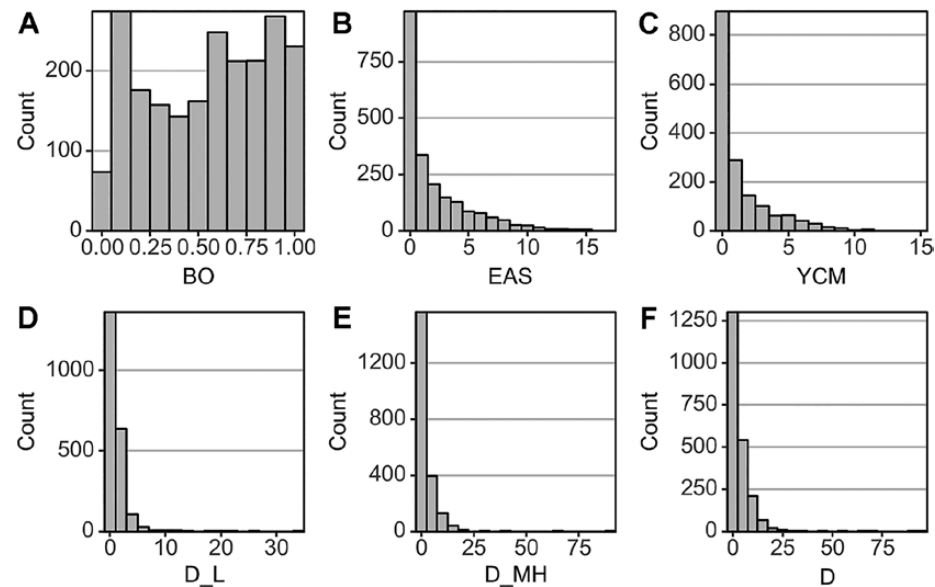
APPENDIX TABLE 5. Summary of model-selection results for initial tests of variable structures within related groups used to characterize sources of variation in breeding dispersal distances of Northern Spotted Owls in Oregon and Washington, USA, 1990–2017. Structures with asterisks were considered in additive models. All models also included random effects of ecophysiological province and time on the intercept. Abbreviations given in Table 1. *k* is number of parameters. *w_i* is Akaike's weight. Dev is the residual deviance.

Variable group	Model	ΔAIC ^a	<i>k</i>	<i>w_i</i>	Dev
Experience	EAS_3groups*	0.0	6	0.644	1738.6
Experience	EAS + EAS ²	1.7	6	0.270	1740.3
Experience	ln(EAS)	4.4	5	0.072	1743.4
Experience	EAS	7.9	5	0.013	1746.6
Experience	EAS_2groups	14.8	5	<0.001	1751.2
Reproductive	MS*	42.2	7	<0.001	1770.2
Experience	ADULT	62.8	5	<0.001	1785.3
Experience	AGECLASS	64.4	6	<0.001	1785.1
Environment	ln(D)*	67.5	5	<0.001	1791.3
Sex	sex*	68.2	5	<0.001	1791.8
Environment	ln(D_LO)	71.5	5	<0.001	1794.4
Reproductive	P	71.7	6	<0.001	1792.5
Environment	ln(D_HI)	72.1	5	<0.001	1794.6
Reproductive	PS	75.0	6	<0.001	1798.1
Environment	D_HI + D_HI ²	78.6	6	<0.001	1799.2
Environment	D_HI	78.8	5	<0.001	1800.8
Environment	D	79.7	5	<0.001	1801.5
Environment	D + D ²	80.1	6	<0.001	1800.2
Barred Owl	BO*	80.5	5	<0.001	1807.9
Barred Owl	ln(BO)	81.4	5	<0.001	1808.8
NULL	intercept-only	84.5	4	<0.001	1806.1
Environment	D_LO	85.6	5	<0.001	1805.7
Environment	D_LO + D_LO ²	86.2	6	<0.001	1804.2
Territory Quality	TQ	86.4	5	<0.001	1806.2

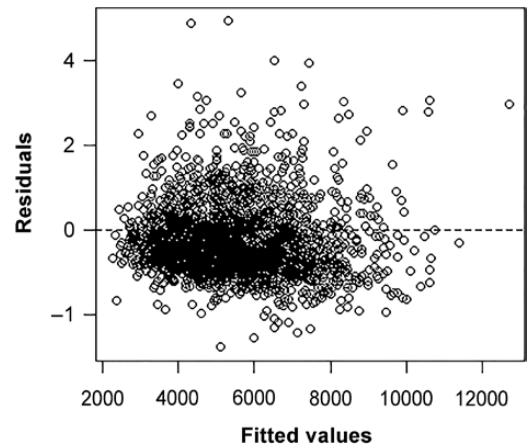
^a Akaike's information criterion (AIC) of top model was 42420.2.



Appendix Figure 6. Boxplots showing proportion of disturbance in sampled pre-dispersal (occupied) territories for Northern Spotted Owls in each ecophysiological province with outliers shown and disturbances from fire overlaid as diamonds. The sample presented here is not representative of disturbance trends within entire study areas or ecophysiological provinces over time.



Appendix Figure 7. Histograms of continuous variables used in analysis of Northern Spotted Owl breeding dispersal distance. Abbreviations: Barred Owl = BO, experience at territory prior to dispersal = EAS, years with mate prior to move = YCM, low-severity disturbance on prior territory = D_L, moderate- to high-severity disturbance on prior territory = D_MH, total disturbance on prior territory = D.



Appendix Figure 8. Residuals plot from top model of breeding dispersal distance in Northern Spotted Owls.