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Western screech-owl occupancy in the face of an invasive predator

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ABSTRACT

Invasive predators can alter ecosystem function and be detrimental to native wildlife by direct predation and through exploitative and interference competition. Barred owls (*Strix varia*), a native species in eastern North America, have expanded their range to Pacific Northwest forests, threatening native owls and community dynamics. The western screech-owl (*Megascops kennicottii*) is a species of conservation concern, and the apparent population decline coincides with the arrival of barred owls. We collected data in 2021 under a broad scale passive acoustic monitoring program at 2482 stations in nine study areas to evaluate western screech-owl distribution and potential threats to population persistence in the Pacific Northwest. We fitted single-species occupancy models to estimate barred owl and western screech-owl landscape use and identify important features of habitat. We quantified effects of barred owls on western screech-owl occupancy and detection probability using co-occurrence models. Barred owls used approximately 0.79 (95 % confidence interval: 0.72, 0.85) of our sampling locations. Western screech-owl occupancy and weekly detection varied by study area from 0.24 (0.15, 0.34) to 0.92 (0.89, 0.95) and 0.12 (0.08, 0.16) to 0.71 (0.69, 0.74), respectively. Western screech-owl detection dropped slightly from 0.36 (0.31, 0.41) to 0.29 (0.26, 0.33) where barred owls were present. Western screech-owls frequently occupied sites used by barred owls but occurred less in older forests where barred owls were present, suggesting they may experience higher predation risk in older forests. Western screech-owls may be unable to avoid habitat used by ubiquitous barred owls, but they may adapt behaviorally to avoid this invasive predator.

1. Introduction

Invasive wildlife can alter ecosystem function and be detrimental to native wildlife by direct predation and through exploitative and interference competition. Barred owls (*Strix varia*), for instance, are a native species of eastern North America and have recently expanded their range into the Pacific Northwest and are now a primary threat to the northern spotted owl (*S. occidentalis caurina*), a native congener and species listed under the US Endangered Species Act (Lesmeister et al., 2018; Franklin et al., 2021). Barred owls are larger, more aggressive, and have been deleterious to northern spotted owl populations with negative impacts on survival, reproduction, territory fidelity, and landscape occupancy (Franklin et al., 2021; Jenkins et al., 2021, 2019a; Rockweit et al., 2023; Wiens et al., 2021). Beyond the impact to northern spotted owls, barred owls may trigger trophic cascades that destabilize forest ecosystems (Baumbusch et al., 2023; Holm et al., 2016).

The western screech-owl (*Megascops kennicottii*) is a small, non-migratory, territorial owl present throughout forests of western

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North America (Cannings et al., 2020). Nine subspecies are currently recognized (Cannings et al., 2020). Two subspecies, *M. k. kennicottii* and *M. k. macfarlanei*, are listed as Threatened in Canada (COSEWIC, 2012), but little is known about population status in the United States. The primary threats to western screech-owls are thought to be habitat loss and interspecific competition and predation by the invasive barred owl (Acker, 2012; COSEWIC, 2012; Elliott, 2006; Er et al., 2005; Holm et al., 2016). Christmas Bird Count data indicates an average 2.11 % decline per year from 1970 to 2021 in the northern Pacific rainforest region (Meehan et al., 2022). Using callback surveys on Bainbridge Island, WA, Acker (2012) reported a significant decline in western screech-owl detections and a significant increase in barred owl detections and sightings. Several studies have found evidence in the region of barred owls preying on small owls including western screech-owls (Baumbusch et al., 2023; Hamer et al., 2007; Wiens et al., 2014). Elliott (2006) suggested that western screech-owls in British Columbia were primarily persisting in small forest fragments of less than 20–30 ha. However, habitat fragmentation may cause local western screech-owl extirpations (Er et al., 2005). Large-scale studies of western screech-owl resource selection, population status, and potential effects of barred owls have been limited by survey methods suited for both species at a landscape scale.

Advances in passive acoustic monitoring have significantly improved the ability to detect multiple vocal species across large spatial and temporal scales (Duchac et al., 2020; Gibb et al., 2019; Ruff et al., 2023, 2021; Tosa et al., 2021). Paired with occupancy models (Bromaghin et al., 2013; MacKenzie et al.,2018; Morin et al., 2020), this methodology can provide consistent, long-term datasets suitable for detecting changes in wildlife populations (Lesmeister et al., 2021; Lesmeister and Jenkins, 2022). A common challenge

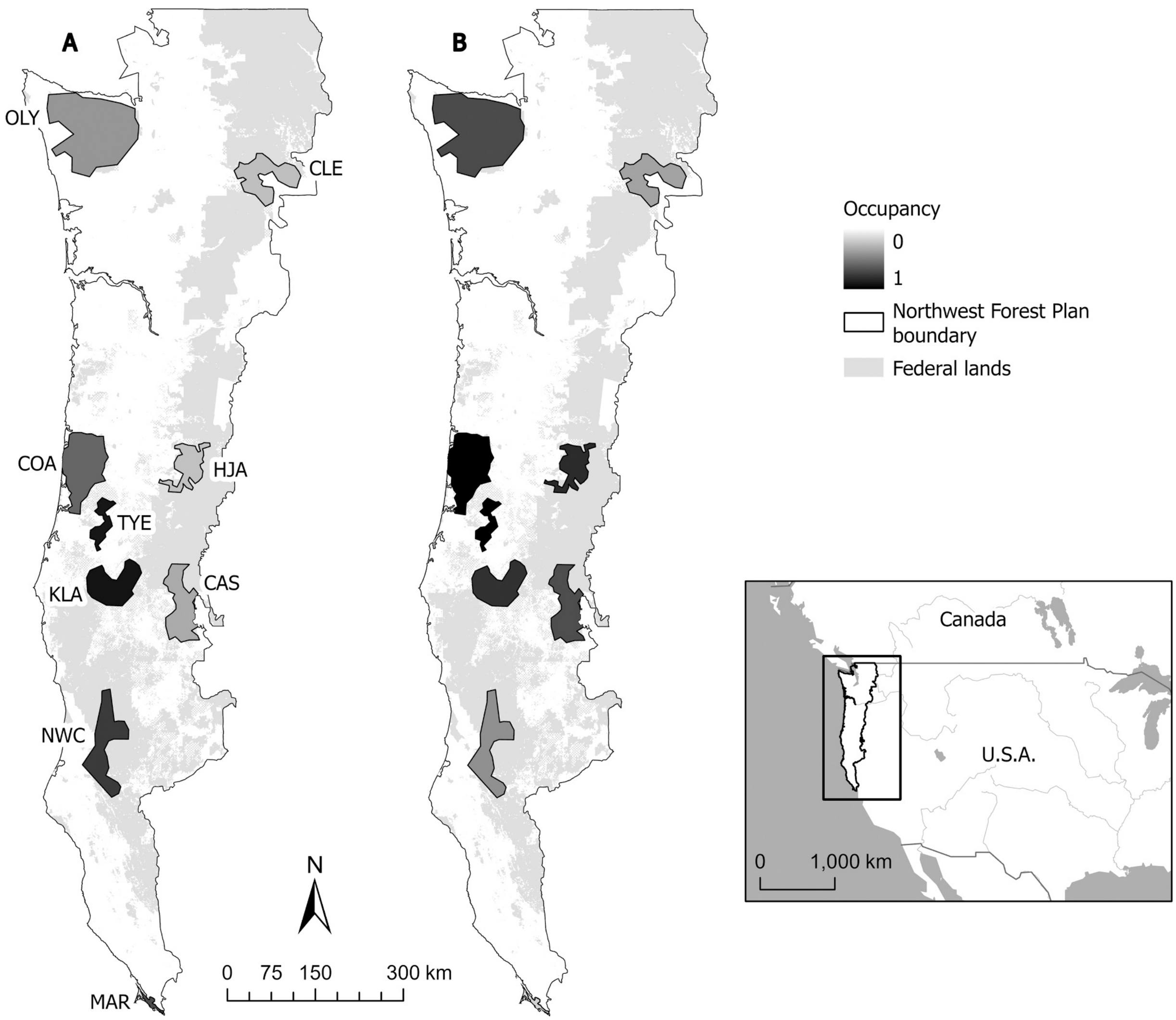

Fig. 1. Study areas within the Northwest Forest Plan boundary with (A) western screech-owl (*Megascops kennicottii*) and (B) barred owl (*Strix varia*) mean occupancy by study area: Olympic Peninsula, WA (OLY), Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Tyee, OR (TYE), Klamath Mountains, OR (KLA), South Oregon Cascades (CAS), Northwest California (NWC), and Marin County, CA (MAR). Occupancy estimates from the most-supported single species single season occupancy models. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

with traditional survey methods for owls is that they are species-specific and not feasible for surveying a significant portion of species' ranges due to the on-the-ground effort required. Passive acoustic monitoring has proven especially effective for broadscale survey efforts for otherwise elusive species and has gradually replaced callback or broadcast surveys for owls in the Pacific Northwest (Duchac et al., 2020).

Here we used data from a large-scale passive acoustic monitoring program to quantify factors that influence western screech-owl distribution in the US Pacific Northwest. We also evaluated the potential impact of barred owl presence on western screech-owl occupancy patterns and detection probability. We hypothesized detection probability for both species would decrease with increased background noise and forest density and increase with increased survey effort (Duchac et al., 2021, 2020; Kissling and Lewis, 2009; MacKenzie et al., 2018). We predicted both species' occupancy would be highest in lower elevation forests with less rugged terrain (Duchac et al., 2021; Elliott, 2006; Kissling and Lewis, 2009). Western screech-owls are often described as an indicator of a healthy riparian system (Cannings et al., 2020; COSEWIC, 2012; Kissling and Lewis, 2009), so we predicted higher occupancy in riparian habitat. We predicted barred owl landscape use would be higher in old-growth forests (Hamer et al., 2007; Livezey, 2009; Singleton et al., 2010) and western screech-owl occupancy may be lower in these forests due to increased presence of barred owls. We predicted western screech-owl occupancy and detection probability would be lower in the presence of barred owls (Acker, 2012; Elliott, 2006; Kissling and Lewis, 2009) and the presence of barred owls may affect additional aspects of western screech-owl resource selection.

2. Methods

2.1. Study area

We collected data in the spring and summer of 2021 under a broad scale passive acoustic monitoring program within nine study areas in the Pacific Northwest: Olympic Peninsula, WA (OLY), Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Tyee, OR (TYE), Klamath Mountains, OR (KLA), South Oregon Cascades (CAS), Northwest California (NWC), and Marin County, CA (MAR; Fig. 1; Table A.1; Lesmeister et al., 2022). These study areas primarily include forest land under federal management by the US Forest Service, US Bureau of Land Management, and US National Park Service. Three study areas (CAS, HJA, CLE) of the Cascades Range and one of the Olympic Mountains (OLY) occurred in high mountains where forests extended up to the tree line >1500 m; the other five study areas (COA, TYE, KLA, NWC, MAR) in the coastal mountains of Oregon and California were lower in elevation <1250 m (Forsman et al., 2011; Table A.1). Climate varied among study areas from relatively warm and dry in California and southern Oregon to extremely wet rainforest on the west side of the Olympic mountains. Most study areas experienced moderately cool and wet winters with some precipitation in the form of snow and dry, warm summers; one study area (CLE) was entirely on the east slope of the Cascades Range and received nearly all its precipitation in snow during the winter (Forsman et al., 2011).

2.2. Acoustic data collection and processing

We used acoustic data collected from 2482 survey stations using Song Meter 4 (Wildlife Acoustics) autonomous recording units (ARUs). Four stations were placed within 5-km^2 hexagons which were randomly chosen to cover 20 % of the federal land within each study area (Lesmeister et al., 2021). The stations were placed ≥200 m from the edge of the hexagon, spaced ≥500 m apart, and ≥50 m from roads, trails, and streams. We conducted surveys at each station over a minimum six-week period during March to mid-September 2021 and scheduled ARUs to record one hour before sunset to three hours after sunset, two hours before sunrise to two hours after sunrise, and 10 min of every hour between the crepuscular periods. The audio data were processed using a multi-step workflow that integrated a trained convolutional neural network model, PNW-Cnet v4, for automated species identification (Lesmeister et al., 2022; Ruff et al., 2023, 2021). PNW-Cnet v4 had high model performance for detecting western screech-owls and barred owls, and predicted detections were verified by technicians to generate weekly encounter histories for both species (Lesmeister et al., 2022).

2.3. Model covariates

We defined survey occasions as one week, resulting in a maximum of nine survey occasions for the season (Table A.1). We recorded the date of surveys (DATE), and quantified mean weekly background noise (NOISE; Duchac et al., 2021, 2020; Lesmeister et al., 2022) and weekly survey effort as the total hours recorded per week (EFFORT) at each station. We log-transformed EFFORT (logEFFORT), hypothesizing that additional recording time significantly improves detection probability initially then stabilizes at a threshold. NOISE was calculated as decibels below full scale (dBFS) using the Kaleidoscope Pro Sound Pressure Level Analysis (SPL) feature between 250 Hz and 1000 Hz, which was averaged daily and then averaged for each survey week (Lesmeister et al., 2022; Wildlife Acoustics, 2021). We compiled climate data for mean weekly temperature (TEMP; Celsius) and weekly precipitation totals (PRECIP; millimeters) using a combination of interpolations and modeling (Daly et al., 2008; PRISM Climate Group, 2022).

We created most occupancy covariates at three buffer scales to represent the potential home range size of western screech-owls. The literature describing likely home range size for western screech-owls is limited and may not represent the variation between subspecies, habitat variation, and latitudinal or longitudinal differences. We used (1) a 250 m buffer to approximate a 20.4 ha breeding season range (Davis and Weir, 2010), (2) a 500 m buffer which approximates an average home range of 64.5–88.6 ha (Davis and Weir, 2010; Kissling and Lewis, 2009), and (3) an 800 m buffer approximating a 200 ha annual home range (COSEWIC, 2012). We calculated terrain covariates from remotely sensed data in ArcGIS (Esri, 2022) including station elevation (ELEV), ruggedness (RUGGED;

standard deviation of elevation within each buffer), topographic position (TOPO; difference of the station elevation relative to the mean elevation within each buffer), and distance to the nearest non-ephemeral stream or waterbody (STREAM). A positive topographic position indicates a station location nearer a ridgetop. We derived forest characteristics in each buffer from the gradient nearest neighbor (GNN; LEMMA, 2020) dataset, including: mean percent canopy cover (FCOVER; using CANCOV data), mean snag density (SDENSE; using SPTH_GE_3 data), and mean forest density (FDENSE; using TPH_GE_3 data). We used GNN Vegetation Class data (LEMMA, 2020) to determine forest type covariates of broadleaves/hardwoods (HDWD), mixed forest (MIX), small conifers (SCON), and giant conifers (GCON; >75 cm quadratic mean diameter). Study area (AREA) and forest density (FDENSE) were used as both occupancy and detection covariates. All candidate models included the categorical covariate AREA to address heterogeneity between study areas. We transformed covariates when appropriate using the scale function in base R (R Core Team, 2022).

2.4. Data analyses

We fitted single-species occupancy models in RPresence (MacKenzie and Hines, 2023) and co-occurrence models in program PRESENCE (Hines, 2006). We first focused on single-species models to determine detectability and habitat factors that affected occupancy for each species, then developed co-occurrence models to evaluate if species interactions improved the model (e.g., Lesmeister et al., 2015). For the single-species models, we used a secondary candidate set strategy (Bromaghin et al., 2013; Morin et al., 2020). We first fitted a set of univariate models and selected the most-supported buffer size and most-supported option among correlated (Spearman rank correlation coefficient greater than ± 0.60) covariates with which to generate multivariate models. We used the resulting general occupancy model structure while developing sub-models for detection, then used the most-supported detection model structure while developing sub-models for occupancy.

To quantify the impact of barred owls on western screech-owl occupancy and detectability, we followed the single-season, two-species occupancy modeling strategy outlined by Richmond et al. (2010) and MacKenzie et al. (2018). We used the most-supported covariates from the top single-species models for each species and evaluated models assuming conditional or unconditional relationships between the two species. We evaluated three biological impacts: barred owl presence affecting western screech-owl occupancy and detection, and barred owl detection affecting western screech-owl detection.

We considered the most-supported models those with the lowest Akaike's information criterion (AIC) and with higher model weight (w; Burnham and Anderson, 2002; MacKenzie et al., 2018; Richmond et al., 2010). For all models, we evaluated covariate beta coefficient estimates and their 95 % confidence intervals (CI) to determine the direction and strength of support for covariates (Burnham and Anderson, 2002; MacKenzie et al., 2018; Richmond et al., 2010). We considered covariate coefficient confidence intervals that widely overlapped zero to have no support (more than 10 %) and those that slightly overlapped zero (less than 10 %) to have little support (Burnham and Anderson, 2002; MacKenzie et al., 2018; Richmond et al., 2010). We report model predicted occupancy and detection estimates by study area and study-wide from most-supported single species models by averaging real estimates and using the delta method to calculate error (Byron et al., 2002). We evaluated the relationship between occupancy or detection with each of the most-supported covariates for top ranked single-species models using the predict function within RPresence (MacKenzie and Hines, 2023).

3. Results

3.1. Western screech-owl

Using PNW-Cnet v4, we estimated 463,009 western screech-owl vocalizations as present in the dataset. We manually validated 14,590 western screech-owl calls, confirming presence at 1107 of 2482 stations and presence in all nine study areas. The most-supported occupancy model included heterogeneity by AREA (Figure A.1), lower SDENSE800 (β = –0.21, CI: –0.37, –0.06), lower GCON800 (β = –1.41, –2.24, –0.58), higher TOPO250 (β = 0.12, 0.01, 0.23), and lower ELEV (β = –0.39, –0.61, –0.16; Table 1, A.2,

Table 1
Top single-species occupancy models for western screech-owl (*Megascops kennicottii*) and barred owl (*Strix varia*) ranked by difference in Akaike's information criterion (ΔAICc), with number of parameters (K), and twice the negative log-likelihood (–2LogL). Occupancy model structure: Ψ(). Detection probability model structure: p(). See Appendix for full model sets and covariate coefficient estimates. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Species	Model structure	AICc	ΔAICc	*w*	K	-2LogL
Western screech-owl	Ψ(AREA + SDENSE800 + GCON800 + ELEV + TOPO250), p(AREA + logEFFORT + NOISE)	12,166.7	0	0.76	24	12,118.18
	Ψ(AREA + SDENSE800 + GCON800 + ELEV), p(AREA + logEFFORT + NOISE)	12,169.1	2.48	0.22	23	12,122.70
Barred owl	Ψ(AREA + FCOVER800 + ELEV + RUGGED800 + TOPO800), p(AREA + logEFFORT + NOISE + TEMP)	16,827.7	0	0.99	25	16,812.82

Notes: Covariates include study AREA; SDENSE800, density of snags within an 800 m radius of each station; GCON800, proportion of giant conifers within an 800 m radius of each station; ELEV, elevation of each station; TOPO250, topographic position within a 250 m radius of each station; TOPO800, topographic position within an 800 m of each station; FCOVER800, canopy cover within an 800 m radius of each station; RUGGED800, terrain ruggedness within an 800 m radius of each station; logEFFORT, log-transformed weekly sampling effort; NOISE, mean weekly background noise in decibels below full scale (dBFS); TEMP, mean weekly temperature.

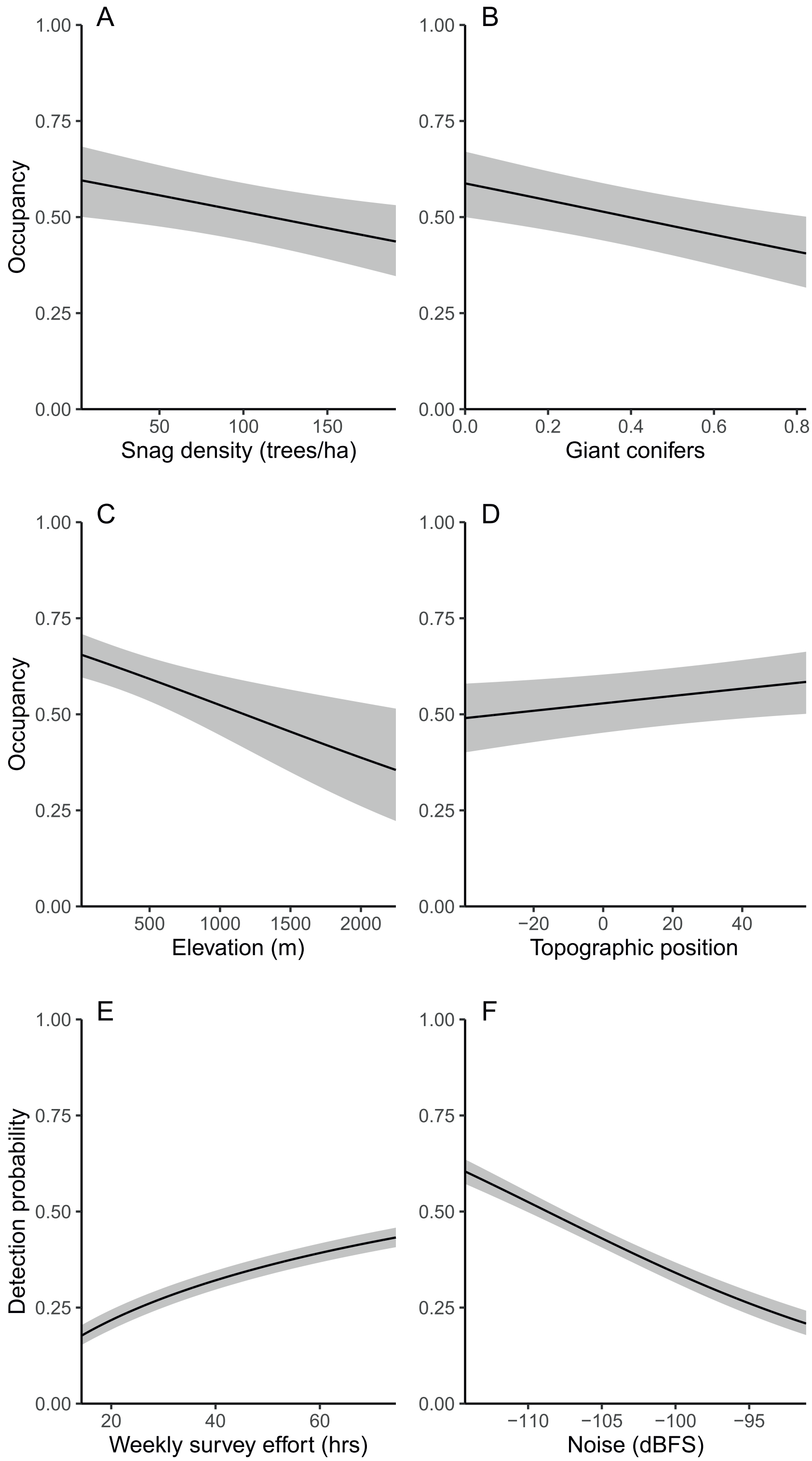

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Fig. 2. Western screech-owl (*Megascops kennicottii*) occupancy and detection probability estimates relative to covariates included in the most-supported single-species model: study area, (A) snag density within an 800 m radius of the station, (B) proportion of giant conifers within an 800 m radius of the station, (C) elevation at the station, (D) topographic position within a 250 m radius of the station, (E) weekly survey effort, and (F) mean weekly background noise measured in decibels below full scale (dBFS). Predictions for each covariate of interest were generated across the 5th to 95th percentile range of study-wide covariate values while other covariates were held at their means, and predictions shown are those for the Oregon Coast Range (COA) study area. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Fig. 2). The average study-wide occupancy rate was 0.50 (0.43, 0.57) and study area occupancy rates were 0.24 in CLE and HJA, 0.32 in CAS, 0.41 in OLY, 0.60 in COA, 0.70 in MAR, 0.76 in NWC, 0.91 in TYE, and 0.92 in KLA (Table A.3; Fig. 1). Weekly detection probability for western screech-owls averaged 0.38 (0.34, 0.41) and varied among study areas from the lowest, 0.12 in CLE, to the highest, 0.71 in KLA (Table A.3). The most-supported model included a negative effect of NOISE (β = –0.50, –0.58, –0.43) and positive effect of logEFFORT (β = 0.77, 0.67, 0.86) on detection probability (Table 1, A.2; Fig. 2).

3.2. Barred owl

Using PNW-Cnet v4, we estimated 223,702 barred owl vocalizations as present in the dataset. We validated 28,092 barred owl calls confirming presence at 1871 of 2482 stations and presence in all nine study areas. The most-supported barred owl model included heterogeneity by AREA (Figure A.1), higher FCOVER800 (β = 0.52, 0.39, 0.65), lower ELEV (β = –0.67, –0.90, –0.45), lower RUGGED800 (β = –0.41, –0.55, –0.27), and higher TOPO800 (β = 0.27, 0.14, 0.40; Table 1, A.2; Fig. 3). The average study-wide landscape use by barred owls was 0.79 (0.72, 0.85) and study area use rates were 0.28 in MAR, 0.46 in CLE, 0.52 in NWC, 0.76 in CAS, 0.77 in OLY, 0.84 in KLA, 0.86 in HJA, 0.97 in COA, and 0.99 in TYE (Table A.3; Fig. 1). Weekly detection probability for barred owls averaged 0.61 (0.58, 0.63) study-wide and varied among study areas from the lowest, 0.37 in CLE, to the highest, 0.87 in TYE (Table A.3). The most-supported barred owl model included the negative effect of NOISE (β = –0.62, –0.68, –0.57) and positive effect of logEFFORT (β = 0.90, 0.83, 0.97; Table 1, A.2; Fig. 3).

3.3. Co-occurrence

The most-supported co-occurrence model assumed western screech-owl occupancy and detection were conditional on barred owl occupancy, and western screech-owl detection was unconditional on barred owl detection (Table 2). Average western screech-owl occupancy was higher where barred owls were present (mean=0.53, CI: 0.45, 0.61) and lower where barred owls were absent (0.36, 0.23, 0.49). Average weekly detection probability for western screech-owls was higher where barred owls were absent (0.36, 0.31, 0.41) and lower where barred owls were present (0.29, 0.26, 0.33; Fig. 4). The most-supported models were within 3 AIC, included all covariates included in the top western screech-owl and barred owl models, and consistently ranked higher than the fully unconditional model with the same parameter dependencies, i.e., the most-supported western screech-owl single-species model (Table 2, A.4). The most-supported model assumed the western screech-owl covariates GCON800, SDENSE800, ELEV, and TOPO250 to be conditional on barred owl occupancy, although the model assuming unconditional covariate relationships ranked within 2 AIC, reducing the support for conditional relationships.

Notes: Covariates include AREA, study area: Southern Oregon Cascades (CAS), Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Klamath Mountains, OR (KLA), Marin County, CA (MAR), Olympic Peninsula, WA (OLY), Tyee, OR (TYE); SDENSE800, density of snags within an 800 m radius of each station; GCON800, proportion of giant conifers within an 800 m radius of each station; ELEV, elevation of each station; TOPO250, topographic position within a 250 m radius of each station; TOPO800, topographic position within an 800 m of each station; FCOVER800, canopy cover within an 800 m radius of each station; RUGGED800, terrain ruggedness within an 800 m radius of each station; logEFFORT, log-transformed weekly sampling effort; NOISE, mean weekly background noise in decibels below full scale (dBFS); TEMP, mean weekly temperature. Occupancy covariates for western screech-owl were either unconditional (U) or conditional (C) on barred owl occupancy. All detection covariates were unconditional on barred owl occupancy or detection.

Western screech-owls avoided higher proportions of giant conifers where barred owls were present (–2.71, –0.92) and not where barred owls were absent (–1.36, 2.99; Fig. 4). Western screech-owls avoided higher densities of snags where barred owls were absent (–1.04, –0.27) and not where barred owls were present (–0.26, 0.08; Fig. 4). Western screech-owls avoided higher elevation where barred owls were present (–0.61, –0.13) and not where barred owls were absent (–0.38, 0.41; Fig. 4). Western screech-owls may have preferred higher topographic position where barred owls were present (–0.02, 0.23) and not where barred owls were absent (–0.12, 0.46; Fig. 4). The second-highest-ranked model differed from the most-supported model only in that it assumed western screech-owl detection was conditional on barred owl detection (Table 2); however, the average weekly detection probability for western screech-owls was 0.30 (0.26, 0.33) when barred owls were detected and 0.29 (0.25, 0.32) when barred owls were not detected. All co-occurrence models included the most-supported detection covariates for each species and assumed they were unconditional on barred owl occupancy and detection (Table 2; A.4). The western screech-owl detection covariates were logEFFORT and NOISE which both effect detection of a call, not call production, and were therefore deemed illogical to depend on barred owl detection. See Appendix for full single-species and co-occurrence model development sets (Tables A.5-A.8).

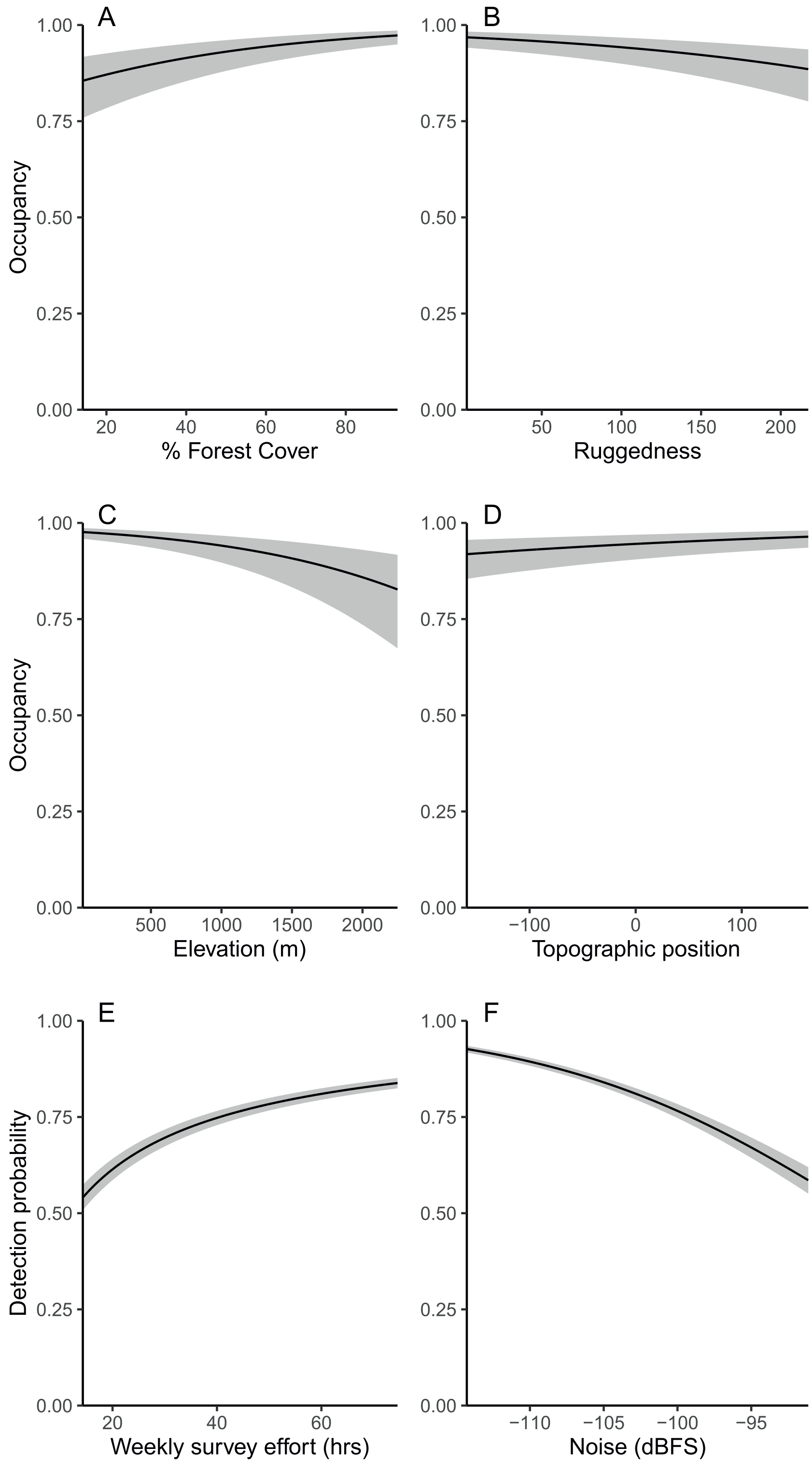

Fig. 3. Barred owl (*Strix varia*) landscape use and detection probability estimates relative to covariates included in the most-supported single-species model: study area, (A) percent forest cover within an 800 m radius of the station, (B) elevation at the station, (C) terrain ruggedness within an 800 m radius of the station, (D) topographic position within an 800 m radius of the station, (E) weekly survey effort, and (F) mean weekly background noise measured in decibels below full scale (dBFS). Predictions for each covariate of interest were generated across the 5th to 95th percentile range of study-wide covariate values while other covariates were held at their means, and predictions shown are those for the Oregon

Coast Range (COA) study area. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Table 2
Top co-occurrence models evaluating the dependence or independence of species interactions between western screech-owl (*Megascops kennicottii*; species B) and barred owl (*Strix varia*; species A) ranked by difference in Akaike's information criterion (ΔAIC), with model weight (*w*) and number of parameters (K). The fully unconditional model is included for comparison. Occupancy parameters tested were (1) occupancy of barred owls (Ψ^A), (2) occupancy of western screech-owls where barred owls were present or absent (Ψ^{BA}, Ψ^{Ba}; equivalent to $\Psi^{BA} \ddagger \Psi^{Ba}$), and (3) occupancy of western screech-owls unconditional on barred owl occupancy (Ψ^B; equivalent to $\Psi^{BA} = \Psi^{Ba}$). Detection parameters tested were (1) detection of barred owls unconditional on western screech-owl occupancy (p^A), (2) detection of western screech-owls conditional on present barred owl detection or non-detection (r^{BA}, r^{Ba}; equivalent to $r^{BA} \ddagger r^{Ba}$), (3) detection of western screech-owls conditional on barred owl occupancy and unconditional on barred owl detection (p^B, r^B; equivalent to $p^B \ddagger r^{BA} = r^{Ba}$), and (4) detection of western screech-owls unconditional on barred owl occupancy and detection (p^B only; equivalent to $p^B = r^{BA} = r^{Ba}$). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Co-occurrence model structure	Occupancy covariates	Detection model structure	Detection covariates	ΔAIC[1]	*w*	K
Ψ^A, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250 (C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^A, p^B, r^B	AREA, NOISE, EFFORT, TEMP[3]	0	0.42	55
Ψ^A, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250 (C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^A, p^B, r^{BA}, r^{Ba}	AREA, NOISE, EFFORT, TEMP[3]	1.21	0.23	56
Ψ^A, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250 (U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^A, p^B, r^B	AREA, NOISE, EFFORT, TEMP[3]	1.26	0.22	51
Ψ^A, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250 (U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^A, p^B, r^{BA}, r^{Ba}	AREA, NOISE, EFFORT, TEMP[3]	2.48	0.12	52
Ψ^A, Ψ^B	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250 (U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^A, p^B	AREA, NOISE, EFFORT, TEMP[3]	42.42	0	49

[1]Lowest AIC = 28,986.58
[2]These covariates were only applied to western screech-owl parameters.
[3]These covariates were only applied to barred owl parameters.

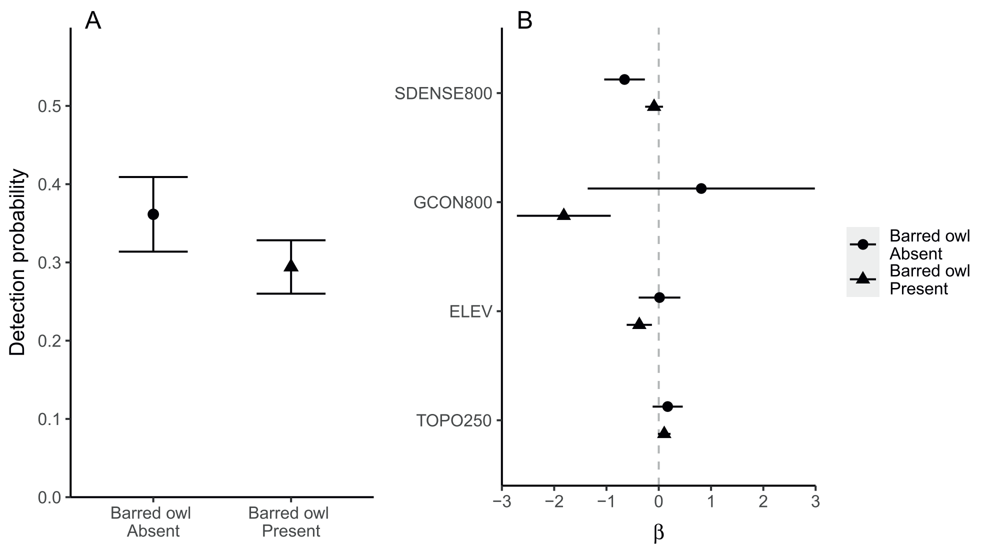

Fig. 4. Conditional effects of barred owl presence on western screech-owl detection probability and occupancy from most-supported co-occurrence model: (A) detection probability averaged from real estimates and (B) covariate coefficient estimates (β) of occupancy covariates chosen from most-supported single-species western screech-owl model. Abbreviations: SDENSE800, snag density within an 800 m radius of the station; GCON800, proportion of giant conifers within an 800 m radius of the station; ELEV, elevation at the station; and TOPO250, topographic position within a 250 m radius of the station. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

4. Discussion

We effectively detected western screech-owls and barred owls across a large area and varied landscapes using passive acoustic monitoring. Western screech-owls were relatively common in low elevation younger forests with limited distribution in high elevations such as the Cascade Mountain range. Barred owls were common throughout low elevation forests in a great diversity of forest types, resulting in very little habitat available for western screech-owls to avoid barred owls and therefore, high co-occurrence rates. In older conifer forests, western screech-owl occupancy was lower where barred owls were present, potentially due to higher competitive exclusion and predation risk.

All three study areas in the Cascade Mountain range had lower western screech-owl occupancy than any other study areas, followed by the Olympic Peninsula, WA where the elevation averaged approximately 681 m with some sites exceeding 1500 m. Western screech-owl occupancy was limited by high elevation, especially where barred owls were present, supporting that the Cascade Mountain range may present a barrier preventing genetic flow between *M. k. kennicottii* and *M. k. macfarlanei* to the east (Gehlbach, 2003). We found higher western screech-owl occupancy in low elevation forests with fewer giant conifers and snags and, contrary to our predictions, found no association with riparian areas. Several of our study areas were coastal mountain ranges where forests are mesic with less distinction between riparian and surrounding landscapes compared to drier forests in the Cle Elum, WA and south Cascades, OR study areas and in other regions outside the Pacific Northwest (Cannings et al., 2020; COSEWIC, 2012). Two of the most-supported western screech-owl occupancy covariates, snag density and giant conifers, were summarized within the 800 m buffer scale, which approximates an average barred owl home range size (200 ha; Singleton et al., 2010). To our knowledge, there have been no studies to estimate western screech owl home range size in our study areas, therefore it's unknown if home ranges are relatively small like those in British Columbia, Canada (64.5 ha; Davis and Weir, 2010) or like the large home ranges in southeast Alaska, USA (551 ha; Kissling and Lewis, 2009). The high support for covariates in the largest buffers could indicate selection at the territory scale.

On a landscape scale, we found higher western screech-owl occupancy of forests used by barred owls. Barred owls used approximately 79 % of our study sites, occurring more frequently in low elevation, less rugged forests with high canopy cover. Our study supports previous barred owl habitat associations found in western North America (Long and Wolfe, 2019) which overlaps significantly with suitable western screech-owl habitat. Like western screech-owls, barred owls had lower occupancy rates in Cle Elum, WA where forests may be less suitable due to higher elevation, more rugged terrain, lower canopy cover, and drier forests. We observed lower landscape use by barred owls in California study areas. We believe this is primarily because these study areas are on the southern edge of the barred owl range expansion and colonized as recently as 2002 (Long and Wolfe, 2019), but the habitat is suitable for continued barred owl colonization. Study-wide, there is little suitable western screech-owl habitat not occupied by barred owls. The two species occur frequently in the same forests, resulting in no overall negative association between barred owl presence and western screech-owl occupancy, contrary to findings by Kissling and Lewis (2009). However, barred owls may affect the relationship between our most-supported covariates and western screech-owl occupancy. Where barred owls were present, we observed a negative relationship between giant conifers and western screech-owl occupancy. Furthermore, in the absence of barred owls, western screech-owl occupancy was lower with higher snag density; in the presence of barred owls, western screech-owls may use habitat they would otherwise avoid. Barred owls often occur in higher densities, use a greater diversity of forest types, and have greater diet diversity than native congeneric spotted owls, exerting greater predation and competitive pressure on native forest communities (Holm et al., 2016; Lesmeister et al., 2018; Jenkins et al., 2019b). Western screech-owls may face higher competitive exclusion or predation risk by barred owls in older conifer forests, leading to altered space use at fine scales.

Western screech-owls are unable to avoid using forests inhabited by the ubiquitous barred owl in the Pacific Northwest but may be adapting behaviorally through fine-scale avoidance to minimize predation. We found western screech-owl detectability decreased where barred owls were present. Kissling and Lewis (2009) found a similar decrease in western screech-owl detection probability in the presence of barred owls or great-horned owls (*Bubo virginianus*). Detection probability for both western screech-owls and barred owls decreased with higher background noise and increased with survey effort. The low detection probability of western screech-owls in some study areas highlights the importance of long duration surveys and accounting for imperfect detection in estimates of occupancy and distribution. These factors indicate the importance of quality data collection and including these factors in other survey types (e.g., Kissling and Lewis, 2009). Existing population estimates for western screech-owls in the Pacific Northwest are mostly based on callback surveys (Acker, 2012) or Christmas Bird Count trends (Meehan et al., 2022), which may not consistently incorporate detection probability. Several studies (Acker, 2012; Elliott, 2006; Meehan et al., 2022) have correlated the timing of apparent western screech-owl declines with the invasion of barred owls. Few studies thus far have accounted for imperfect detection of western screech-owls, especially as related to the presence of barred owls. Therefore, population trend estimates for western screech-owls could be impacted by changes in detection probability in the face of a novel predator rather than true changes in the population. However, beyond changes in detection probability, barred owls may still negatively affect western screech-owl occupancy trends. In southeast Alaska, western screech-owl occupancy increased in some sites from a historical period (1986–1992) to a recent period (2005–2008) but decreased in more southern sites (Kissling and Lewis, 2009) where barred owls were more established.

Invasive barred owls have been the focus of recent conservation actions in western North America to benefit northern spotted owls (e.g., Wiens et al., 2021), however, the broader impact on native wildlife communities is largely unknown. Our study supports the finding that western screech-owl populations are negatively impacted by barred owls (Acker, 2012; COSEWIC, 2012; Elliott, 2006; Kissling and Lewis, 2009), and conservation actions focused on reducing ecological impact of barred owls may also benefit western screech-owls. The barred owl range expansion and establishment in the Pacific Northwest is still recent (Livezey, 2009) and yet we observed western screech-owls behaving in a way that could be an adaptation to reduce predation risk when co-occurring with barred owls. A robust, long-term study that incorporates detection probability with barred owl occupancy could provide further insights into western screech-owl behavioral adaptations and population trends in the region. Additional contribution of broadscale passive acoustic monitoring will be understanding barred owl effects on other small owls, including northern saw-whet owls (*Aegolius acadicus*) and northern pygmy owls (*Glaucidium gnoma*), that may experience similar pressure in the Pacific Northwest (Acker, 2012; Baumbusch et al., 2023; Wiens et al., 2014).

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Damon B. Lesmeister: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix

Table A.1
Summary of station detection histories and mean values for most-supported covariates by study area. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Study Area	Number of Stations	Mean survey weeks per station (min, max)	Western screech-owl only	Barred owl only	Both species	No detections	SDENSE 800[1]	GCON 8001	ELEV	TOPO 250[1]	FCOVER 800[2]	RUGGED 800[2]	TOPO 800[2]	NOISE	EFFORT	TEMP[2]
CAS	380	6.81 (1, 9)	18	188	89	85	33.27	0.10	1498.57	1.87	68.11	42.44	4.05	−106.84	67.27	11.59
CLE	298	7.45 (1, 9)	9	89	32	168	32.21	0.02	1231.78	3.14	63.21	72.20	9.86	−98.64	68.79	12.63
COA	476	6.93 (1, 9)	5	192	260	19	27.56	0.29	344.90	10.79	66.32	59.50	31.61	−106.44	65.40	12.37
HJA	279	7.00 (1, 9)	7	179	53	40	30.64	0.23	964.62	5.41	73.93	75.75	13.45	−104.37	65.63	13.09
KLA	276	7.58 (5, 9)	41	19	212	4	15.52	0.07	687.51	8.78	68.45	71.50	23.83	−108.51	64.56	13.87
MAR	27	6.63 (3, 8)	8	0	8	11	33.64	0.31	207.55	2.97	62.63	54.84	3.47	−105.40	63.90	11.71
NWC	121	6.35 (1, 8)	45	14	42	20	20.37	0.04	1054.96	9.23	68.66	88.84	21.31	−103.86	62.29	15.96
OLY	473	6.71 (1, 9)	15	216	126	116	39.69	0.25	681.08	7.57	82.48	100.70	18.51	−103.20	67.45	13.25
TYE	156	7.43 (2,9)	1	15	140	0	10.03	0.12	368.87	8.89	65.32	64.59	16.09	−107.63	65.83	13.76
Total	2482	7.01 (1, 9)	149	912	962	463	28.93	0.17	834.09	6.79	70.40	71.10	17.62	−104.89	66.28	12.95

[1]These covariates were only applied to western screech-owl parameters.
[2]These covariates were only applied to barred owl parameters.

Abbreviations: SDENSE800, density of snags (trees/hectare) within an 800 m radius of each station; GCON800, proportion of giant conifers within an 800 m radius of each station; ELEV, elevation (meters) of each station; TOPO250, topographic position within a 250 m radius of each station; FCOVER800, canopy cover within an 800 m radius of each station; RUGGED800, terrain ruggedness within an 800 m radius of each station; TOPO800, topographic position within an 800 m of each station, NOISE, mean weekly background noise in decibels below full scale (dBFS); weekly survey effort in hours; and TEMP, mean weekly temperature in Celsius.

Table A.2
Top single-species occupancy models for western screech-owl (*Megascops kennicottii*) and barred owl (*Strix varia*) ranked by difference in Akaike's information criterion (ΔAICc), with model coefficient estimates (β) for occupancy covariates (Ψ) and detection covariates (*p*), standard error (SE), and lower and upper 95 % confidence limits (LCL; UCL). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Species	Model structure	ΔAICc	*w*	K	Covariate[3]	β	SE	LCL	UCL
Western screech-owl[1]	Ψ(AREA+SDENSE800 +GCON800 +ELEV+TOPO250), *p*(AREA+logEFFORT+NOISE)	0	0.76	24	intercept (Ψ)	0.03	0.21	–0.39	0.44
					AREA: CLE (Ψ)	–0.72	0.28	–1.28	–0.17
					AREA: COA (Ψ)	0.33	0.31	–0.29	0.94
					AREA: HJA (Ψ)	–0.74	0.24	–1.21	–0.28
					AREA: KLA (Ψ)	2.22	0.31	1.61	2.83
					AREA: MAR (Ψ)	0.88	0.70	–0.49	2.25
					AREA: NWC (Ψ)	1.31	0.28	0.76	1.85
					AREA: OLY (Ψ)	–0.04	0.28	–0.60	0.51
					AREA: TYE (Ψ)	1.81	0.40	1.03	2.58
					SDENSE800 (Ψ)	–0.21	0.08	–0.37	–0.06
					GCON800 (Ψ)	–1.41	0.42	–2.24	–0.58
					ELEV (Ψ)	–0.39	0.11	–0.61	–0.16
					TOPO250 (Ψ)	0.12	0.06	0.01	0.23
					intercept (*p*)	–4.31	0.22	–4.75	–3.87
					AREA: CLE (*p*)	–0.55	0.22	–0.97	–0.12
					AREA: COA (*p*)	0.73	0.11	0.53	0.94
					AREA: HJA (*p*)	0.48	0.15	0.19	0.76
					AREA: KLA (*p*)	1.91	0.11	1.70	2.12
					AREA: MAR (*p*)	0.10	0.28	–0.45	0.64
					AREA: NWC (*p*)	1.70	0.13	1.44	1.96
					AREA: OLY (*p*)	–0.12	0.12	–0.37	0.12
					AREA: TYE (*p*)	1.88	0.12	1.65	2.11
					logEFFORT (*p*)	0.77	0.05	0.67	0.86
					NOISE (*p*)	–0.50	0.04	–0.58	–0.43
	Ψ(AREA+SDENSE800 +GCON800 +ELEV), p(AREA+logEFFORT+NOISE)	2.48	0.22	23	intercept (Ψ)	–0.06	0.21	–0.47	0.35
					AREA: CLE (Ψ)	–0.69	0.28	–1.25	-0.14
					AREA: COA (Ψ)	0.47	0.31	–0.13	1.07
					AREA: HJA (Ψ)	–0.68	0.24	–1.15	–0.22
					AREA: KLA (Ψ)	2.32	0.31	1.72	2.92
					AREA: MAR (Ψ)	0.87	0.66	–0.43	2.17
					AREA: NWC (Ψ)	1.40	0.27	0.86	1.93
					AREA: OLY (Ψ)	0.07	0.28	–0.48	0.61
					AREA: TYE (Ψ)	1.92	0.39	1.15	2.69
					SDENSE800 (Ψ)	–0.22	0.08	–0.38	–0.07
					GCON800 (Ψ)	–1.37	0.42	–2.19	–0.54
					ELEV (Ψ)	–0.37	0.11	–0.59	–0.14
					intercept (*p*)	–4.31	0.22	–4.75	-3.87
					AREA: CLE (*p*)	–0.55	0.22	–0.97	–0.13
					AREA: COA (*p*)	0.73	0.11	0.53	0.94
					AREA: HJA (*p*)	0.48	0.15	0.19	0.76
					AREA: KLA (*p*)	1.91	0.11	1.70	2.12
					AREA: MAR (*p*)	0.12	0.27	–0.41	0.65
					AREA: NWC (*p*)	1.70	0.13	1.44	1.96
					AREA: OLY (*p*)	–0.13	0.12	–0.37	0.12
					AREA: TYE (*p*)	1.88	0.12	1.65	2.11
					logEFFORT (p)	0.77	0.05	0.67	0.86

(*continued on next page*)

Table A.2 (*continued*)

Species	Model structure	ΔAICc	*w*	K	Covariate[3]	β	SE	LCL	UCL
					NOISE (*p*)	–0.50	0.04	–0.58	–0.43
Barred owl[2]	Ψ(AREA+FCOVER800 +ELEV+RUGGED800 +TOPO800), *p*(AREA+logEFFORT+NOISE+TEMP)	0	0.99	25	intercept (Ψ)	2.04	0.24	1.57	2.51
					AREA: CLE (Ψ)	–1.26	0.22	–1.70	–0.82
					AREA: COA (Ψ)	0.77	0.44	–0.08	1.63
					AREA: HJA (Ψ)	0.05	0.28	–0.50	0.60
					AREA: KLA (Ψ)	–0.42	0.32	–1.04	0.20
					AREA: MAR (Ψ)	–3.69	0.58	–4.84	–2.55
					AREA: NWC (Ψ)	–1.40	0.30	–1.99	–0.82
					AREA: OLY (Ψ)	–1.07	0.32	–1.70	–0.44
					AREA: TYE (Ψ)	2.64	1.06	0.57	4.71
					FCOVER800 (Ψ)	0.52	0.07	0.39	0.65
					ELEV (Ψ)	–0.67	0.11	–0.90	–0.45
					RUGGED800 (Ψ)	–0.41	0.07	–0.55	–0.27
					TOPO800 (Ψ)	0.27	0.07	0.14	0.40
					intercept (*p*)	–3.97	0.16	–4.28	–3.66
					AREA: CLE (*p*)	0.13	0.09	–0.05	0.31
					AREA: COA (*p*)	1.74	0.07	1.61	1.88
					AREA: HJA (*p*)	0.68	0.08	0.53	0.83
					AREA: KLA (*p*)	0.80	0.07	0.65	0.94
					AREA: MAR (*p*)	0.35	0.31	–0.25	0.95
					AREA: NWC (*p*)	0.46	0.12	0.22	0.71
					AREA: OLY (*p*)	0.76	0.07	0.62	0.90
					AREA: TYE (*p*)	2.07	0.11	1.87	2.28
					logEFFORT (p)	0.90	0.04	0.83	0.97
					NOISE (*p*)	–0.62	0.03	–0.68	–0.57
					TEMP (*p*)	–0.06	0.02	–0.10	–0.02

[1]Lowest western screech-owl model AICc = 12166.67

[2]Lowest barred owl model AICc = 16863.35

[3]Intercept indicates study area Southern Oregon Cascades (CAS). AREA, study area: Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Klamath Mountains, OR (KLA), Marin County, CA (MAR), Olympic Peninsula, WA (OLY), Tyee, OR (TYE); SDENSE800, density of snags within an 800 m radius of each station; GCON800, proportion of giant conifers within an 800 m radius of each station; ELEV, elevation of each station; TOPO250, topographic position within a 250 m radius of each station; TOPO800, topographic position within an 800 m of each station; FCOVER800, canopy cover within an 800 m radius of each station; RUGGED800, terrain ruggedness within an 800 m radius of each station; logEFFORT, log-transformed total weekly sampling effort in hours; NOISE, mean weekly background noise in decibels below full scale (dBFS); and TEMP, mean weekly temperature in Celcius.

Table A.3
Mean occupancy (ψ) and detection probability (p) estimates for western screech-owl (Megascops kennicottii) and barred owl (Strix varia) by study area with standard error (SE) and lower and upper 95 % confidence limits (LCL; UCL) calculated from most-supported single-species models. Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

	Area	Ψ	SE	LCL	UCL	Area	*p*	SE	LCL	UCL
Western screech-owl	CAS	0.32	0.032	0.26	0.39	CAS	0.28	0.017	0.25	0.31
	CLE	0.24	0.047	0.15	0.34	CLE	0.12	0.020	0.08	0.16
	COA	0.60	0.032	0.53	0.66	COA	0.43	0.012	0.40	0.45
	HJA	0.24	0.027	0.19	0.29	HJA	0.34	0.022	0.29	0.38
	KLA	0.92	0.018	0.89	0.95	KLA	0.71	0.012	0.69	0.74
	MAR	0.70	0.126	0.45	0.95	MAR	0.27	0.044	0.19	0.36
	NWC	0.76	0.042	0.68	0.85	NWC	0.59	0.019	0.55	0.62
	OLY	0.41	0.040	0.34	0.49	OLY	0.22	0.013	0.19	0.24
	TYE	0.91	0.025	0.86	0.96	TYE	0.71	0.015	0.68	0.73
	Mean	0.50	0.037	0.43	0.57	Mean	0.38	0.017	0.34	0.41
	Median	0.44	0.037	0.37	0.51	Median	0.34	0.017	0.30	0.37
Barred Owl	CAS	0.76	0.030	0.70	0.82	CAS	0.49	0.011	0.47	0.51
	CLE	0.46	0.041	0.38	0.54	CLE	0.37	0.015	0.34	0.40
	COA	0.97	0.010	0.95	0.99	COA	0.81	0.008	0.79	0.82
	HJA	0.86	0.024	0.81	0.91	HJA	0.57	0.012	0.55	0.60
	KLA	0.84	0.028	0.79	0.90	KLA	0.68	0.011	0.65	0.70
	MAR	0.28	0.090	0.10	0.46	MAR	0.53	0.061	0.41	0.65
	NWC	0.52	0.053	0.41	0.62	NWC	0.49	0.021	0.45	0.54
	OLY	0.77	0.031	0.71	0.83	OLY	0.58	0.009	0.56	0.60
	TYE	0.99	0.007	0.98	1.01	TYE	0.87	0.010	0.85	0.89
	Mean	0.79	0.031	0.72	0.85	Mean	0.61	0.01	0.58	0.63
	Median	0.85	0.031	0.79	0.91	Median	0.63	0.01	0.60	0.66

Notes: Study areas include Southern Oregon Cascades (CAS), Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Klamath Mountains, OR (KLA), Marin County, CA (MAR), Olympic Peninsula, WA (OLY), and Tyee, OR (TYE).

Table A.4

Complete set of 12 co-occurrence models evaluating the dependence or independence of species and covariate interactions between western screech-owl (Megascops kennicottii; species B) and barred owl (Strix varia; species A) ranked by difference in Akaike's information criterion (ΔAIC), with model weight (w) and number of parameters (K). Occupancy parameters tested were (1) occupancy of barred owls (Ψ^{A}), (2) occupancy of western screech-owls when barred owls were present or absent (Ψ^{BA}, Ψ^{Ba}; equivalent to Ψ^{BA} ‡ Ψ^{Ba}), and (3) occupancy of western screech-owls unconditional on barred owl occupancy (Ψ^{B}; equivalent to $\Psi^{BA}=\Psi^{Ba}$). Detection parameters tested were (1) detection of barred owls unconditional on western screech-owl occupancy (p^{A}), (2) detection of western screech-owls conditional on present barred owl detection or non-detection (r^{BA}, r^{Ba}; equivalent to r^{BA} ‡ r^{Ba}), (3) detection of western screech-owls conditional on barred owl occupancy and unconditional on barred owl detection (p^{B}, r^{B}; equivalent to p^{B} ‡ $r^{BA} = r^{Ba}$), and (4) detection of western screech-owls unconditional on barred owl occupancy and detection (p^{B}; equivalent to $p^{B} = r^{BA} = r^{Ba}$). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

Occupancy model	Occupancy covariates	Detection model	Detection covariates	ΔAIC[1]	w	K
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250(C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{B}	AREA, NOISE, EFFORT, TEMP[3]	0	0.42	55
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250(C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{BA}, r^{Ba}	AREA, NOISE, EFFORT, TEMP[3]	1.21	0.23	56
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250(U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{B}	AREA, NOISE, EFFORT, TEMP[3]	1.26	0.22	51
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250(U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{BA}, r^{Ba}	AREA, NOISE, EFFORT, TEMP[3]	2.48	0.12	52
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250(C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}	AREA, NOISE, EFFORT, TEMP[3]	18.45	0	54
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250(U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}	AREA, NOISE, EFFORT, TEMP[3]	19.6	0	50
Ψ^{A}, Ψ^{B}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250(C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{B}	AREA, NOISE, EFFORT, TEMP[3]	25.36	0	54
Ψ^{A}, Ψ^{B}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250(C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{BA}, r^{Ba}	AREA, NOISE, EFFORT, TEMP[3]	26.63	0	55
Ψ^{A}, Ψ^{B}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250(U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{B}	AREA, NOISE, EFFORT, TEMP[3]	34.31	0	50
Ψ^{A}, Ψ^{B}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250(U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}, r^{BA}, r^{Ba}	AREA, NOISE, EFFORT, TEMP[3]	35.61	0	51
Ψ^{A}, Ψ^{B}	AREA(U), ELEV(C), SDENSE800(C)[2], GCON800(C)[2], TOPO250(C)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}	AREA, NOISE, EFFORT, TEMP[3]	36.89	0	53
Ψ^{A}, Ψ^{B}	AREA(U), ELEV(U), SDENSE800(U)[2], GCON800(U)[2], TOPO250(U)[2], FCOVER800[3], RUGGED800[3], TOPO800[3]	p^{A}, p^{B}	AREA, NOISE, EFFORT, TEMP[3]	42.42	0	49

[1]Lowest AIC = 28986.58

[2]These covariates were only applied to western screech-owl parameters.

[3]These covariates were only applied to barred owl parameters.

Notes: Covariates include AREA, study area: Southern Oregon Cascades (CAS), Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Klamath Mountains, OR (KLA), Marin County, CA (MAR), Olympic Peninsula, WA (OLY), Tyee, OR (TYE); SDENSE800, density of snags within an 800 m radius of each station; GCON800, proportion of giant conifers within an 800 m radius of each station; ELEV, elevation of each station; TOPO250, topographic position within a 250 m radius of each station; TOPO800, topographic position within an 800 m of each station; FCOVER800, canopy cover within an 800 m radius of each station; RUGGED800, terrain ruggedness within an 800 m radius of each station; logEFFORT, log-transformed weekly sampling effort; NOISE, mean weekly background noise in decibels below full scale (dBFS); TEMP, mean weekly temperature. Occupancy covariates for western screech-owl were either unconditional (U) or conditional (C) on barred owl occupancy. All detection covariates were unconditional on barred owl occupancy or detection.

Table A.5

Detection model subset of single-species models for western screech-owl (Megascops kennicottii) ranked by difference in Akaike's information criterion (ΔAICc), with model weight (w), and number of parameters (K). Occupancy model structure (ψ) is held as the general model while testing detection submodels (p). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

	Model	ΔAICc[1]	w	K	-2LogL
1	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+logEFFORT+NOISE)	0.00	1	27	12124.18
2	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+logEFFORT+PRECIP)	148.71	0	27	12272.89
3	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+logEFFORT+TEMP)	159.36	0	27	12283.54
4	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+logEFFORT)	160.46	0	26	12286.68

(*continued on next page*)

Table A.5 (*continued*)

	Model	ΔAICc[1]	w	K	-2LogL
5	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+logEFFORT+DATE)	160.74	0	27	12284.92
6	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+logEFFORT+FDENSE)	162.50	0	27	12286.68
8	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+NOISE)	311.39	0	26	12437.61
9	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+EFFORT)	371.08	0	26	12497.30
10	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+DATE)	445.78	0	26	12572.01
11	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+TEMP)	457.27	0	26	12583.50
12	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+PRECIP)	458.26	0	26	12584.48
14	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(AREA)	458.86	0	25	12587.13
15	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p (AREA+FDENSE)	460.85	0	26	12587.07
16	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800, p(logEFFORT)	1268.42	0	18	13410.94
17	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(NOISE)	1298.70	0	18	13441.22
19	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(TEMP)	1455.89	0	18	13598.41
20	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(DATE)	1475.84	0	18	13618.36
21	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(PRECIP)	1484.73	0	18	13627.25
22	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(FDENSE)	1485.29	0	18	13627.80
23	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(.)	1486.77	0	18	13629.29
24	ψ(AREA+ELEV+FCOVER800 +RUGGED800 +TOPO250 +FDENSE250 +SDENSE800 +MIX800), p(EFFORT)	1510.81	0	17	13655.35
25	ψ(.), p(.)	2302.65	0	2	14477.44

[1]Lowest AICc = 12178.79

Table A.6

Occupancy model subset of single-species models for western screech-owl (*Megascops kennicottii*) ranked by difference in Akaike's information criterion (ΔAICc), with model weight (*w*), and number of parameters (K). Detection model structure (p) is held as the top-ranked detection model structure while testing occupancy submodels (ψ). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

	Model	ΔAICc[1]	w	K	-2LogL
1	ψ(AREA+SDENSE800 +GCON800 +ELEV+TOPO250), p(AREA+logEFFORT+NOISE)	0.00	0.76	24	12118.18
2	ψ(AREA+SDENSE800 +GCON800 +ELEV), p(AREA+logEFFORT+NOISE)	2.48	0.22	23	12122.70
3	ψ(AREA+SDENSE800 +ELEV+TOPO250), p(AREA+logEFFORT+NOISE)	9.19	0.01	23	12129.40
4	ψ(AREA+SDENSE800 +GCON800 +TOPO250), p(AREA+logEFFORT+NOISE)	9.66	0.01	23	12129.88
5	ψ(AREA+SDENSE800 +GCON800), p(AREA+logEFFORT+NOISE)	11.00	0	22	12133.26
6	ψ(AREA+SDENSE800 +ELEV), p(AREA+logEFFORT+NOISE)	11.12	0	22	12133.37
7	ψ(AREA+SDENSE800 +TOPO250), p(AREA+logEFFORT+NOISE)	14.52	0	22	12136.77
8	ψ(AREA+SDENSE800), p(AREA+logEFFORT+NOISE)	15.66	0	21	12139.95
9	ψ(AREA+SDENSE800 +HDWD800), p(AREA+logEFFORT+NOISE)	16.47	0	22	12138.72
10	ψ(AREA+SDENSE800 +MIX800), p(AREA+logEFFORT+NOISE)	17.41	0	22	12139.67
11	ψ(AREA+ELEV), p(AREA+logEFFORT+NOISE)	31.37	0	21	12155.66
12	ψ(AREA+GCON800), p(AREA+logEFFORT+NOISE)	32.50	0	21	12156.79
13	ψ(AREA+MIX800), p(AREA+logEFFORT+NOISE)	49.56	0	21	12173.85
14	ψ(AREA+TOPO250), p(AREA+logEFFORT+NOISE)	50.85	0	21	12175.14
15	ψ(AREA+HDWD800), p(AREA+logEFFORT+NOISE)	50.92	0	21	12175.21
16	ψ(AREA+RUGGED250), p(AREA+logEFFORT+NOISE)	51.83	0	21	12176.13
18	ψ(AREA), p(AREA+logEFFORT+NOISE)	52.06	0	20	12178.39
19	ψ(AREA+SCON500), p(AREA+logEFFORT+NOISE)	52.07	0	21	12176.36
20	ψ(AREA+FDENSE250), p(AREA+logEFFORT+NOISE)	53.87	0	21	12178.16
21	ψ(AREA+FCOVER800), p(AREA+logEFFORT+NOISE)	54.07	0	21	12178.36
22	ψ(SDENSE800), p(AREA+logEFFORT+NOISE)	255.08	0	13	12395.60
23	ψ(SDENSE500), p(AREA+logEFFORT+NOISE)	284.09	0	13	12424.61
24	ψ(MIX800), p(AREA+logEFFORT+NOISE)	304.38	0	13	12444.90
25	ψ(MIX500), p(AREA+logEFFORT+NOISE)	325.97	0	13	12466.49
26	ψ(SDENSE250), p(AREA+logEFFORT+NOISE)	337.41	0	13	12477.93
27	ψ(MIX250), p(AREA+logEFFORT+NOISE)	348.74	0	13	12489.26
28	ψ(ELEV), p(AREA+logEFFORT+NOISE)	359.31	0	13	12499.83
29	ψ(HDWD800), p(AREA+logEFFORT+NOISE)	390.54	0	13	12531.06
30	ψ(HDWD500), p(AREA+logEFFORT+NOISE)	415.87	0	13	12556.39
31	ψ(GCON800), p(AREA+logEFFORT+NOISE)	433.74	0	13	12574.26
32	ψ(GCON500), p(AREA+logEFFORT+NOISE)	442.51	0	13	12583.03
33	ψ(SCON500), p(AREA+logEFFORT+NOISE)	446.58	0	13	12587.10
34	ψ(SCON800), p(AREA+logEFFORT+NOISE)	448.07	0	13	12588.58

(*continued on next page*)

Table A.6 (*continued*)

	Model	ΔAICc[1]	w	K	-2LogL
35	ψ(GCON250), p(AREA+logEFFORT+NOISE)	463.09	0	13	12603.61
36	ψ(HDWD250), p(AREA+logEFFORT+NOISE)	464.81	0	13	12605.33
37	ψ(FCOVER800), p(AREA+logEFFORT+NOISE)	472.33	0	13	12612.85
38	ψ(SCON250), p(AREA+logEFFORT+NOISE)	478.62	0	13	12619.14
39	ψ(TOPO250), p(AREA+logEFFORT+NOISE)	483.57	0	13	12624.09
40	ψ(FCOVER500), p(AREA+logEFFORT+NOISE)	484.38	0	13	12624.90
41	ψ(TOPO500), p(AREA+logEFFORT+NOISE)	493.92	0	13	12634.44
42	ψ(RUGGED250), p(AREA+logEFFORT+NOISE)	494.42	0	13	12634.94
43	ψ(TOPO800), p(AREA+logEFFORT+NOISE)	498.61	0	13	12639.13
44	ψ(FCOVER250), p(AREA+logEFFORT+NOISE)	500.52	0	13	12641.04
45	ψ(FDENSE250), p(AREA+logEFFORT+NOISE)	503.96	0	13	12644.48
46	ψ(FDENSE500), p(AREA+logEFFORT+NOISE)	504.24	0	13	12644.76
47	ψ(FDENSE800), p(AREA+logEFFORT+NOISE)	505.58	0	13	12646.10
48	ψ(RUGGED800), p(AREA+logEFFORT+NOISE)	505.91	0	13	12646.43
49	ψ(RUGGED500), p(AREA+logEFFORT+NOISE)	506.25	0	13	12646.77
50	ψ(.), p(AREA+logEFFORT+NOISE)	506.27	0	12	12648.81
51	ψ(STREAM), p(AREA+logEFFORT+NOISE)	507.48	0	13	12648.00
52	ψ(.), p(.)	2314.78	0	2	14477.44

[1]Lowest AICc = 12166.67

Table A.7

Detection model subset of single-species models for barred owl (*Strix varia*) ranked by difference in Akaike's information criterion (ΔAICc), with model weight (*w*), and number of parameters (K). Occupancy model structure (ψ) is held as the general model while testing detection submodels (p). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

	Model	ΔAICc[1]	w	K	-2LogL
1	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+logEFFORT+NOISE+TEMP)	0.00	0.93	29	16804.4
2	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+logEFFORT+NOISE)	5.97	0.05	28	16812.4
3	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+logEFFORT+NOISE+DATE)	7.72	0.02	29	16812.1
4	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+logEFFORT+DATE)	467.51	0	28	17274.0
5	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+logEFFORT+TEMP)	489.18	0	28	17295.6
6	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+logEFFORT)	497.65	0	27	17306.2
7	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+NOISE)	778.56	0	27	17587.1
8	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+TEMP)	1233.32	0	27	18041.8
9	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+DATE)	1239.67	0	27	18048.2
11	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA)	1240.00	0	26	18050.6
12	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+FDENSE)	1241.18	0	27	18049.7
13	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(AREA+PRECIP)	1241.24	0	27	18049.7
14	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(logEFFORT)	1678.30	0	19	18503.1
15	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(NOISE)	1721.64	0	19	18546.5
18	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(EFFORT)	2196.21	0	19	19021.0
19	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(FDENSE)	2283.17	0	19	19108.0
20	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(PRECIP)	2303.49	0	19	19128.3
21	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(DATE)	2314.68	0	19	19139.5
22	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(TEMP)	2322.22	0	19	19147.0
23	ψ(AREA+ELEV+MIX500 +FDENSE800 +TOPO800 +RUGGED800 +FCOVER800 +SDENSE800 + STREAM), p(.)	2332.32	0	18	19159.2

[1]Lowest AICc = 16863.12

Table A.8
Occupancy model subset of single-species models for barred owl (*Strix varia*) ranked by difference in Akaike's information criterion (ΔAICc), with model weight (w), and number of parameters (K). Detection model structure (p) is held as the top-ranked detection model structure while testing occupancy submodels (ψ). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

	Model	ΔAICc[1]	w	K	-2LogL
1	ψ(AREA+FCOVER800 +ELEV+RUGGED800 +TOPO800), p(AREA+logEFFORT+NOISE+TEMP)	0.00	1	25	16812.82
2	ψ(AREA+FCOVER800 +ELEV+RUGGED800), p(AREA+logEFFORT+NOISE+TEMP)	15.06	0	24	16829.92
3	ψ(AREA+FCOVER800 +ELEV+RUGGED800 +SDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	15.68	0	25	16828.50
4	ψ(AREA+FCOVER800 +ELEV+RUGGED800 +MIX500), p(AREA+logEFFORT+NOISE+TEMP)	15.91	0	25	16828.72
5	ψ(AREA+FCOVER800 +RUGGED800), p(AREA+logEFFORT+NOISE+TEMP)	43.34	0	23	16860.23
6	ψ(AREA+FCOVER800 +ELEV), p(AREA+logEFFORT+NOISE+TEMP)	48.29	0	23	16865.19
7	ψ(AREA+FCOVER800 +SDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	79.15	0	23	16896.05
8	ψ(AREA+FCOVER800 +MIX500), p(AREA+logEFFORT+NOISE+TEMP)	87.26	0	23	16904.15
9	ψ(AREA+FCOVER800 +TOPO800), p(AREA+logEFFORT+NOISE+TEMP)	88.81	0	23	16905.70
10	ψ(AREA+FCOVER800), p(AREA+logEFFORT+NOISE+TEMP)	95.34	0	22	16914.28
11	ψ(AREA+FCOVER800 +SCON800), p(AREA+logEFFORT+NOISE+TEMP)	96.68	0	23	16913.57
12	ψ(AREA+FCOVER800 +FDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	97.00	0	23	16913.90
13	ψ(AREA+ELEV), p(AREA+logEFFORT+NOISE+TEMP)	103.25	0	22	16922.19
14	ψ(AREA+RUGGED800), p(AREA+logEFFORT+NOISE+TEMP)	120.65	0	22	16939.59
15	ψ(AREA+SDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	132.36	0	22	16951.30
16	ψ(AREA+MIX500), p(AREA+logEFFORT+NOISE+TEMP)	133.70	0	22	16952.64
17	ψ(AREA+FDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	137.65	0	22	16956.59
18	ψ(AREA+SCON800), p(AREA+logEFFORT+NOISE+TEMP)	138.61	0	22	16957.55
19	ψ(AREA+TOPO800), p(AREA+logEFFORT+NOISE+TEMP)	144.06	0	22	16962.99
21	ψ(AREA), p(AREA+logEFFORT+NOISE+TEMP)	153.38	0	21	16974.35
22	ψ(AREA+GCON800), p(AREA+logEFFORT+NOISE+TEMP)	154.19	0	22	16973.13
23	ψ(AREA+HDWD250), p(AREA+logEFFORT+NOISE+TEMP)	154.57	0	22	16973.50
24	ψ(ELEV), p(AREA+logEFFORT+NOISE+TEMP)	326.64	0	14	17161.82
25	ψ(SDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	463.13	0	14	17298.31
26	ψ(SDENSE500), p(AREA+logEFFORT+NOISE+TEMP)	468.29	0	14	17303.47
27	ψ(FCOVER800), p(AREA+logEFFORT+NOISE+TEMP)	471.37	0	14	17306.55
28	ψ(SDENSE250), p(AREA+logEFFORT+NOISE+TEMP)	475.78	0	14	17310.96
29	ψ(FCOVER500), p(AREA+logEFFORT+NOISE+TEMP)	475.97	0	14	17311.15
30	ψ(RUGGED800), p(AREA+logEFFORT+NOISE+TEMP)	478.26	0	14	17313.44
31	ψ(FCOVER250), p(AREA+logEFFORT+NOISE+TEMP)	485.55	0	14	17320.73
32	ψ(GCON800), p(AREA+logEFFORT+NOISE+TEMP)	486.20	0	14	17321.37
33	ψ(TOPO800), p(AREA+logEFFORT+NOISE+TEMP)	490.31	0	14	17325.49
34	ψ(GCON250), p(AREA+logEFFORT+NOISE+TEMP)	491.63	0	14	17326.80
35	ψ(GCON500), p(AREA+logEFFORT+NOISE+TEMP)	491.82	0	14	17327.00
36	ψ(FDENSE800), p(AREA+logEFFORT+NOISE+TEMP)	492.87	0	14	17328.05
37	ψ(MIX500), p(AREA+logEFFORT+NOISE+TEMP)	493.26	0	14	17328.44
38	ψ(RUGGED500), p(AREA+logEFFORT+NOISE+TEMP)	493.35	0	14	17328.53
39	ψ(FDENSE500), p(AREA+logEFFORT+NOISE+TEMP)	494.20	0	14	17329.37
40	ψ(MIX800), p(AREA+logEFFORT+NOISE+TEMP)	495.75	0	14	17330.93
41	ψ(FDENSE250), p(AREA+logEFFORT+NOISE+TEMP)	496.79	0	14	17331.97
42	ψ(TOPO500), p(AREA+logEFFORT+NOISE+TEMP)	498.90	0	14	17334.07
43	ψ(TOPO250), p(AREA+logEFFORT+NOISE+TEMP)	501.74	0	14	17336.91
44	ψ(MIX250), p(AREA+logEFFORT+NOISE+TEMP)	508.23	0	14	17343.40
45	ψ(RUGGED250), p(AREA+logEFFORT+NOISE+TEMP)	513.16	0	14	17348.33
46	ψ(HDWD250), p(AREA+logEFFORT+NOISE+TEMP)	519.62	0	14	17354.80
47	ψ(HDWD500), p(AREA+logEFFORT+NOISE+TEMP)	521.17	0	14	17356.34
48	ψ(HDWD800), p(AREA+logEFFORT+NOISE+TEMP)	521.89	0	14	17357.07
49	ψ(SCON800), p(AREA+logEFFORT+NOISE+TEMP)	521.92	0	14	17357.10
50	ψ(SCON250), p(AREA+logEFFORT+NOISE+TEMP)	522.55	0	14	17357.73
51	ψ(.), p(AREA+logEFFORT+NOISE+TEMP)	522.77	0	13	17359.97
52	ψ(STREAM), p(AREA+logEFFORT+NOISE+TEMP)	522.86	0	14	17358.04
53	ψ(SCON500), p(AREA+logEFFORT+NOISE+TEMP)	523.82	0	14	17359.00

[1]Lowest AICc = 16863.35

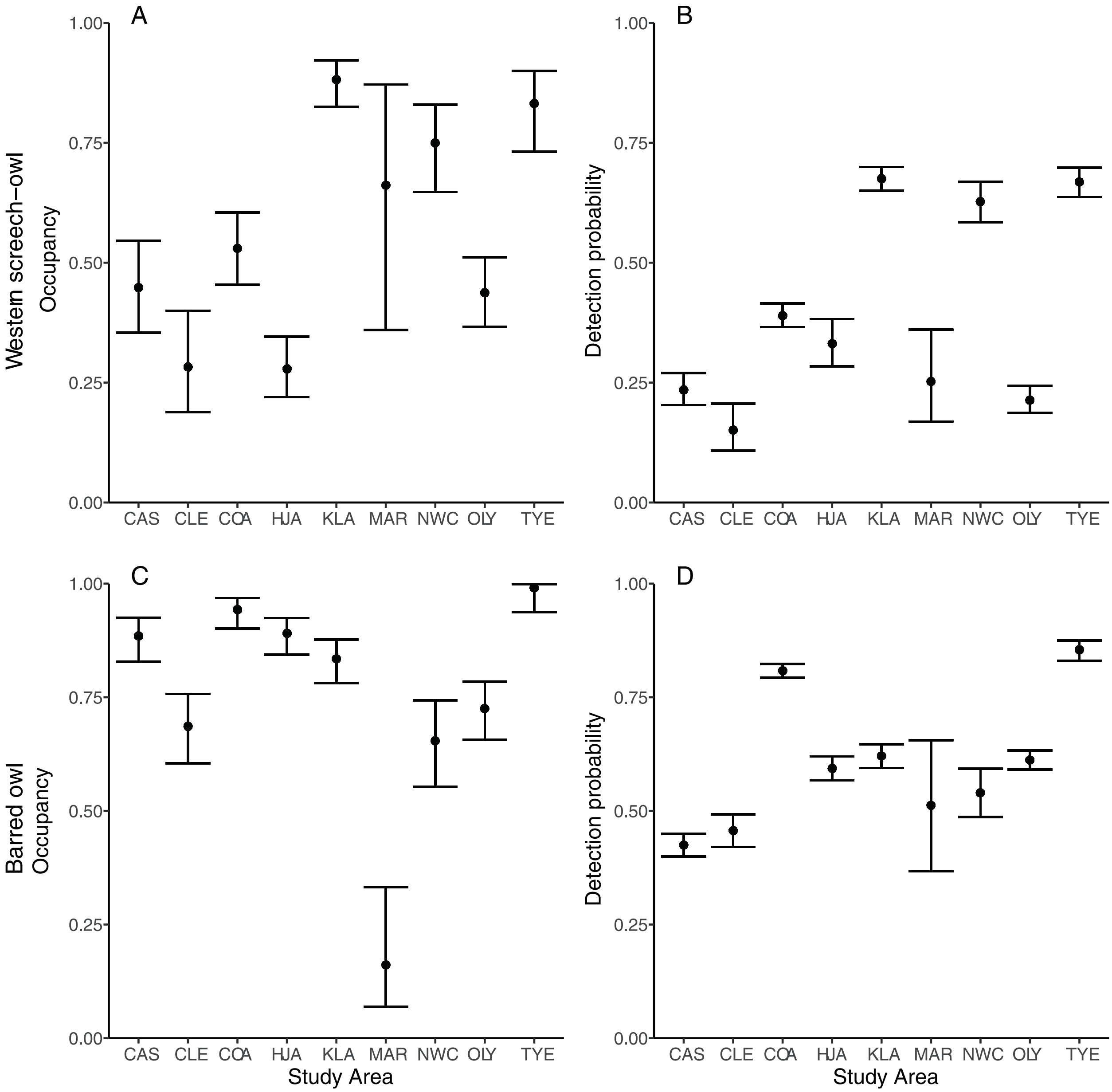

Figure A.1. Predicted occupancy and detection probability estimates relative to study area effect for western screech-owl (*Megascops kennicottii*; A and B, respectively) and barred owl (*Strix varia*; C and D, respectively) calculated using most-supported model structure while holding other covariates at their means. Study area abbreviations: Oregon Cascades (CAS), Cle Elum, WA (CLE), Oregon Coast Range (COA), H. J. Andrews Experimental Forest, OR (HJA), Klamath Mountains, OR (KLA), Marin County, CA (MAR), Olympic Peninsula, WA (OLY), Tyee, OR (TYE). Data collected in 2021 from 2482 stations in the US Pacific Northwest under a broad scale monitoring program (Lesmeister et al., 2022).

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