THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 122, 2020, pp. 1–22
DOI: 10.1093/condor/duaa017

RESEARCH ARTICLE

Passive acoustic monitoring effectively detects Northern Spotted Owls and Barred Owls over a range of forest conditions

Leila S. Duchac,[1,2,*] Damon B. Lesmeister,[1] Katie M. Dugger,[3] Zachary J. Ruff,[1] and Raymond J. Davis[4]

[1] USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA
[2] Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[3] U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[4] USDA Forest Service, Pacific Northwest Region, Corvallis, Oregon, USA
*Corresponding author: leila.duchac@oregonstate.edu

Submission Date: October 10, 2019; Editorial Acceptance Date: March 5, 2020; Published April 27, 2020

ABSTRACT

Passive acoustic monitoring using autonomous recording units (ARUs) is a fast-growing area of wildlife research especially for rare, cryptic species that vocalize. Northern Spotted Owl (*Strix occidentalis caurina*) populations have been monitored since the mid-1980s using mark–recapture methods. To evaluate an alternative survey method, we used ARUs to detect calls of Northern Spotted Owls and Barred Owls (*S. varia*), a congener that has expanded its range into the Pacific Northwest and threatens Northern Spotted Owl persistence. We set ARUs at 30 500-ha hexagons (150 ARU stations) with recent Northern Spotted Owl activity and high Barred Owl density within Northern Spotted Owl demographic study areas in Oregon and Washington, and set ARUs to record continuously each night from March to July, 2017. We reviewed spectrograms (visual representations of sound) and tagged target vocalizations to extract calls from ~160,000 hr of recordings. Even in a study area with low occupancy rates on historical territories (Washington's Olympic Peninsula), the probability of detecting a Northern Spotted Owl when it was present in a hexagon exceeded 0.95 after 3 weeks of recording. Environmental noise, mainly from rain, wind, and streams, decreased detection probabilities for both species over all study areas. Using demographic information about known Northern Spotted Owls, we found that weekly detection probabilities of Northern Spotted Owls were higher when ARUs were closer to known nests and activity centers and when owls were paired, suggesting passive acoustic data alone could help locate Northern Spotted Owl pairs on the landscape. These results demonstrate that ARUs can effectively detect Northern Spotted Owls when they are present, even in a landscape with high Barred Owl density, thereby facilitating the use of passive, occupancy-based study designs to monitor Northern Spotted Owl populations.

Keywords: autonomous recording unit, bioacoustics, detection probability, occupancy models, population monitoring

El monitoreo acústico pasivo detecta eficazmente a *Strix occidentalis caurina* y *S. varia* en un rango de condiciones boscosas

RESUMEN

El monitoreo acústico pasivo usando unidades de grabación autónomas (UGAs) es un área de investigación de vida silvestre en rápido crecimiento, especialmente para especies crípticas raras que vocalizan. Las poblaciones de *Strix occidentalis caurina* han estado monitoreadas desde medidos de los 1980s usando métodos de marcado y recaptura. Para evaluar un método de muestreo alternativo, usamos UGAs para detectar llamadas de *S. o. caurina* y *S. varia*, un congénere que ha expandido su rango hacia el noroeste del Pacífico y amenaza la persistencia de *S. o. caurina*. Establecimos UGAs en 30 hexágonos de 500 ha (150 estaciones UGA) con actividad reciente de *S. o. caurina* y alta densidad de *S. varia* dentro de áreas de estudio de demografía de *S. o. caurina* en Oregón y Washington, y configuramos las UGAs para registrar continuamente cada noche desde marzo a julio de 2017. Revisamos los espectrogramas (representaciones visuales de sonido) y etiquetamos las vocalizaciones de interés para extraer llamados a partir de ~160,000 hr de grabación. Incluso en un área de estudio con bajas tasas de ocupación en territorios históricos (Península Olímpica de Washington), la probabilidad de detectar un individuo de *S. o. caurina* cuando estuvo presente en un hexágono excedió 0.95 luego de 3 semanas de grabación. El ruido ambiental, principalmente de lluvia, viento y arroyos, disminuyó las probabilidades de detección para ambas especies a lo largo de todas las áreas de estudio. Usando información demográfica sobre individuos conocidos de *S. o. caurina*, encontramos que las probabilidades de detección semanales de *S. o. caurina* fueron más altas cuando las UGAs estuvieron más cerca de nidos y centros de actividad conocidos y cuando los búhos estuvieron en pareja, sugiriendo que los datos acústicos pasivos por sí solos podrían ayudar a localizar parejas de *S. o. caurina* en el

Copyright © American Ornithological Society 2020. All rights reserved. For permissions, e-mail: journals.permissions@oup.com.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

paisaje. Estos resultados demuestran que las UGAs pueden detectar eficazmente a *S. o. caurina* cuando está presente, incluso en un paisaje con alta densidad de *S. varia*, facilitando así el uso de diseños de estudio pasivos basados en la ocupación para monitorear las poblaciones de *S. o. caurina*.

Palabras clave: bio-acústica, modelos de ocupación, monitoreo poblacional, probabilidad de detección, unidad de grabación autónoma

INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) is an old forest specialist that was federally listed as threatened under the U.S. Endangered Species Act in 1990 because of the extensive loss of habitat throughout the subspecies' range (United States Fish and Wildlife Service 1990). Subsequently, the Northwest Forest Plan was designed to protect mature and old-growth forest ecosystems on federal lands in the Pacific Northwest while allowing for sustainable use of forest resources (USDA Forest Service and USDOI Bureau of Land Management 1994). Since 1994, when the Northwest Forest Plan was first implemented, the rate of Northern Spotted Owl habitat loss from timber harvest has slowed dramatically on federal lands (Davis et al. 2016). However, Northern Spotted Owl populations continue to decline, partly due to the recent range expansion and subsequent high density of Barred Owls (*S. varia*) throughout the Pacific Northwest (Dugger et al. 2016).

The Barred Owl (*S. varia*) has expanded its range from eastern North America over the past century and now occupies the entire range of the Northern Spotted Owl (Livezey 2009). Barred Owls are slightly larger, and have more generalized diet and habitat requirements (Gutiérrez et al. 2007, Singleton et al. 2010, Dugger et al. 2011), thereby requiring less space (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014) to produce >4 times as many offspring (Wiens et al. 2014) compared with Northern Spotted Owls. The presence of Barred Owls has been associated with declines in Northern Spotted Owl survival, occupancy, breeding propensity, and, to a lesser extent, reproductive success (e.g., Olson et al. 2004, Wiens et al. 2014, Dugger et al. 2016, Mangan et al. 2019, Yackulic et al. 2019).

As part of the Effectiveness Monitoring Program for the Northwest Forest Plan, Northern Spotted Owl demography is monitored on 8 study areas, making up ~8% of the subspecies range and comprised primarily of federal lands in Washington, Oregon, and California (Lint et al. 1999, Dugger et al. 2016). In addition to capturing, marking, and resighting birds, field crews perform callback surveys to locate territorial Northern Spotted Owls and generate data for demographic analyses, including estimates of site occupancy dynamics (Dugger et al. 2016). State and federal agencies, as well as private contractors, also perform similar roadside surveys to meet pre-timber harvest protocols. The Effectiveness Monitoring Program has proven to be highly effective at estimating trends in basic vital rates within study areas as well as identifying drivers associated with those trends (e.g., Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016). However, as Northern Spotted Owl occupancy and detection probabilities have decreased, the costs and effort required by highly trained personnel to locate owls has increased, including the need for increased numbers of nocturnal roadside callback surveys. Several Northern Spotted Owl populations have declined to the level where few individuals occupy and reproduce in the historical territories monitored under the existing program (Dugger et al. 2016). As a result, mark–recapture methods for monitoring Northern Spotted Owls were discontinued in 2019 for Washington's Olympic Peninsula demographic study area.

There are general drawbacks associated with the use of callback surveys for birds, including changes in behavior and decreased overall fitness (Conway and Gibbs 2005). Territorial avian species (e.g., owls, marsh birds, and passerines) often leave their nest sites to approach the broadcast source, potentially exposing themselves and the nest to predation (Haug and Didiuk 1993, Takats et al. 2001, Moulton et al. 2004, Langham et al. 2006, Conway et al. 2008). In addition, since response to these types of surveys is strongest when birds are paired and defending territories, callbacks may be less effective at detecting nonterritorial individuals in a population (e.g., Great Horned Owls [*Bubo virginianus*], Rohner 1997; Eagle Owls [*Bubo bubo*], Martínez and Zuberogoitia 2002). Finally, broadcast surveys are species-specific, and incidental detections of other species during those surveys may not accurately represent the occupancy patterns of those species (e.g., Wiens et al. 2011).

There are additional potential consequences to the use of callback surveys for Northern Spotted Owls because Barred Owls will approach and may react aggressively to the source of a broadcast call, or the responding Northern Spotted Owl (Herter and Hicks 2000, Piorecky and Prescott 2004, Van Lanen et al. 2011, Wiens et al. 2011). As a result, Northern Spotted Owl responses to callbacks in areas where Barred Owls occur could increase the negative interactions between the 2 species (Gutiérrez et al. 2007, Van Lanen et al. 2011). Evaluating alternative survey methods is especially warranted as, in addition to detectability issues associated with declining populations, callback surveys for Northern Spotted Owls place them at increased risk of injury or interference from Barred Owls.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

Both Northern Spotted Owls and Barred Owls use vocalization to establish and defend territories, find mates, and for communication between pairs (Forsman et al. 1984, Odom and Mennill 2010). While they are similar, differences between the Northern Spotted Owl stereotypic 4-note hoot and the Barred Owl 8-note hoot, the most common call types for both species, are sufficient to distinguish the 2 without visual confirmation (Forsman et al. 1984, Odom and Mennill 2010). Both species respond to callback surveys with a variety of vocalizations (Gutiérrez et al. 1995, Wiens et al. 2011), but relatively little is known about the vocal habits of these birds when surveyors are not actively eliciting responses.

Passive acoustic monitoring using autonomous recording units (ARUs) is a fast-growing area of wildlife research (Laiolo 2010, Shonfield and Bayne 2017), and has been especially useful in surveys of species that are rare, nocturnal, occur in remote areas, or are difficult to detect by traditional means (Blumstein et al. 2011, Bayne and Stralberg 2015, Wood et al. 2019a). Much bioacoustic work originated in marine environments and researchers have implemented sophisticated artificial intelligence programs for automated detection in this context (e.g., Bergler et al. 2019, Bermant et al. 2019). However, in recent years researchers have developed similar tools for automated detection of terrestrial mammals and avian species (Stowell et al. 2019, Znidersic et al. 2020). It is now feasible to use automated detection software to efficiently extract detections from large acoustic datasets (Blumstein et al. 2011, Katz et al. 2016, Kahl et al. 2017, Ruff et al. 2019).

Other advantages to using ARUs compared to vocal response (callback) methods for owls include (1) all fieldwork can take place during daylight hours regardless of target species' diel activity patterns; (2) biological training and expertise needed for field crews is usually less than for vocal response surveys, point counts, and demographic studies; and (3) the resulting sound data provide a permanent record of all vocal species at each ARU location, which both allows for verification of species identification by experts, and can provide data on non-focal species for additional analyses. Furthermore, owls and other species are detected at their natural calling locations, rather than at locations where callbacks may have "lured" the animals. This has the potential to bias subsequent analyses if the elicited response to broadcasts moves the target species into atypical habitat.

ARUs have been used to monitor Northern Spotted Owls and other forest owls (Rognan et al. 2012, Whyte et al. 2015), and similar work exists for California Spotted Owls (*S. occidentalis occidentalis*; Wood et al. 2019b), but no studies have explored the spatio-temporal effort required to achieve precise detection probability estimates suitable for monitoring Northern Spotted Owls at the landscape scale. Here, we evaluated the effectiveness of passive acoustic surveys using ARUs to detect Northern Spotted and Barred Owls and to quantify factors influencing detection probabilities at 2 spatial scales: the area around each ARU station, and the broader 500-ha survey hexagon. We expected Northern Spotted Owl detection probabilities to decrease as distance from known nesting locations or activity centers increased, as relative probability of use appears to follow this same pattern (Wiens et al. 2014). Northern Spotted Owl response rates to callback surveys appear to decrease when Barred Owls are present, so we expected their detection probabilities to decrease when Barred Owls were detected (e.g., Olson et al. 2005, Crozier et al. 2006, Kroll et al. 2010, Dugger et al. 2011, 2016). We predicted that detection probabilities would decrease with increased background noise from streams, wind, and rain, as these factors decrease the range at which sounds are clearly audible and may also affect calling behavior (Kriebel 1972, Forsman 1983, Digby et al. 2013, Shonfield and Bayne 2017, Yip et al. 2017a). Dense vegetation and rugged terrain act as barriers to sound transmission, so we predicted that detection probabilities would differ between study areas due to variation in these conditions (Rasmussen 1985, Albert 2004, Peng et al. 2014). We also predicted higher detection probabilities from locations on upper slopes and ridgetops with fewer obstructions to sound travel. We evaluated these influences to inform potential design of effective passive monitoring schemes using ARUs to detect Northern Spotted Owls.

METHODS

Study Area

We conducted this study in western Oregon and Washington on lands under federal ownership administered by the U.S. Forest Service, the U.S. Bureau of Land Management, and National Park Service, which make up a portion of the lands surveyed as part of the Northern Spotted Owl Effectiveness Monitoring Program under the Northwest Forest Plan (Lint et al. 1999). The 3 Northern Spotted Owl demography study areas chosen for our study include the Klamath (KLA), Oregon Coast Range (COA), and Olympic Peninsula (OLY) (Figure 1). All 3 of these study areas have been included in the numerous meta-analyses conducted to understand the status and trends of Northern Spotted Owl populations across the subspecies' range (e.g., Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016). These 3 study areas represent a range of population conditions for Northern Spotted Owl populations; populations in KLA have been relatively stable, COA population estimates are steadily declining, and OLY has few remaining owls and a low probability of population persistence (Dugger et al. 2016, Yackulic et al. 2019).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

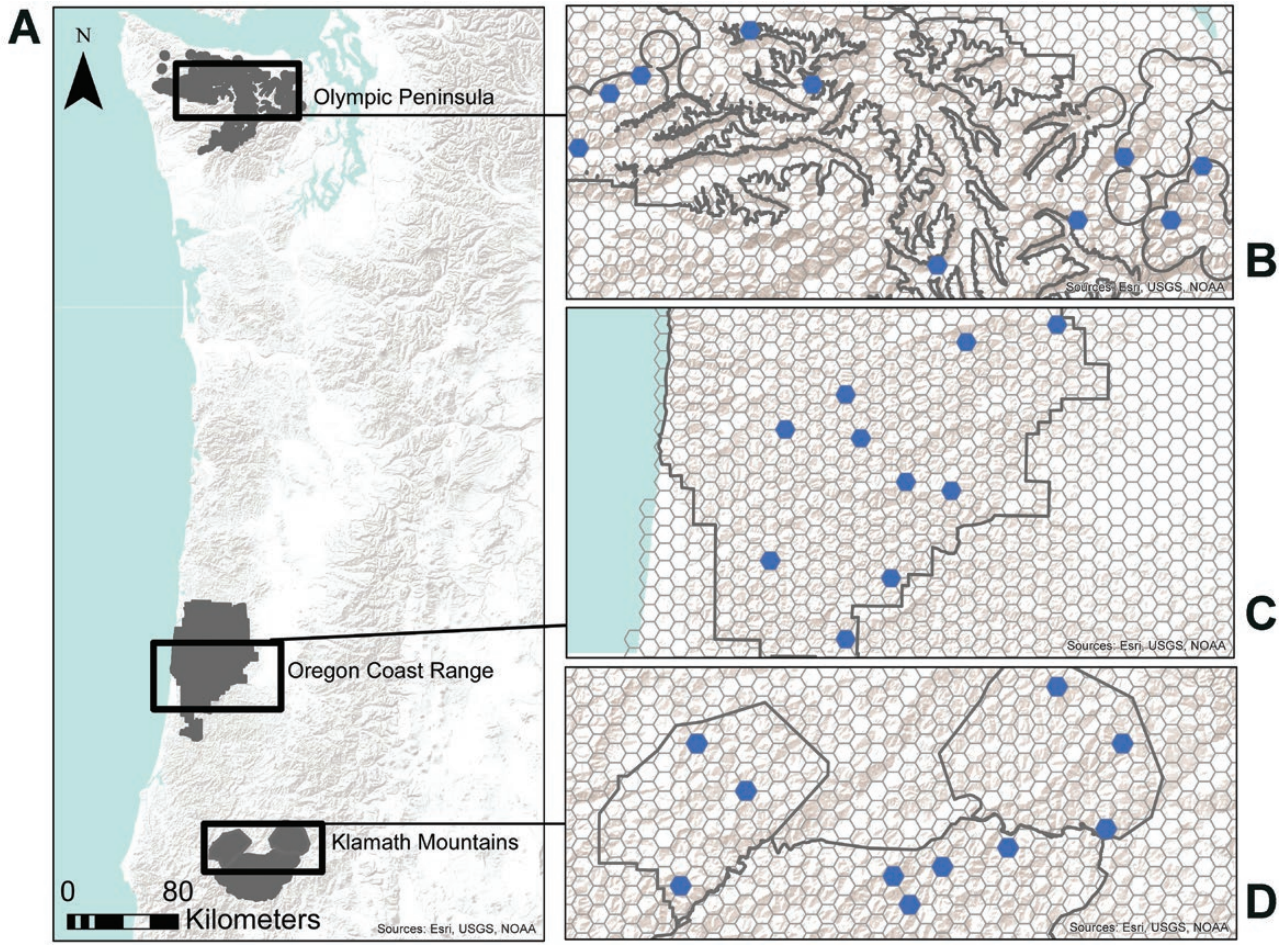

FIGURE 1. (**A**) At left, map showing 3 study areas (in dark gray) in Oregon and Washington, USA, where Northern Spotted Owl populations have been monitored since ~1990 and where 150 autonomous recording units were deployed in 2017 to survey for Northern Spotted Owls and Barred Owls. Locations of 500-ha hexagon grids with 10 hexagons surveyed at each study area highlighted in blue for (top to bottom) (**B**) Klamath Mountains, (**C**) Oregon Coast Range, and (**D**) Olympic Peninsula.

All lands within OLY that were monitored for Northern Spotted Owls were federally administered and characterized by contiguous forested landscapes (Forsman et al. 2011). The forests were primarily comprised of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*) (Forsman et al. 2011). Over 60% of the landscape is covered by mature and old-growth (over 200 yr old) forest with large trees and multilayered canopies (Forsman et al. 2011). Elevations in this area extend up to timberline, above 1,500 m (Dugger et al. 2016). Climate in this region is wet, especially on the western side of the study area where annual precipitation averages 300 cm yr^{-1} (Western Regional Climate Center 2018, wrcc.dri.edu), with much of the winter precipitation occurring as snow at higher elevations (Forsman et al. 2011). Precipitation on the eastern side of OLY is much more moderate (average = 140 cm; Western Regional Climate Center 2018).

COA and KLA comprise mountainous regions of western Oregon with elevations below 1,250 m (Forsman et al. 2011). COA forests are dominated by Sitka spruce, Douglas fir, and western hemlock (Franklin and Dyrness 1973), while KLA forests are made up of a diverse mixture of conifers and hardwoods (see Forsman et al. 2011 for details). Climate is generally warmer in KLA than COA, but both are warm and dry during summer, and cool and wet during winter, with most annual precipitation (~219 cm in COA; ~120 cm in KLA) falling as rain (Forsman et al. 2011). A patchwork matrix of federal, state, and private land ownership in both Oregon study areas results in more forest fragmentation due to private timber harvest and agriculture compared with OLY (Forsman et al. 2011).

Sampling Design and Acoustic Data Collection

We used Wildlife Acoustics Song Meter 4s (SM4; Wildlife Acoustics 2018) to collect acoustic data because they are portable, weatherproof, and easily programmable with 2

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

built-in microphones, a large memory capacity, and ~350-hr battery life. SM4 SMM-A2 internal microphones have a signal-to-noise ratio of ~80 dB and record sound between 20 Hz and 48 kHz at decibel levels of approximately −33.5 to 122 dB (Wildlife Acoustics 2018), while human hearing ranges from ~20 Hz to 20 kHz between ~0 and 100 dB (Goldstein 2010). While factors like internal microphone noise can affect the listening ability of some ARUs, Song Meter SM3s and SM4s "hear" nearly as well as human listeners in field tests of listening distance and have returned similar results in other comparative analyses (Shonfield and Bayne 2017, Yip et al. 2017b). Both models of ARU have been widely used to monitor a range of amphibian, avian, and mammalian species (Zwart et al. 2014, Sidie-Slettedahl et al. 2015, Kalan et al. 2016, Courtois et al. 2016, Ross et al. 2017).

Our ARU monitoring sites consisted of 500-ha hexagons. This hexagon size corresponds to the mean home range size reported for Barred Owls in the Pacific Northwest (Hamer et al. 2007, Singleton et al. 2010). This is smaller than a Northern Spotted Owl home range, but larger than a territory core area around a primary activity center or nest tree (Glenn et al. 2004, Schilling et al. 2013). Thus, 500-ha hexagons reflect ecologically relevant space use by both Northern Spotted Owls and Barred Owls during the breeding season. Because Northern Spotted Owls and Barred Owl territories were likely to overlap more than one hexagon, we did not survey adjacent hexagons to minimize the probability of detecting the same owl in multiple hexagons during the same breeding season.

Using nesting and activity center data from the 2012–2016 survey seasons of the Northern Spotted Owl demographic studies, we identified 10 hexagons in each study area with documented Northern Spotted Owl activity in the previous year. Within each hexagon we randomly selected 5 locations to deploy ARUs with a rule set as follows: stations were (1) on federal land, (2) ≥500 m apart, (3) ≥200 m from the hexagon's edge, and (4) on mid- and upper-slopes (Figure 1B–D). To classify slope position and avoid placing ARUs in lower-slope areas, we separated a 450 m-resolution Topographic Position Index (TPI) layer in ArcMap version 10.3.1 (Esri 2015) into 3 classes and eliminated points in the lowest class from consideration. This index is calculated as the difference in elevation of the point compared with the mean elevation within a 450 m radius (Glenn et al. 2017). Negative index values represent lower-slope locations, and positive values indicate higher slope (nearer to ridgetops). We calculated these classes separately for each study area; TPI values for the lower-slope class ranged from −203 to −28 m in KLA, from −235 to −24 m in COA, and from −349 to −27 m in OLY. The combined mid- and upper-slope class ranged from −28 to 251 m, −24 to 234 m, and from −27 to 470 m in KLA, COA, and OLY, respectively. While both species of owls could potentially vocalize in the lower-slope areas, deploying ARUs on mid-slopes and ridgetops reduced stream noise that could interfere with the recordings and likely increased listening radii compared with lower-slope locations. We determined that these benefits outweighed any risk of missing occasional low-slope vocalizations from either species. The 200 m buffer around the edge of the hexagon ensured that the vocalizations recorded primarily came from within the hexagon, rather than from the area outside the hexagon's edge.

We conducted ARU surveys between mid-March to late July, 2017, and scheduled recordings to occur nightly beginning 1 hr before sunset and ending 2 hr after sunrise. ARUs recorded at a sample rate of 32 kHz, allowing us to detect sounds in the frequency range of 0–16 kHz. We mounted ARUs ~1.5 m above the ground on small trees with diameter ~15–20 cm, which allowed microphones to extend past the bole for unobstructed recording ability. If the random point fell within 50 m from roads, trails, or streams, we moved the station >50 m from those sources of potential vandalism or excessive noise. Each ARU held one 512 GB SD memory card and 4 D-cell batteries, which powered the ARUs for ~350 hr of recording. We visited ARUs every 4 weeks for battery and SD card replacement.

Modeling Covariates

We used a suite of site- and survey-level covariates derived from field observations, remotely sensed data, and Northern Spotted Owl demographic surveys to model landscape use and detection probability of Spotted and Barred Owls (Table 1). Site-level covariates derived from remotely sensed data in ArcMap included terrain ruggedness (RUGGED), and topographic position (TOPO). Terrain ruggedness was the standard deviation of the mean elevation within a hexagon, calculated using the values from a 30 m-resolution Digital Elevation Model and the Zonal Statistics tool in ArcMap. Topographic position was a continuous variable of relative position on the slope for each ARU extracted from the 450 m-resolution TPI raster described above (Glenn et al. 2017). We also calculated distance in meters to the nearest stream from each ARU station using ArcMap's Euclidean Distance tool. From field observations, we created a binary covariate to indicate whether consistent noise from a road (ROAD) was audible from the ARU station and created a categorical AREA covariate with 3 study areas (COA, KLA, and OLY).

We compiled mean weekly precipitation (PRECIP) in millimeters for each hexagon and ARU station from daily PRISM precipitation data, which are generated using a combination of modeling and interpolation methods (Daly et al. 2008) and are available nationally at 63-ha resolution (Prism Climate Group 2019, prismclimate.org). We summarized mean weekly temperature data (TEMP) from HOBO data loggers (HOBOWare 2017) that we deployed

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

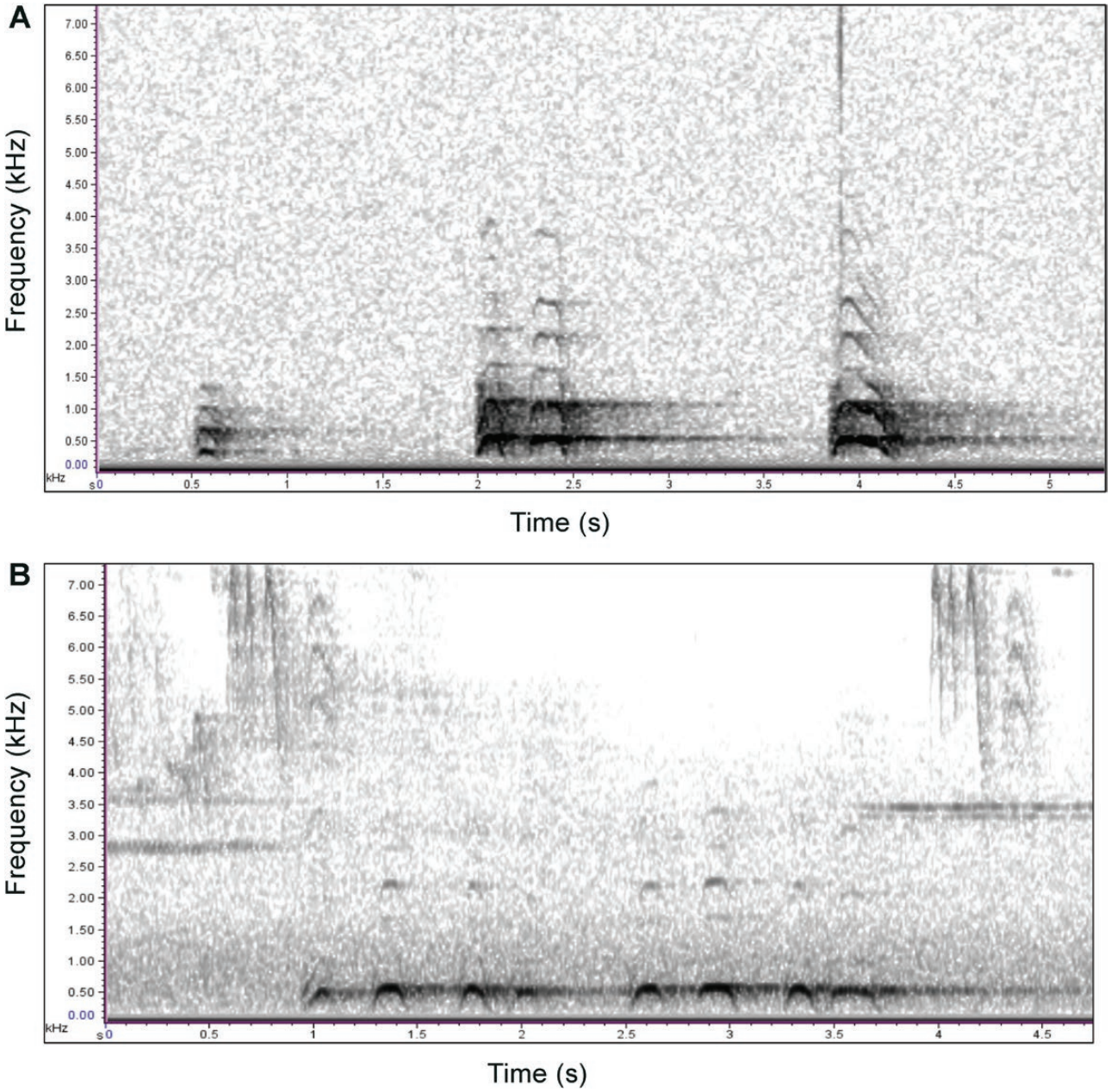

FIGURE 2. A visual representation (spectrogram) of (**A**) Northern Spotted Owl 4-note call, recorded in the Klamath Mountains study area, and (**B**) Barred Owl 8-note call, recorded in the Olympic Peninsula study area. The *x*-axis represents time in seconds, *y*-axis shows frequency (0–5.5 kHz), and darkness of color indicates amplitude (volume) of sound.

at the ARU station nearest to the center of each hexagon. HOBO loggers collected temperature data every 2 hr over the survey season.

We used Kaleidoscope Pro version 4.5.4 software's noise analysis feature (Wildlife Acoustics 2019) to estimate weekly background noise levels (NOISE) directly from recordings at each ARU station. Noise analysis reports mean decibel levels in decibels below full scale (dBFS) within a selected frequency range (here, 220–1,200 Hz; range of owl vocalizations) for each hour of recording. In dBFS, 0 is the maximum possible digital level, and as such all decibel levels are negative on this scale (Wildlife Acoustics 2019). We calculated daily mean NOISE, then averaged those weekly for each station. Finally, we used a temporal covariate (WEEK) to model weekly detection probability through the season.

Regular callback surveys for Barred Owls were conducted on COA and KLA as part of another study during 2017 (Wiens et al. 2018). A review of our acoustic dataset after it was collected revealed that Barred Owl survey

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

TABLE 1. Site- and survey-specific covariates for autonomous recording unit (ARU) stations and hexagons, to model detection probabilities using data from ARUs in 3 Northern Spotted Owl demographic study areas for the 2017 breeding season.

Variable	Description	Site or survey var.
area	Categorical variable of 3 demographic study areas.	Site
Rugged	Terrain ruggedness; standard deviation of elevation in the area within each hexagon. Derived from GIS data.[a]	Site
road	Binary, 1 if road noise is audible from ARU station—recorded in field upon deployment.	Site
Topo	Topographic position within 450 m radius; continuous variable of relative position on slope, with the mid-slope as zero, upper slope values positive, and lower-slope values negative. Derived from GIS data.	Site
stream	Distance in meters from ARU station to nearest stream or river—derived from GIS.	Site
NSO-loc	Distance in meters from ARU station to the nearest 2017 Northern Spotted Owl nest location (if nesting) or estimated activity center (if not nesting)—from demographic study survey data.	Site
NSO-nest	Distance in meters from ARU station to nearest known 2017 Northern Spotted Owl nest location—from demographic study survey data.	Site
nso-hex	Binary, 1 if nearest known Northern Spotted Owl location was within survey hexagon, 0 otherwise.	Site
NSO-pair-ST	Pair status from demographic surveys of Northern Spotted Owl territories—assigned from territory that overlapped each survey station: No Owl Detected, Single Owl, Non-nesting Pair, Nesting Pair.	Site
NSO-PAIR-HEX	Pair status from demographic surveys of Northern Spotted Owl territories—if survey hexagon overlapped multiple territories, assigned as highest status from overlapping territories: No Owls Detected, Single Owl Detected, Non-nesting Pair Detected, Nesting Pair Detected.	Site
noise	Measure of average weekly background noise in decibels below full scale (dBFS, 0 is maximum possible digital volume) from each ARU station between 220 Hz and 1,200 Hz. Calculated by Kaleidoscope Pro software.	Survey
Temp	Hexagon-scale temperature data in Celsius (°C) collected every 2 hr by HOBO data loggers deployed on the ARU nearest to center of each hexagon, averaged weekly.	Survey
week	Numbered week of the survey season (1–18).	Survey
Precip	Daily precipitation in millimeters derived from PRISM climate data (PRISM Climate Group 2018, prismclimate.org) averaged weekly per hexagon. PRISM precipitation data are reported in a grid with units of 0.63 km^2 or 63 ha. Approximately 14 PRISM grid cells fall fully or partly within each 500-ha hexagon.	Survey
BO-hex	Binary: 0 = no Barred Owl broadcast surveys within ARU hexagon in survey week, 1 = 1 or more Barred Owl broadcast surveys within hexagon.	Survey
BO-adj	Count of Barred Owl broadcast surveys in 6 hexagons adjacent to ARU hexagon in a survey week.	Survey
BO-any	Binary: 0 = no Barred Owl broadcast surveys in ARU survey hexagon or 6 adjacent hexagons within survey week, 1 = 1 or more Barred Owl surveys.	Survey

[a] GIS = Geographic Information Science. We used ArcMap version 10.3.1 (Esri 2015) to access GIS data and build covariates.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

broadcasts were detected several kilometers away and could potentially affect owl vocalization behavior in adjacent hexagons. Thus, using information provided by these other researchers (K. Dilione personal communication), we quantified the weekly intensity of Barred Owl broadcast surveys at each hexagon using 3 survey-level covariates. BO-INHEX was a binary covariate; 1 indicated that one or more Barred Owl surveys were performed within the survey hexagon in a week, and 0 indicated no survey occurred. BO-ADJ was the total number of Barred Owl surveys that occurred in the adjacent 6 hexagons to the survey hexagon within the week. BO-ANY was binary, indicating whether one or more Barred Owl surveys had occurred in the survey hexagon or any of the 6 adjacent hexagons.

We summarized seasonal data from 2017 Northern Spotted Owl demographic surveys (included nighttime callbacks and daytime walk-ins to identify marked individuals) in the 3 study areas to create 5 ARU station- and hexagon-scale covariates. The first 3 addressed locations of known Northern Spotted Owls during the survey season: (1) NSO-LOC, distance in meters from each ARU station to the nearest known activity center or nest; (2) NSO-NEST, distance in meters from each ARU station to the nearest known nest location; and (3) NSO-HEX, a binary covariate at the hexagon scale with 1 indicating that the nearest known activity center was within the survey hexagon, and 0 indicating that the activity center was outside the hexagon. We included both NSO-LOC and NSO-NEST to clarify whether detection probability depended on proximity to any Northern Spotted Owl regardless of nesting status (NSO-LOC), or if only distance from nesting pairs (NSO-NEST) affected the probability of detection. The final 2 covariates were the status of known Northern Spotted Owls from data collected by demography field crews: (4) NSO-PAIR-ST, a categorical covariate indicating known status in the territory overlapping the ARU station: no owl detected (used as the reference in this analysis), single owl, non-nesting pair, or nesting pair; and (5) NSO-PAIR-HEX, derived as described for NSO-PAIR-ST, but summarized at the hexagon scale by applying the highest status of any territory that overlapped the survey hexagon.

Sound Processing

We processed sound files for the calls of both owl species using the *simple clustering* feature of Kaleidoscope Pro software, which uses a hidden Markov model to categorize sound clips into "clusters" based on similar characteristics, without targeting any particular type of sound or vocalization (Wildlife Acoustics 2019). Using a fast Fourier-transform, Kaleidoscope displays the sound clips as spectrograms (Figure 2A,B) that are visually scanned for relevant content; this allows for much more rapid tagging of clips than would be possible by listening to each sound file.

We set the signal parameters for clustering in Kaleidoscope Pro as follows: we restricted the frequency range to 0–1,200 Hz, as this is the range of most Barred and Northern Spotted Owl vocalizations. We set the range for sound clip length to 0.5–7.5 s to capture both short and longer vocalizations from the 2 owl species. We set the inter-syllable gap (breaks between notes of a single call) to 2 s to prevent, for example, a 4-note Northern Spotted Owl hoot generating 4 separate clips. Cluster Analysis settings were left at the default values: maximum distance from center of cluster to be included in cluster = 1.0, maximum number of states = 12, maximum distance to cluster center for building clusters = 0.5, maximum number of clusters = 500. Next, we manually scanned through all cluster output and tagged all vocalizations (typical 4- and 8-note hoots as well as other positively identifiable calls) from either a Barred Owl or Northern Spotted Owl. Finally, we rechecked our tagged output to exclude or correct any mistagged clips. We summarized those final tagged clips into the encounter histories we used for further analyses.

In all 3 study areas, we identified Northern Spotted Owl vocalizations that overlapped with known demographic survey occasions and manually eliminated vocalizations that were non-authentic (broadcasts from electronic callers, human-voice imitations). By contrast, we removed all Barred Owl detections (authentic and non-authentic) from the acoustic dataset that overlapped spatially and temporally with Barred Owl surveys. These broadcast events were more frequent, longer in duration, and generally played at a higher volume compared with those in Northern Spotted Owl surveys, and, as a result, identification and removal of non-authentic Barred Owl vocalizations while leaving authentic responses would have been time-consuming and logistically unfeasible. Considering the frequency of true Barred Owl vocalizations detected by the ARUs each week, we deemed insignificant any potential loss of true Barred Owl vocalizations associated with this filtering related to Barred Owl callback surveys.

Data Analyses

We used single-season, single-species occupancy models with the logit link (MacKenzie et al. 2018) to identify factors affecting detection probability (p) for Northern Spotted Owls and Barred Owls independently, and the probability of use (ψ) for Barred Owls. Here, we defined ψ as probability of use, the probability that at least one owl used the area around an ARU station or the area within a hexagon during the survey season. We defined p as the probability of detecting an owl within a survey period if at least one owl used that survey site (MacKenzie et al. 2018). Due to the non-random selection of hexagons in this study, Northern Spotted Owl estimates of ψ are not informative. We focused on modeling p for Northern Spotted Owls and used either the null model (.) or a study area model

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

(AREA) for ψ, depending on which had more support. For Barred Owl analyses, we determined that modeling ψ was unbiased as we based our non-random hexagon selection only on Northern Spotted Owl demographic information, not on any prior knowledge of Barred Owls in these areas.

We z-transformed all continuous covariates to improve model convergence and make model coefficients for all covariates comparable. Before building a priori model sets, we checked for correlation between covariates using the *corrplot* package in R (R Core Team 2018). We did not combine covariates in models if correlation exceeded 0.60. For all models, we generated output and model selection results using the *RPresence* package (R Core Team 2018). We considered 1 week of acoustic data as a survey occasion in all models. We chose this time scale to increase the number of survey occasions and thus identify changes in detection probability through the season, but balance this with maintaining a reasonable probability of detecting an owl if it was present within a survey period. With a rare species such as Northern Spotted Owls and a much shorter survey period (e.g., a single day), detection probability during each survey may have been ~0, which could lead to issues with model estimates (MacKenzie and Royle 2005, Hamel et al. 2012). For Barred Owls, we fit models at the scale of the ARU station (n = 150), and for Northern Spotted Owls, we fit separate models at the scale of the ARU station as well as hexagon (n = 30; i.e. clusters of 5 stations) to examine the relationship between p at the station and hexagon scales.

We used a single-season, co-occurrence occupancy model with the logit link (MacKenzie et al. 2018) for Northern Spotted Owls and Barred Owls to estimate p for each species relative to the presence and detection probability of the other species. In this analysis, we considered each ARU station to be a sampling unit (n = 150), and the model parameterization that estimates conditional ψ and p for a dominant species, Species A (Barred Owls, referred to in these models as BO), and a subordinate species, Species B (Northern Spotted Owls, NSO in models) following Richmond et al. (2010). The conditional estimates of ψ from this model are as follows: probability of use by Barred Owls (ψ_{BO}), probability of use by Northern Spotted Owls if Barred Owls are not present ($\psi_{NSO|bo}$), and probability of use by Northern Spotted Owls if Barred Owls are present ($\psi_{NSO|BO}$). As in the single-species models discussed above, estimates of ψ for Northern Spotted Owls in these models are uninformative given hexagons were chosen based on known recent Northern Spotted Owl activity. This model also estimates 5 different conditional detection probabilities: (1) p_{BO} and (2) p_{NSO}, species-specific detection probability when each species is the only species present at a sample location; (3) r_{BO}, Barred Owl detection probability if Northern Spotted Owls are also present at a location; (4) $r_{NSO|bo}$, Northern Spotted Owl detection probability if Barred Owls are present at a location but not detected during a survey week; and (5) $r_{NSO|BO}$, Northern Spotted Owl detection probability if Barred Owls are present at a location and also detected during a survey week. The basic structure of this co-occurrence model allows detection probability to vary between species (SP), and based on occurrence (INT_OCC) and detection (INT_DET) of the other species. We estimated rho (ρ), a detection interaction factor, to quantify if Northern Spotted Owl detections were dependent on the detection of Barred Owls. Thus, $\rho > 1$ indicates that weekly detection probabilities of Northern Spotted Owls are higher when Barred Owls are also detected in the same survey.

We used an information-theoretic approach to evaluate a priori model sets that included models containing the factors hypothesized to affect probability of detection (table 2.1 in Burnham and Anderson 2002) for each of our analyses, and those affecting use for Barred Owls. We ranked models in our a priori model set using Akaike's information criterion corrected for small sample size (AIC_c), and evaluated model support using differences between model AIC_c and the model with the lowest AIC_c (ΔAIC_c) and Akaike's model weights (w_i) (Burnham and Anderson 2002). We examined 95% confidence intervals (CIs) on coefficients in competitive models to evaluate the strength of evidence for specific covariate effects (Forsman et al. 2011, Dugger et al. 2016). We considered covariates with coefficient CIs that did not overlap zero to have the strongest support, while those with CIs that slightly overlapped zero (<10%) were considered to have weaker support, and those coefficients with CIs that widely overlapped were considered to have no support (e.g., Forsman et al. 2011, Dugger et al. 2016).

For Northern Spotted Owls we identified the best performing models under 2 separate criteria: (1) including covariates with information provided by overlapping demographic surveys of Northern Spotted Owls regarding Northern Spotted Owl location and status within the hexagon (no owl detected, single owl, non-nesting pair, nesting pair), and (2) a model set without this external knowledge. Taking advantage of known Northern Spotted Owl demographic information could reveal insights about underlying ecological processes or owl behavior, but it may obscure the effects of environmental covariates on p that would inform ARU deployment design in areas where demographic information was not available.

RESULTS

We collected a total of 161,448 hr of recordings from 150 ARU stations over 18 survey weeks from March 20, 2017 to July 23, 2017. We detected 19,713 Northern Spotted Owl vocalizations with the highest number from KLA

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

(n = 15,712), followed by COA (n = 3,414), and then OLY (n = 587). We documented more Barred Owl vocalizations (n = 67,264), and the highest number were detected on COA (n = 46,307), followed by KLA (n = 13,772), and then OLY (n = 7,185). We detected Northern Spotted Owls at 50% (n = 75) of all ARU stations and within 87% (n = 26) of all hexagons. Barred Owls were detected at 82% (n = 123) of ARU stations and 93% (n = 28) of hexagons. At the station-scale, mean latency (number of recording weeks prior to first detection) for Northern Spotted Owls was 4.3 weeks (range: 0–14 weeks, 0.50 standard error [SE]), and for Barred Owls was 2.3 weeks (range: 0–13 weeks, 0.25 SE). We did not detect strong increasing or decreasing trends in detection probability through the March–July survey season for either species. Weekly detection histories for Barred Owls varied among ARU stations, but when summarizing encounter histories at the hexagon scale (i.e. if a Barred Owl was detected at ≥1 of the hexagon's 5 ARU stations within a survey week, the hexagon received a "1" for that week), we detected Barred Owl vocalizations too frequently (mean = 84% of survey weeks) to effectively model detection probability for this species at the hexagon scale (i.e. the weekly probability of detection was functionally ~1.0). As a result, we only modeled Barred Owl use and probability of detection at the ARU-station scale.

Single-Species Probability of Detection

Weekly probability of detection (with 95% CIs) at the station-scale for Northern Spotted Owls was highest in KLA (0.463, CI: 0.423–0.503) followed by COA (0.270, CI: 0.229–0.316) and OLY (0.257, CI: 0.178–0.257); whereas for Barred Owls the probability of detection was highest in COA (0.722, CI: 0.689–0.754) followed by KLA (0.565, CI: 0.528–0.602) and OLY (0.397, CI: 0.344–0.452). With 5 ARUs per hexagon and an average of 11 weeks of deployment in this study season, the estimated probability of detecting either Northern Spotted Owls or Barred Owls at least one time over the entire season (Mackenzie et al. 2018) when they were present within a hexagon approached 1.0 on all 3 study areas. Using the simple AREA model (detection probability does not vary between ARUs within a hexagon) and reducing to a 4-ARU design for sampling a hexagon, seasonal probability of detection at the hexagon scale exceeded 0.95 for Northern Spotted Owls within 2 weeks of surveys at KLA and 3 weeks of surveys at COA and OLY. Barred Owl seasonal probability of detection using 4-ARU design exceeded 0.95 for all study areas within 1–2 weeks.

The best performing station-scale Northern Spotted Owl probability of detection model was additive with NOISE and NSO-LOC (Table 2; Appendix Table 3A), with detection probability decreasing with increasing distance to a Northern Spotted Owl activity center (NSO-LOC; $\wedge\beta = -1.151$; CI: –1.422 to –0.880) and increasing background noise (NOISE; $\wedge\beta = -0.727$; CI: –0.887 to –0.568; Figure 3A). Excluding demographic knowledge of Northern Spotted Owl activity, the most supported probability of detection model included an additive relationship between NOISE ($\wedge\beta = 1.055$; CI: –1.196 to –0.914) and topographic position on slope (TOPO; $\wedge\beta = 0.109$, CI: –0.014 to 0.232; Appendix Table 3B). In single-species station-scale Barred Owl models, probability of detection differed by AREA (highest in COA, similar in KLA and OLY) and was inversely related to NOISE ($\wedge\beta = -1.158$, CI: –1.311 to –1.005; Figure 3B; Table 2; Appendix Table 4).

Using knowledge from the concurrent Northern Spotted Owl demographic study in hexagon-scale models (Appendix Table 5), we found that Northern Spotted Owl detection probability decreased as noise increased ($\wedge\beta = -1.108$, CI: –1.410 to –0.804), and differed relative to pair status (NSO-PAIR; Figure 4; Appendix Table 5A). There was little support for a difference in effect between probability of detection at sites where demographic surveys detected a single owl (Single owl; $\wedge\beta = 0.390$, CI: –1.150–1.930) compared with the reference, No Owl Detected (sites where demographic surveys did not detect any Northern Spotted Owls but, in some cases, ARUs did detect owls; $\wedge\beta = -2.862$, CI: –3.894 to –1.830). By contrast, there was a strong positive effect of similar magnitude on detection probability at sites with non-nesting territorial pairs (Non-nesting pair; $\wedge\beta = 4.037$, CI: 3.010–5.154), and known nesting pairs of Northern Spotted Owls (Nesting pair; $\wedge\beta = 3.474$, CI: 2.368–4.581; Figure 4) compared with the reference (No Owl Detected). Without including the information from demography crews, the most-supported probability of detection model at the hexagon scale for Northern Spotted Owls had additive effects of NOISE ($\wedge\beta = -1.108$, CI: –1.410 to –0.804) and AREA with p on KLA > COA > OLY (Table 2; Appendix Table 5B).

Barred Owl Landscape Use

The most-supported model for Barred Owl landscape use included only the negative effect of rugged terrain, with a maximum estimate of probability of use of 0.973 (CI: 0.931–0.990) at the hexagon with the least rugged terrain, and a minimum estimate of 0.133 (CI: 0.0381–0.371) in the most rugged hexagon. The second most-supported model ($\Delta AIC_c = 3.16$) for Barred Owl landscape use included both RUGGED and differences by AREA, with estimated probability of use when RUGGED was held at the mean varying from the highest use on COA, followed by KLA, and lowest use at OLY ($\wedge\psi_{COA} = 0.958$, CI: 0.748–0.994; $\wedge\psi_{KLA} = 0.911$, CI: 0.761–0.971; $\wedge\psi_{OLY} = 0.850$, CI: 0.638–0.948).

Detection Probability, 2-Species Co-occurrence

The 2-species co-occurrence model of detection probability that was most supported included the interaction between species (SP) and NOISE, such that p_{BO} and p_{NSO}

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

TABLE 2. Model coefficients ($\wedge\beta$) and upper and lower 95% confidence limits (UCL; LCL) from the most-supported model estimating the probability of detection from autonomous recording unit (ARU) data for Northern Spotted Owls or Barred Owls on 3 study areas in Washington (Olympic [OLY]), and Oregon (Coast Ranges [COA]; Klamath [KLA]) during 2017. See full model sets in Appendix Tables 3–6. At the ARU and hexagon scales, Northern Spotted Owl results show first the most-supported model using location and pair status information from concurrent Northern Spotted Owl demographic surveys (NSO Information), then the most-supported model without this additional information (No NSO Information).

Model set	Model structure	Covariate [a]	($\wedge\beta$)	UCL	LCL
Northern Spotted Owl: Station-Scale (NSO Information)	NOISE + NSO-LOC	NOISE	–0.731	–0.571	–0.890
		NSO-LOC	–1.147	–0.883	–1.410
Northern Spotted Owl: Station-Scale (No NSO Information)	NOISE + TOPO	NOISE	–1.055	–0.914	–1.195
		TOPO	0.109	0.233	–0.015
Northern Spotted Owl: Hexagon-Scale (NSO Information)	NSO-PAIR-HEX + NOISE	No Owl Detected [e]	–2.862	–1.830	–3.894
		Single Owl	0.390	1.930	–1.150
		Non-nesting Pair	4.037	5.154	3.010
		Nesting Pair	3.474	4.581	2.368
		NOISE	–1.108	–0.804	–1.410
Northern Spotted Owl: Hexagon-Scale (No NSO Information)	AREA + NOISE	AREA-COA [e]	–0.222	0.123	–0.567
		AREA-KLA	1.441	1.969	0.913
		AREA-OLY	–0.528	0.127	–1.183
		NOISE	–0.457	–0.159	–0.754
Barred Owl: Station-Scale [b]	AREA + NOISE	AREA-COA [e]	0.920	1.094	0.746
		AREA-KLA	–1.229	–0.974	–1.485
		AREA-OLY	–1.087	–0.781	–1.392
		NOISE	–1.158	–1.005	–1.311
Two-Species Co-occurrence: Station-Scale	SP + INT_OCC + INT_DET + SP * INT_OCC + NOISE +	p_{BO} [d]	0.286	0.469	0.103
	SP * NOISE [c]	p_{NSO}	0.239	1.219	–0.741
		r_{BO}	–0.135	0.130	–0.400
		$r_{NSO\|BO}$	-1.141	-0.165	-2.117
		$r_{NSO\|bo}$	-0.411	-0.103	-0.719
		$NOISE_{BO}$	-1.097	-0.949	-1.245
		$NOISE_{NSO}$	0.384	0.615	0.153

[a] See Table 1 for descriptions of environmental covariates included in models.
[b] Most-supported model included covariate to model use (ψ), full model structure: ψ_{RUGGED}, $p_{AREA + NOISE. RUGGED}$, β: –1.379, CI: –1.933 to –0.824.
[c] Co-occurrence model structure: SP: allows occupancy and detection probability to differ between species; INT: allows for interactive effect of occupancy by one species on occupancy of the other species; INT_OCC: detection interaction between species depending on presence of other species; INT_DET: detection interaction between species depending on detection of other species.
[d] Beta estimates refer to each other as such: p_{BO} first intercept with p_{NSO} and r_{BO} magnitude and direction of effects referring to p_{BO}. $r_{NSO|BO}$ effect refers to p_{NSO}, and $r_{NSO|bo}$ effect refers to $r_{NSO|BO}$.
[e] Indicates intercept in models with categorical covariates.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

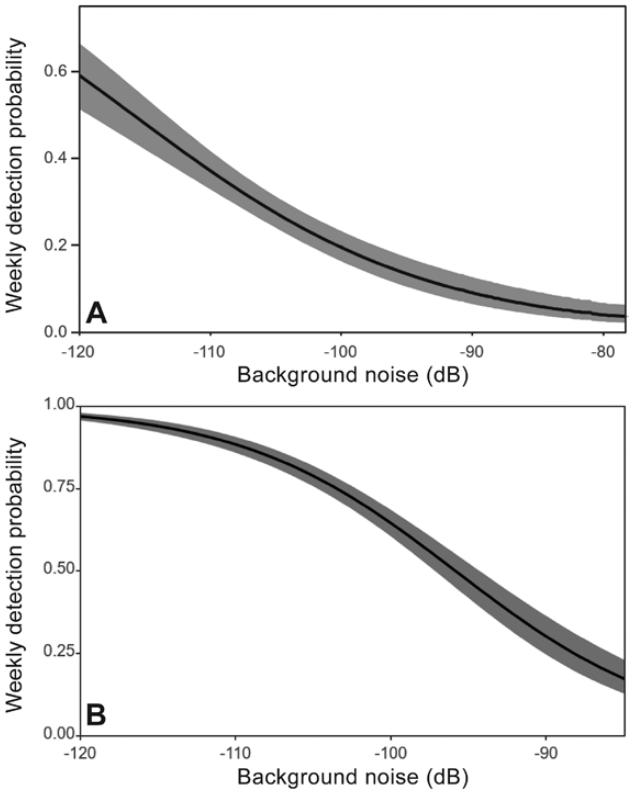

FIGURE 3. Change in (**A**) Northern Spotted Owl and (**B**) Barred Owl detection probability (*p*) with NOISE at the station scale. Northern Spotted Owl estimates are from additive Distance to Known Spotted Owl + NOISE model, at mean Distance to Known Spotted Owl; Barred Owl estimates are from additive NOISE + Study Area model, using estimates from Coast Range study area. NOISE was measured with Kaleidoscope Pro software as the average weekly background noise level in decibels below full scale (dBFS; 0 is the maximum possible digital level so –80 dB is noisier than –110 dB) from each station between 220 and 1,200 Hz.

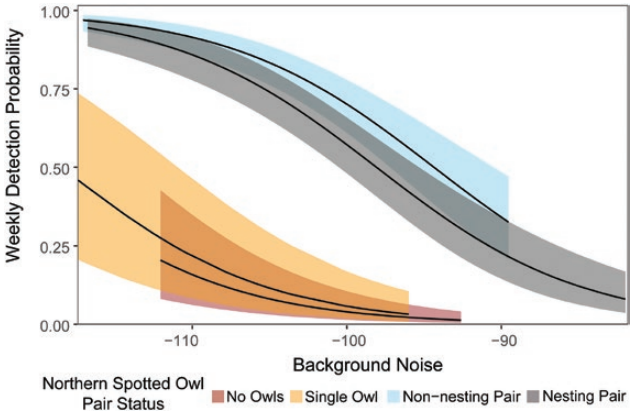

FIGURE 4. Northern Spotted Owl hexagon-scale detection probability (y-axis) with NOISE on the x-axis and pair status from NSO-PAIR-HEX (see Table 1 for covariate definitions) labeled by color. Estimates from most-supported hexagon-scale model: additive NSO-PAIR-HEX + NOISE. NOISE was measured with Kaleidoscope Pro software as the average weekly background noise level in decibels below full scale (dBFS; 0 is the maximum possible digital level so –80 dB is noisier than –110 dB) from each station between 220 and 1,200 Hz.

were estimated independently with a species-specific NOISE effect (SP*NOISE; Figure 5; Appendix Table 6). In addition, detection probability was allowed to vary for both species depending on whether the other species was present at a station (e.g., $p_{BO} \neq r_{BO;}$ INT_OCC), and for Northern Spotted Owls, in relation to whether Barred Owls were detected within a survey week ($r_{NSO|BO} \neq r_{NSO|bo}$; INT_DET).

As in previous models, NOISE negatively affected probability of detection for both species, with a somewhat stronger effect for Barred Owls than for Northern Spotted Owls (Table 2). At mean NOISE levels, detection probabilities were similar between species if only that species was present at a station ($\hat{p}_{BO}$=0.57, CI: 0.525–0.614; $\hat{p}_{NSO}$=0.628, CI: 0.388–0.817), but SE was large for the Northern Spotted Owl-only model coefficient due to small sample size (7 stations where only Northern Spotted Owls and no Barred Owls were present). The 95% CIs for coefficients overlapped, but for Barred Owls at mean NOISE levels we observed slightly higher $\hat{p}_{BO}$ (only Barred Owls present; 0.571, CI: 0.525–0.614) than $\hat{r}_{BO}$ (both species present; 0.537 CI: 0.496–0.577; Table 2).

Northern Spotted Owl detection probabilities were negatively associated with Barred Owl presence at a station (Figure 5). At mean NOISE levels, probability of detection was lowest if a Barred Owl was present but not detected at a station in a survey week ($\hat{r}_{NSO|bo}$ = 0.238, CI: 0.195–0.286; Figure 5), and higher if Barred Owls were present and detected in a survey week ($\hat{r}_{NSO|bo}$ = 0.320, CI: 0.277–0.366; Figure 5). The detection interaction factor, rho (ρ), was estimated at 1.51, indicating that within a survey week detection of Northern Spotted Owls was more likely if Barred Owls were also detected.

DISCUSSION

In this study we demonstrated that passive acoustic monitoring can be an effective method of detecting Northern Spotted Owls and Barred Owls at multiple spatial scales (station and 500-ha hexagon). The probability of detecting Northern Spotted Owls decreased as background noise and distance to known Northern Spotted Owl locations increased. Detection probability increased if the nearest known Northern Spotted Owls were paired rather than single individuals and when ARUs were nearer to ridgetops. Finally, detection probability varied by study area, with estimates for KLA highest and OLY lowest. Barred Owl detection probability also depended on background noise and study area (in this case, with COA highest and OLY lowest) but comparatively, this species had overall higher

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

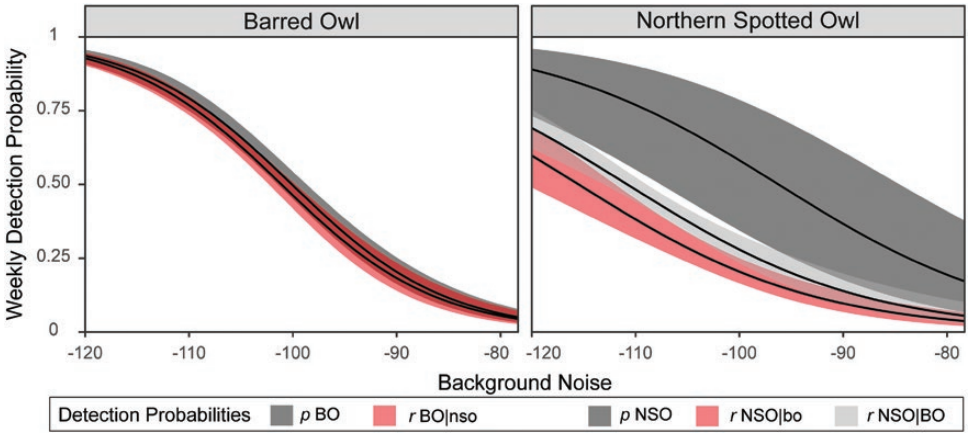

FIGURE 5. Barred Owl and Northern Spotted Owl conditional detection probabilities from 2-species co-occurrence occupancy model estimates over a range of NOISE on the x-axis. Estimates are from the most-supported co-occurrence model: SP + INT_OCC + INT_DET +SP * INT_OCC + NOISE + SP * NOISE. Here, SP models occupancy and detection probability separately for each species, INT is the interactive effect of occupancy by one species on occupancy of the other species, INT_OCC is the detection interaction between species depending on presence of other species, INT_DET is the detection interaction between species depending on detection of other species. Conditional detection probabilities are defined as: p_{BO}, Barred Owl *p* when only Barred Owls are present; $r_{BO|nso}$, Barred Owl *p* when Northern Spotted Owls are also present; p_{NSO}, Northern Spotted Owl *p* when only Northern Spotted Owls are present; $r_{NSO|bo}$, Northern Spotted Owl *p* when Barred Owls are also present but not detected in a survey week; and $r_{NSO|BO}$, Northern Spotted Owl *p* when Barred Owls are also present and detected in a survey week. NOISE was measured with Kaleidoscope Pro software as the average weekly background noise level in decibels below full scale (dBFS; 0 is the maximum possible digital level so –80 dB is noisier than –110 dB) from each station between 220 and 1,200 Hz.

probabilities of detection. Northern Spotted Owl detection probabilities were lower at ARU stations where Barred Owls were also present. At those stations where Northern Spotted Owls co-occurred with Barred Owls, Northern Spotted Owl detection probabilities were higher during weeks when ARUs detected Barred Owls.

Detection Probability

In all model sets the effect of background noise was negatively associated with probability of detection. Background noise likely decreased effective listening distance of ARUs (e.g., Yip et al. 2017a, Darras et al. 2018), but calling activity by both Northern Spotted Owls and Barred Owls may decrease during times of inclement weather (wind, storms) and near sources of excessive noise (e.g., rivers/streams). Background noise during avian breeding surveys is unavoidable in the Pacific Northwest because incubation and nesting periods occur during the end of the rainy season (March–June). Future study designs will be most effective by reducing potential bias in estimating detection probability through modeling efforts as well as considering strategic placement of ARUs away from rivers and streams to decrease the effect of these sources of background noise.

As we hypothesized, the probability of detecting Northern Spotted Owls generally increased at higher topographic positions and by study area, but similar models for Barred Owls failed to reveal any relationship between Barred Owl probability of detection and position on the slope. This may indicate a behavioral difference between the species in that, relative to mid- or lower-slope locations, Northern Spotted Owls call more often higher up the slope, and are thus more easily detected nearer to ridgetops. This observation could also reflect an unmodeled pattern in space use by Northern Spotted Owls, but those investigations are beyond the scope of this study. Estimated detection probabilities also varied between study areas for both species, although in different patterns (e.g., highest probability of detection for Barred Owls at COA, but for Northern Spotted Owls the highest detection probability was at KLA). These patterns are similar to occupancy estimates from previous research (Dugger et al. 2016, Wiens et al. 2018, Yackulic et al. 2019).

Decreased probability of detection relative to increased distance from the nearest known Northern Spotted Owl was expected and has also been observed using callback surveys (Wiens et al. 2014). The strength of this pattern highlights the skill of demographic surveyors to locate Northern Spotted Owls in historical territories when they are present, as well as the ability of the ARUs to detect these same birds. Estimates of detection probability from our models incorporating known Northern Spotted Owl location data could be informative if the goal is to approximate the location of activity centers or nest sites within a hexagon from passive acoustic data. Given that weekly detection probabilities vary between ARU stations within a hexagon, stations with higher estimated detection probability could indicate a shorter distance to a nest or activity center relative to other ARUs in the hexagon. Among

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

other uses, this distance/detection relationship could help narrow on-the-ground searches for individual owls, or inform the establishment of boundaries for protected areas used by Northern Spotted Owls.

At the hexagon scale, models indicated a striking difference in weekly probability of detection between known paired and unpaired Northern Spotted Owls in surveyed territories that overlapped ARU hexagons. We found little support for differences in detection probability between the "No Owl" category (locations in which foot and call-back surveys did not detect any Northern Spotted Owls in the 2017 season) and the "Single Owl" category as documented by demography crews. This suggests that we could not distinguish between single, territorial owls and non-territorial owls based on passive acoustic data. The findings here may support previous descriptions of non-territorial Northern Spotted Owls, sometimes known as "floaters", which appear to vocalize infrequently and range more widely on the landscape than territorial pairs (Dugger et al. 2016). Attempts to account for sporadic detections of non-territorial individuals can reduce potential bias in occupancy estimates of territorial owls (Berigan et al. 2019). Alternatively, these detections in "No Owl" hexagons could represent vocalizations of known owls from nearby occupied territories.

We observed little difference between detection probabilities from ARUs in hexagons that overlapped territories of non-nesting and nesting pairs of Northern Spotted Owls, which allowed us to simply consider detection probabilities for 2 categories of known owl status in a hexagon: territorial pairs and individual owls. The 2 groups show widely different patterns of weekly detection probability, likely due to the vocal behaviors associated with paired status (territorial defense and intra-pair communication). The slightly higher weekly detection probability of non-nesting vs. nesting pairs of Northern Spotted Owls could reflect more movement within a territory from non-nesting Northern Spotted Owls. Nesting pairs tend to remain near a nest tree in a territory core (Glenn et al. 2004, Schilling et al. 2013), and while there is frequent communication within pairs and from parents to nestlings, these vocalizations are more localized. As such, an ARU must be nearer to a nest to detect these vocalizations than to detect the calls of non-nesting territorial Northern Spotted Owls within a hexagon. For example, one ARU in the Klamath study area was randomly placed ~20 m from an active Northern Spotted Owl nest tree, and that ARU recorded Northern Spotted Owl vocalizations virtually every night, including pair communications, nestling begging, and apparent responses to Barred Owls, totaling 6,438 individual vocalizations. However, from the other 4 ARUs in the same hexagon we detected 0, 0, 6, and 16 Northern Spotted Owl vocalizations throughout the season. In this study, we tagged all Northern Spotted Owl vocalizations but did not separate these by call type. A focused study of vocalization types between nesting and non-nesting pairs of Northern Spotted Owls could further elucidate these differences and may allow for distinction between these 2 categories based on acoustic data. Additional research is needed to determine whether breeding status of otherwise unknown Northern Spotted Owls can be inferred using only passive acoustic monitoring.

Barred Owl Use

Variation in the probability of use for Barred Owls relative to terrain ruggedness supports previous work that reported Barred Owl habitat selection for flatter terrain (Wiens et al. 2014, Jenkins et al. 2019). Northern Spotted Owls use areas with steeper slopes (Jenkins et al. 2019) and our non-random hexagon selection was based on recent Northern Spotted Owl use; thus, the average ruggedness of these hexagons may not be fully representative of the surrounding landscape. As such, these results could reveal variation in use by Barred Owls at the high end of the ruggedness spectrum. Additionally, the most rugged sites in this study were primarily in the Olympic Peninsula study area. Thus, spatial trends in landscape use observed here may provide insight about why we detected fewer Barred Owls on the Olympic Peninsula, especially considering they colonized this region earlier relative to the other study areas (Livezey 2009).

Co-occurrence Detection Probability

After accounting for the effect of background noise, our results indicated that Northern Spotted Owl detection probabilities were higher when Barred Owls were not present. This finding supports multiple previous studies of Barred Owl and Northern Spotted Owl dynamics (e.g., Olson et al. 2005, Crozier et al. 2006, Kroll et al. 2010, Dugger et al. 2011, 2016). However, the structure of this co-occurrence model allows for more nuanced examination of detection probabilities of the subordinate species (here, Northern Spotted Owls) conditional not only on Barred Owl presence in the hexagon over the survey season, but detection of Barred Owls during a particular survey week as well. Where both species occurred but Barred Owls were not detected during the survey week, Northern Spotted Owl probability of detection within that week was lowest. However, where both species occurred and Barred Owls were detected within a survey week, Northern Spotted Owl weekly detection probabilities increased. We selected survey hexagons with a high likelihood of pair occupancy based on demographic information, so most of the known Northern Spotted Owls in this study were territorial pairs. As such, the patterns in detection probability seen here may be a result of at least 2 non-mutually exclusive mechanisms. First, it may have been that when Barred Owls vocalized, territorial Northern Spotted Owls responded

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

in territorial defense. A previous study found that in some cases, Northern Spotted Owls appeared to respond more readily to Barred Owl broadcasts than to conspecific broadcasts in the same survey occasion (Crozier et al. 2006), suggesting that Northern Spotted Owls may reduce calling in response to conspecific calls in the presence of Barred Owls, but then increase calling in response to interspecific vocalizations. If this hypothesis is true, then where Northern Spotted Owls remain in the landscape they may be actively defending nesting territories in the face of pressure from Barred Owls. A second hypothesis is that both species were responding to unmodeled environmental conditions that increased calling activity simultaneously for both species. A focused analysis of temporal calling patterns at sites where both species overlap could more clearly reveal the mechanism behind this observation. Measuring vocal activity at a fine scale (e.g., 5-min intervals) could quantify the proportion of direct interspecific interactions, while a somewhat more coarse scale (e.g., 1 day) could clarify the effect of vocal Barred Owls on Northern Spotted Owl detection probability.

Summary

The findings from this study showed that passive acoustic monitoring can not only detect Northern Spotted Owls and Barred Owls with high probability over a breeding season, but that the high-resolution data collected by this method can reveal spatial and temporal patterns in detection probability beyond what roadside callback surveys provide. As such, this proves to be a promising step toward a non-invasive method for monitoring forest owl populations, especially for a rare and cryptic species such as Northern Spotted Owls. Current work on automating detection of vocalizations through machine learning has greatly reduced the processing time of acoustic data in multiple contexts (e.g., Bergler et al. 2019, Ruff et al. 2019, Stowell et al. 2019), making it possible to increase the scale of future monitoring using these methods. As sound processing time continues to decrease, various hybrid designs that combine passive acoustic monitoring with more traditional methods could prove highly effective; for example, ARU data could identify Northern Spotted Owls on the landscape, then surveyors could locate owls on foot and determine pair and reproductive status. Approximating distance of each detection from ARU data (Yip et al. 2019) may allow for estimates of density using passive acoustic methods. Finally, incorporating the number of detections (counts) within a sampling time period into occupancy models to develop call thresholds (Berigan et al. 2019) that can distinguish between singles, pairs, and even breeding pairs has the potential to increase the applicability of acoustic methods to the monitoring of Northern Spotted Owl populations across their range.

ACKNOWLEDGMENTS

The authors thank M. Corr, D. Culp, E. Guzmán, E. Johnston, and K. McLaughlin for help with field data collection. T. Levi and E. M. Bayne provided feedback and support during study development, data processing, and analysis. Two anonymous reviewers provided valuable feedback and thoughtful questions, which improved the quality and clarity of this manuscript. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official U.S. Department of Agriculture or U.S. Government determination or policy. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Funding statement: Funding for this project was provided by a cooperation between the U.S. Forest Service Pacific Northwest Research Station and Oregon State University, as well as by Region 6 of the U.S. Forest Service, U.S. Department of the Interior Bureau of Land Management, the Oregon Cooperative Fish and Wildlife Research Unit, and the Northwest Scientific Association.

Ethics statement: We did not require permits or approvals to conduct this study and we conducted all fieldwork on federal lands.

Author contributions: D.B.L., K.M.D., and R.J.D. designed the study; L.S.D. collected data; L.S.D. and Z.J.R. processed and analyzed data; D.B.L., K.M.D., and L.S.D. developed methods; D.B.L. and K.M.D. provided funding and materials; L.S.D. wrote the manuscript; D.B.L, K.M.D., R.J.D., and Z.J.R. edited the manuscript.

Data depository: Analyses reported in this article can be reproduced using the data provided by Duchac et al. (2020).

LITERATURE CITED

Albert, D. G. (2004). Past Research on Sound Propagation Through Forests. Cold Regions Research and Engineering Laboratory, U. S. Army Corps of Engineers Engineer Research and Development Center, Hanover, NH, USA.

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. (2006). Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildlife Monographs 163:1–48.

Bayne, E. M., and D. Stralberg (2015). Bird Community Composition Along Elevation and Latitudinal Gradients in Alberta's Mixedwood Forests: Analogues for Our Future Climate? Progress Report, Biodiversity Management and Climate Change Adaptation Project. Alberta Biodiversity Monitoring Institute, Edmonton, Alberta, Canada.

Bayne, E. M., D. Stralberg, and A. Nixon (2015). Adapting Monitoring to More Effectively Assess the Impacts of Climate Change on Alberta's Biodiversity. Prepared for the Biodiversity Management and Climate Change Adaptation project. Alberta Biodiversity Monitoring Institute, Edmonton, Alberta, Canada.

Bergler, C., H. Schroter, R. X. Cheng, V. Barth, M. Weber, E. Noth, H. Hofer, and A. Maier (2019). ORCA-SPOT: An automatic killer

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

whale sound detection toolkit using deep learning. Scientific Reports 9. Doi:10.1038/s41598-019047335-w

Berigan, W. J., G. M. Jones, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery (2019). Cryptic wide-ranging movements lead to upwardly biased occupancy in a territorial species. Journal of Applied Ecology 56:470–480.

Bermant, P. C., M. M. Bronstein, R. J. Wood, S. Gero, and D. F. Gruber (2019). Deep machine learning techniques for the detection and classification of sperm whale bioacoustics. Scientific Reports 9:12588. doi:10.1038/s41598-019-48909-4

Blumstein, D. T., D. J. Mennill, P. Clemins, L. Girod, K. Yao, G. Patricelli, J. L. Deppe, A. H. Krakauer, C. Clark, K. A. Cortopassi, et al. (2011). Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus. Journal of Applied Ecology 48:758–767.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information–Theoretical Approach, second edition. Springer-Verlag, New York, NY, USA.

Conway, C. J., and J. P. Gibbs (2005). Effectiveness of call-broadcast surveys for monitoring marsh birds. The Auk 122:26–35.

Conway, C. J., V. Garcia, M. D. Smith, and K. Hughes (2008). Factors affecting detection of Burrowing Owl nests during standardized surveys. The Journal of Wildlife Management 72:688–696.

Courtois, E. A., E. Michel, Q. Martinez, K. Pineau, M. Dewynter, G. F. Ficetola, and A. Fouquet (2016). Taking the lead on climate change: Modelling and monitoring the fate of an Amazonian frog. Oryx 50:450–459.

Crozier, M. L., M. E. Seamans, R. J. Gutiérrez, P.J. Loschl, R. B. Horn, S. G. Sovern, and E. D. Forsman (2006). Does the presence of Barred Owls suppress the calling behavior of Northern Spotted Owls? The Condor 108:760–769.

Daly, C., M. Hableib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

Darras, K., P. Batary, B. Furnas, A. Celis-Murillo, S. L. Van Wilgenburg, Y. A. Mulyani, and T. Tscharntke (2018). Comparing the sampling performance of sound recorders versus point counts in bird surveys: A meta-analysis. Journal of Applied Ecology 55:2575–2586.

Davis, R. J., B. Hollen, J. Hobson, J. E. Gower, and D. Keenum (2016). Northwest Forest Plan--the First 20 Years (1994–2013): Status and Trends of Northern Spotted Owl Habitats. Gen. Tech. Rep. PNW-GTR-929, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, USA.

Digby, A., M. Towsey, B. D. Bell, and P. D. Teal (2013). A practical comparison of manual and autonomous methods for acoustic monitoring. Methods in Ecology and Evolution 4:675–683.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, Z. J. Ruff, and R. J. Davis (2020). Data from: Passive acoustic monitoring effectively detects Northern Spotted Owls and Barred Owls over a range of forest conditions. The Condor: Ornithological Applications 122:1–22. doi:10.5061/dryad.qnk98sfcd

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 the long-term population demographics of Northern Spotted Owls. The Condor: Ornithological Applications 118:57–116.

Dugger, K. M., R. G. Anthony, and L. S. Andrews (2011). Transient dynamics of invasive competition: Barred Owls, Northern Spotted Owls, habitat, and the demons of competition present. Ecological Applications 21:2459–2468.

ESRI (2015). ArcGIS Desktop: Release 10.3.1. Environmental Systems Research Institute, Redlands, CA, USA.

Forsman, E. D. (1983). Methods and Materials, for Locating and Studying Spotted Owls. USDA Forest Service, Pacific Northwest Research Station General Technical Report PNW-GTR-162, Portland, OR, USA.

Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwartz, 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., E. C. Meslow, and H. M. Wight (1984). Distribution and biology of the Northern Spotted Owl in Oregon. Wildlife Monographs 48:1–64.

Franklin, J. F., and C. T. Dyrness (1973). Natural Vegetation of Oregon and Washington. General Technical Report PNW-8. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, USA.

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.

Glenn, E. M., M. C. Hansen, and R. G. Anthony (2004). Northern Spotted Owl home-range and habitat use in young forests of western Oregon. The Journal of Wildlife Management 68:33–50.

Goldstein, E. B. (2010). Encyclopedia of Perception, volume 1. SAGE Publishing, University of Pittsburgh, Pittsburgh, PA, USA.

Gutiérrez, R. J., A. B. Franklin, and W. S. Lahaye (1995). Spotted Owl (*Strix occidentalis*), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.

Gutiérrez, R. J., M. L. Cody, S. P. Courtney, and A.B. Franklin (2007). The invasion of the Barred Owl and its potential effect on the Northern Spotted Owl: A conservation conundrum. Biological Invasions 9:181–196.

Hamel, S., S. T. Killengreen, J. Henden, N. E. Eide, L. Roed-Eriksen, R. A. Ims, and N. G. Yoccoz (2012). Towards good practice guidance in using camera-traps in ecology: Influence of sampling design on validity of ecological inferences. Methods in Ecology and Evolution 4:105–113.

Hamer, T. E., E. D. Forsman, and E. M. Glenn (2007). Home range attributes and habitat selection of Barred Owls and Northern Spotted Owls in an area of sympatry. The Condor 109:750–768.

Haug, E. A., and A. B. Didiuk (1993). Use of recorded calls to detect Burrowing Owls. Journal of Field Ornithology 64:188–194.

Herter, D. R., and L. L. Hicks (2000). Barred Owl and Northern Spotted Owl populations and habitat in the Central Cascade range of Washington. Journal of Raptor Research 34:279–286.

HOBOWare (2017). http://www.onsetcomp.com/products/data-loggers/ua-002-64

Jenkins, J. M. A., D. B. Lesmeister, J. D. Wiens, J. T. Kane, V. R. Kane, and J. Verschuyl (2019). Three-dimensional partitioning of resources by congeneric forest predators with recent sympatry. Scientific Reports 9:6036.

Kahl, S., T. Wilhelm-Stein, H. Hussein, H. Klinck, D. Kowerko, M. Ritter, and M. Eibl (2017). Large-scale bird sound classification using convolutional neural networks. BirdCLEF 2017:1–14. https://arxiv.org/abs/1804.07177

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

Kalan, A. K., A. K. Piel, R. Mundry, R. M. Wittig, C. Boesch, and H. S. Kuhl (2016). Passive acoustic monitoring reveals group ranging and territory use: A case study of wild chimpanzees (*Pan troglodytes*). Frontiers in Zoology 13. Doi: 10.1186/s12983-016-0167-8

Katz, J., S. D. Hafner, and T. Donovan (2016). Tools for automated acoustic monitoring within the R package monitoR. Bioacoustics 25:197–210.

Kriebel, A. R. (1972). Refraction and attenuation of sound by wind and thermal profiles over a ground plane. Journal of the Acoustical Society of America 51. Doi: 10.1121/1.1912816

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. The Journal of Wildlife Management 74:1264–1274.

Laiolo, P. (2010). The emerging significance of bioacoustics in animal species conservation. Biological Conservation 143:1635–1645.

Langham, G. M., T. A. Contreras, and K. E. Sieving (2006). Why pishing works: Titmouse (*Paridae*) scolds elicit a generalized response in bird communities. Ecoscience 13:485–496.

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. PNW-GTR-440. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA.

Livezey, K. B. (2009). Range expansion of Barred Owls, Part I: Chronology and distribution. The American Midland Naturalist 161:49–56.

MacKenzie, D. I., and J. A. Royle (2005). Designing occupancy studies: General advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines (2018). Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence, second edition. Elsevier, Academic Press, Burlington, MA, USA.

Mangan, A. O., T. Chestnut, J. C. Vogeler, I. K. Breckheimer, W. M. King, K. E. Bagnall, and K. M. Dugger (2019). Factors related to occupancy dynamics and breeding propensity of Northern Spotted Owls in a protected area: Habitat, weather and presence of Barred Owls. The Condor: Ornithological Applications 121:1–20.

Martínez, J. A., and I. Zuberogoitia (2002). Factors affecting the vocal behaviour of Eagle Owls *Bubo bubo:* Effects of sex and territorial status. Ardeola 49:1–9.

Moulton, C. E., R. S. Brady, and J. R. Belthoff (2004). Territory defense of nesting Burrowing Owls: Responses to simulated conspecific intrusion. Journal of Field Ornithology 75:288–295.

Odom, K. J., and D. J. Mennill (2010). A quantitative description of the vocalization and vocal activity of the Barred Owl. The Condor 112:549–560.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Akers, 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 effect of Barred Owls. The Journal of Wildlife Management 69:918–932.

Olson, G.S., E.M. Glenn, R.G. Anthony, E. D. Forsman, J. A. Reid, P. J. Loschl, and W. J. Ripple (2004). Modeling demographic performance of Northern Spotted Owls relative to forest habitat in Oregon. The Journal of Wildlife Management 68:1039–1053.

Peng, J., R. Bullen, and S. Kean (2014). The Effects of Vegetation on Road Traffic Noise. Inter-Noise 2014, Melbourne, Australia, 16–19 November.

Piorecky, M. D., and D. R. C. Prescott (2004). Distribution, Abundance and Habitat Selection of Northern Pygmy and Barred Owls Along the Eastern Slopes of the Alberta Rocky Mountains. Alberta Species at Risk Report No. 91, Alberta Sustainable Resource Development.

Rasmussen, K. B. (1985). On the effect of terrain profile on sound propagation outdoors. Journal of Sound and Vibration 98:35–44.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Richmond, O. M. W., J. E. Hines, and S. R. Beissinger (2010). Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. Ecological Applications 20:2036–2046.

Rognan, C. B., J. M. Szewczak, and M. L. Morrison (2012). Autonomous recording of Great Gray Owls in the Sierra Nevada. Northwestern Naturalist 93:138–144.

Rohner, C. (1997). Non-territorial "floaters" in Great Horned Owls: Space use during a cyclic peak of snowshoe hares. Animal Behavior 53:901–912.

Ross, S. R. P. J., N. R. Friedman, K. L. Dudley, M. Yoshimura, T. Yoshida, and E. P. Economo (2017). Listening to ecosystems: Data-rich acoustic monitoring through landscape-scale sensor networks. Ecological Research 33:135–147.

Ruff, Z. J., D. B. Lesmeister, L. S. Duchac, B. K. Padmaraju, and C. M. Sullivan (2019). Automated identification of avian vocalizations with deep convolutional neural networks. Remote Sensing in Ecology and Conservation. doi: 10.1002/rse2.125

Schilling, J. W., K. M. Dugger, and R. G. Anthony (2013). Survival and home-range size of Northern Spotted Owls in southwestern Oregon. Journal of Raptor Research 47:1–14.

Shonfield J., and E. M. Bayne (2017). Autonomous recording units in avian ecological research: Current use and future applications. Avian Conservation and Ecology 12:14.

Sidie-Slettedahl, A. M., K. C. Jensen, R. R. Johnson, T. A. Arnold, J. E. Austin, and J. D. Stafford (2015). Evaluation of autonomous recording units for detecting 3 species of secretive marsh birds: Marsh Bird Surveys. Wildlife Society Bulletin 39:626–634.

Singleton, P. H., J. F. Lehmkuhl, W. L. Gaines, and S. A. Graham (2010). Barred Owl space use and habitat selection in the eastern Cascades, Washington. The Journal of Wildlife Management 74:285–294.

Stowell, D., Y. Stylianou, M. D. Wood, H. Pamuła, and H. Glotin (2019). Automatic acoustic detection of birds through deep learning: The first Bird Audio detection challenge. Methods in Ecology and Evolution 10:363–380.

Takats, D. L., C. M. Francis, G. L. Holroyd, J. R. Duncan, K. M. Mazur, R. J. Cannings, W. Harris, and D. Holt (2001). Guidelines for Nocturnal Owl Monitoring in North America. Beaverhill Bird Observatory and Bird Studies Canada. Edmonton, Alberta, Canada.

United States Fish and Wildlife Service (1990). Endangered and threatened wildlife and plants: Determination of threatened status for the Northern Spotted Owl. Federal Register 55:26114–26194.

USDA Forest Service and USDOI Bureau of Land Management (1994). Final Supplemental Impact Statement on Management

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

of Habitat for Late-Successional and Old-Growth Forest Related Species Within the Range of the Northern Spotted Owl. USDA Forest Service and USDOI Bureau of Land Management, Portland, OR, USA.

Van Lanen N. J., A. B. Franklin, K. P. Huyvaert, R. F. Reiser, and P. C. Carlson (2011). Who hits and hoots at whom? Potential for interference competition between Barred and Northern Spotted owls. Biological Conservation 144:2194–2201.

Whyte, K. H., C. E. Ross, and S. R. Mohren (2015). Crater Lake National Park Biological Sound Station Research: 2015 Annual Report. National Park Service, Crater Lake National Park, Crater Lake, OR, USA.

Wiens, J. D., K. M. Dugger, D. B. Lesmeister, K. E. Dilione, and D. C. Simon (2018). Effects of Experimental Removal of Barred Owls on Population Demography of Northern Spotted Owls in Washington and Oregon—2017 Progress Report. Open-File Report 2016-1041. U.S. Department of the Interior, U.S. Geological Survey.

Wiens, J. D., R. G. Anthony, and E. D. Forsman (2011). Barred Owl occupancy surveys within the range of the Northern Spotted Owl. The Journal of Wildlife Management 75:531–538.

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: Competition Between Spotted and Barred Owls. Wildlife Monographs 185:1–50.

Wildlife Acoustics, Inc. (2018). Song Meter SM4 Bioacoustics Recorder User Guide, updated March 2018. https://www.wildlifeacoustics.com/images/documentation/SM4-USER-GUIDE.pdf

Wildlife Acoustics, Inc. (2019). Kaleidoscope Pro 5 User Guide. http://condor.wildlifeacoustics.com/Kaleidoscope.pdf.

Wood, C. M., R. J. Gutiérrez, and M. Z. Peery (2019a). Acoustic monitoring reveals a diverse forest owl community, illustrating its potential for basic and applied ecology. Ecology 100:e02764.

Wood, C. M., V. D. Popescu, H. Klinck, J. J. Keane, R. J. Gutiérrez, S. C. Sawyer, and M. Z. Peery (2019b). Detecting small changes in populations at landscape scales: A bioacoustic site-occupancy framework. Ecological Indicators 98:492–507.

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 29:1–8.

Yip, D. A., E. C. Knight, E. Haave-Audet, S. J. Wilson, C. Carchuk, C. D. Scott, P. Solymos, and E. M. Bayne (2019). Sound level measurements from audio recordings provide objective distance estimates for distance sampling wildlife populations. Remote Sensing in Ecology and Conservation. doi: 10.1002/rse2.118

Yip, D. A., E. M. Bayne, P. Solymos, and A. Grover (2017a). Sound attenuation in forest and roadside environments: implications for avian point-count surveys. The Condor: Ornithological Applications 119:73–84.

Yip, D. A., L. Leston, E. M. Bayne, P. Solymos, and A. Grover (2017b). Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. Avian Conservation and Ecology 12:11.

Znidersic, E., M. Towsey, W. K. Roy, S. E. Darling, A. Truskinger, P. Roe, and D. M. Watson (2020). Using visualization and machine learning methods to monitor low detectability species—The Least Bittern as a case study. Ecological Informatics 55(101014):1–9.

Zwart, M. C., A. Baker, P. J. K. McGowan, M. J. Whittingham, and S. G. Willis (2014). The use of automated bioacoustic recorders to replace human wildlife surveys: An example using nightjars. PLoS One 9:e102770.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

APPENDIX

APPENDIX TABLE 3. Northern Spotted Owl station-scale detection models. Model selection results including -2 log likelihood (-2LogL), number of parameters (*k*), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAICc; adjusted for small sample size), and Akaike weights (wi) from detection probability models (null (.) and AREA on ψ) for Northern Spotted Owls from 150 autonomous recording unit (ARU) stations surveyed at 18 1-week intervals from March–July, 2017. ARU stations were clustered in groups of 5 within 30 500-ha hexagons in 3 study areas in western Oregon and Washington. Table 3A shows models using knowledge of Northern Spotted Owl locations and pair status from concurrent demographic surveys; Table 3B shows models without this knowledge. ΔAIC_c between the most-supported model in Table 3A and the most-supported model in Table 3B is 68.46.

	Model [a]	ΔAIC_c	w_i	*k*	−2LogL
Table 3A					
1	ψ (AREA), *p*(NSO-LOC + NOISE)	0	1	6	1,466.23
2	ψ (AREA), *p*(NOISE + NSO-PAIR-ST)	54.11	0	8	1,515.9
3	ψ (AREA), *p*(NSO-LOC + AREA)	55.96	0	7	1,519.99
4	ψ (AREA), *p*(NSO-LOC + PRECIP)	70.22	0	6	1,536.45
5	ψ (AREA), *p*(NSO-LOC + TOPO)	83.05	0	6	1,549.28
6	ψ (AREA), *p*(NSO-LOC)	87.85	0	5	1,556.25
7	ψ (AREA), *p*(NSO-LOC + RUGGED)	87.88	0	6	1,554.11
8	ψ (AREA), *p*(NSO-LOC + ROAD)	90	0	6	1,556.22
9	ψ (AREA), *p*(NSO-PAIR-ST * BO-ANY)	111.8	0	11	1,566.7
10	ψ (AREA), *p*(NSO-PAIR-ST + TOPO)	117.96	0	8	1,579.76
11	ψ (AREA), *p*(NSO-PAIR-ST + NSO-NEST)	125.85	0	8	1,587.64
12	ψ (AREA), *p*(WEEK + NSO-PAIR-ST)	128.49	0	24	1,549.71
13	ψ (AREA), *p*(NSO-NEST + AREA)	130.57	0	7	1,594.59
14	ψ (AREA), *p*(NSO-PAIR-ST)	145.09	0	7	1,609.12
15	ψ (AREA), *p*(NSO-PAIR-ST + BO-ANY)	147.3	0	8	1,609.1
16	ψ (AREA), *p*(NSO-PAIR-ST * BO-ANY)	151.5	0	11	1,606.4
17	ψ (AREA), *p*(NSO-NEST)	154.75	0	5	1,623.15
18	ψ (.), *p*(NSO-NEST)	189.06	0	3	1,661.71
19	ψ (.), *p*(.)	204.67	0	2	1,679.41
Table 3B					
1	ψ (AREA), *p*(NOISE + TOPO)	0	0.9853	6	1,526.7
2	ψ (AREA), *p*(AREA + NOISE)	9.36	0.0091	7	1,533.86
3	ψ (AREA), *p*(NOISE + RUGGED)	10.36	0.0056	6	1,537.06
4	ψ (AREA), *p*(NOISE)	29.7	0	5	1,558.58
5	ψ (AREA), *p*(AREA * TOPO)	33.77	0	9	1,553.77
6	ψ (AREA), *p* (AREA + WEEK)	46.4	0	23	1,530.93
7	ψ (AREA), *p*(AREA + PRECIP)	59.73	0	7	1,584.23
8	ψ (AREA), *p*(TOPO + PRECIP)	61.48	0	6	1,588.18
9	ψ (AREA), *p*(AREA + STREAM)	66.77	0	7	1,591.27
10	ψ (AREA), *p*(AREA)	69.41	0	6	1,596.11
11	ψ (AREA), *p*(AREA + RUGGED)	70.02	0	7	1,594.52
12	ψ (AREA), *p*(TOPO)	83.59	0	5	1,612.46
13	ψ (AREA), *p*(PRECIP + WEEK)	84.32	0	22	1,571.64
14	ψ (AREA), *p*(PRECIP)	85.17	0	5	1,614.04
15	ψ (AREA), *p*(RUGGED + PRECIP)	86.81	0	6	1,613.51
16	ψ (AREA), *p*(TEMP)	90.17	0	5	1,619.04
17	ψ (AREA), *p*(WEEK)	92.87	0	21	1,582.94
18	ψ (.), *p*(AREA)	100.35	0	21	1,631.37
19	ψ (AREA), *p*(STREAM)	109.07	0	5	1,637.94
20	ψ (AREA), *p*(RUGGED)	110.29	0	5	1,639.16
21	ψ (AREA), *p*(BO-ADJ)	111.30	0	5	1,640.17
22	ψ (AREA), *p*(BO-HEX)	111.96	0	5	1,640.83
23	ψ (AREA), *p*(BO-ANY)	112.15	0	5	1,641.02
24	ψ (.), *p*(WEEK)	126.08	0	19	1,621.52
25	ψ (.), *p*(.)	144.20	0	2	1,679.41

[a] AREA = study area; ROAD = binary whether road audible from ARU station; RUGGED = terrain ruggedness measured as the standard deviation of elevation within each hexagon; TOPO = topographic position relative to a 450 m radius around each station; STREAM = distance in meters to the nearest stream; ELEV = elevation in meters at each station; PRECIP = daily precipitation in mm averaged weekly at each station; TEMP = temperature measured hourly and averaged weekly at each station; NOISE = measure of average weekly background noise between 200 and 1,000 Hz; NSO-LOC = distance to nearest known Spotted Owl nest or activity center; NSO-NEST = distance to nearest known Spotted Owl nest; NSO-PAIR-ST = pair status of historical Spotted Owl territory overlapping ARU station; BO-ADJ = number of Barred Owl broadcast surveys in 6 adjacent hexagons within a survey week; BO-HEX = binary, 1 if Barred Owl broadcast survey occurred within ARU hexagon in a survey week; BO-ANY = binary, 1 if Barred Owl broadcast survey occurred in ARU hexagon or 6 adjacent hexagons in a survey week; WEEK = numbered week of the survey season (1–18).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

APPENDIX TABLE 4. Barred Owl station-scale detection and use models. Model selection results including −2 log likelihood (−2LogL), number of parameters (*k*), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c; adjusted for small sample size), and Akaike weights (w_i) from detection probability (*p*) and use (ψ) models for Barred Owls from 150 autonomous recording unit (ARU) stations surveyed at 18 1-week intervals from March to July, 2017. ARU stations were clustered in groups of 5 within 30 500-ha hexagons in 3 study areas in western Oregon and Washington. We included a limited set of single-effect and additive ψ models.

	Model [a]	ΔAIC_c	w_i	*k*	−2LogL
1	ψ (RUGGED), *p*(AREA + NOISE)	0	0.7958	6	2,069.21
2	ψ (AREA + RUGGED), *p*(AREA + NOISE)	3.16	0.1643	8	2,067.93
3	ψ (AREA + NSO-LOC), *p*(AREA + NOISE)	6.44	0.0318	8	2,071.22
4	ψ (AREA), *p*(AREA + NOISE)	9.17	0.0081	7	2,076.18
5	ψ (AREA), *p*(NOISE + RUGGED	54.47	0	6	2,123.68
6	ψ (AREA), p(NOISE + WEEK)	105.81	0	22	2,135.64
7	ψ (AREA), *p*(TOPO + NOISE)	118.27	0	6	2,187.48
8	ψ (AREA), *p*(NOISE)	119.05	0	5	2,190.43
9	ψ (AREA), *p*(WEEK + RUGGED)	201.75	0	22	2,231.58
10	ψ (AREA), *p*(AREA + WEEK)	213.37	0	23	2,240.4
11	ψ (AREA), *p*(AREA + PRECIP)	246.73	0	7	2,313.74
12	ψ (AREA), *p*(AREA + RUGGED)	254.43	0	7	2,321.44
13	ψ (AREA), *p*(RUGGED)	260.8	0	5	2,332.18
14	ψ (AREA), *p*(AREA)	276.8	0	6	2,346.01
15	ψ (AREA), *p*(AREA + TOPO)	278.87	0	7	2,345.88
16	ψ (.), *p*(AREA)	306.27	0	4	2,379.79
17	ψ (AREA), *p*(WEEK)	345.28	0	21	2,377.86
18	ψ (AREA), *p*(TEMP)	355.95	0	5	2,427.33
19	ψ (AREA), *p*(PRECIP)	361.85	0	5	2,433.24
20	ψ (AREA), *p*(BO-HEX)	372.57	0	5	2,443.95
21	ψ (AREA), *p*(.)	376.84	0	4	2,450.36
22	ψ (AREA), *p*(BO-ADJ)	377.6	0	5	2,448.98
23	ψ (AREA), *p*(TOPO)	378.22	0	5	2,449.6
24	ψ (AREA), *p*(BO-ANY)	378.63	0	5	2,450.01
25	ψ (.), *p*(.)	407.69	0	2	2,485.41

[a] AREA = study area; ROAD = binary whether road audible from ARU station; RUGGED = terrain ruggedness measured as the standard deviation of elevation within each hexagon; TOPO = topographic position relative to a 450 m radius around each station; STREAM = distance in meters to the nearest stream; ELEV = elevation in meters at each station; PRECIP = daily precipitation in mm averaged weekly at each station; TEMP = temperature measured hourly and averaged weekly at each station; NOISE = measure of average weekly background noise between 200 and 1,000 Hz; NSO-LOC = distance to nearest known Spotted Owl nest or activity center; NSO-NEST = distance to nearest known Spotted Owl nest; NSO-PAIR-HEX = highest pair status of historical Spotted Owl territory overlapping ARU hexagon; BO-ADJ = number of Barred Owl broadcast surveys in 6 adjacent hexagons within a survey week; BO-HEX = binary, 1 if Barred Owl broadcast survey occurred within ARU hexagon in a survey week; BO-ANY = binary, 1 if Barred Owl broadcast survey occurred in ARU hexagon or 6 adjacent hexagons in a survey week; WEEK = numbered week of the survey season (1–18).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

APPENDIX TABLE 5. Northern Spotted Owl hexagon-scale detection models. Model selection results including −2 log likelihood (−2LogL), number of parameters (*k*), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c; adjusted for small sample size), and Akaike weights (w_i) from detection probability (*p*) models (null (.) and AREA on ψ) for Northern Spotted Owls from 30 500-ha hexagons surveyed at 18 1-week intervals from March to July, 2017, in western Oregon and Washington. Hexagon-scale models combine data from 5 autonomous recording unit stations within each hexagon in 3 study areas. Table 5A shows models using knowledge of Northern Spotted Owl locations and pair status from concurrent demographic surveys, Table 5B shows models without this knowledge. ΔAIC_c between the most-supported model in Table 5A and the most-supported model in Table 5B is 78.68.

	Model [a]	ΔAIC_c	w_i	*k*	−2LogL
Table 5A					
1	ψ (.), *p*(NSO-PAIR-HEX + NOISE)	0	1	6	381.15
2	ψ (.), *p*(BO-ANY + NSO-PAIR-HEX)	55.27	0	6	436.42
3	ψ (.), *p*(NSO-PAIR-HEX)	57.79	0	5	442.09
4	ψ (.), *p*(NSO-HEX + NSO-PAIR-HEX)	58.12	0	6	439.26
5	ψ (AREA), *p*(NSO-PAIR-HEX)	61.39	0	7	439.1
6	ψ (.), *p*(NSO-IN-HEX + NOISE)	89.89	0	4	477.09
7	ψ (.), *p*(NSO-IN-HEX + PRECIP)	123.25	0	4	510.45
8	ψ (.), *p*(NSO-IN-HEX)	127.5	0	3	517.37
9	ψ (AREA), *p*(NSO-IN-HEX)	130.12	0	5	514.42
10	ψ (.), *p*(.)	159.71	0	2	552.06
11	ψ (.), *p*(NSO-PAIR-HEX + WEEK)	212.4	0	22	420.62
Table 5B					
1	ψ (.), *p*(NOISE + AREA)	0	0.9293	5	462.98
2	ψ (.), *p*(AREA)	6.04	0.0454	4	471.92
3	ψ (.), *p*(AREA + PRECIP)	8	0.017	5	470.98
4	ψ (AREA), *p*(AREA)	9.46	0.0082	6	469.29
5	ψ (.), *p*(NOISE)	38.43	0	3	506.99
6	ψ (.), *p*(RUGGED + NOISE)	40.94	0	4	506.82
7	ψ (AREA), *p*(NOISE)	41.62	0	5	504.6
8	ψ (.), *p*(PRECIP + RUGGED)	63.06	0	4	528.94
9	ψ (AREA), *p*(RUGGED)	74.32	0	5	537.3
10	ψ (AREA), *p*(TEMP)	74.77	0	5	537.75
11	ψ (AREA), *p*(ROAD)	76.97	0	5	539.95
12	ψ (AREA), *p*(BO-ANY)	77.07	0	5	540.05
13	ψ (AREA), *p*(PRECIP)	77.46	0	5	540.44
14	ψ (.), *p*(.)	81.03	0	2	552.06
15	ψ (AREA), *p*(BO-ADJ)	83.65	0	5	546.63
16	ψ (AREA), *p*(BO-HEX)	85.03	0	5	548.01
17	ψ (.), *p*(AREA + WEEK)	131.55	0	21	449.53
18	ψ (AREA), *p*(WEEK)	215.6	0	21	533.58

[a] AREA = study area; ROAD = binary whether road audible from autonomous recording unit (ARU) station; RUGGED = terrain ruggedness measured as the standard deviation of elevation within each hexagon; TOPO = topographic position relative to a 450 m radius around each station; STREAM = distance in meters to the nearest stream; ELEV = elevation in meters at each station; PRECIP = daily precipitation in mm averaged weekly at each station; TEMP = temperature measured hourly and averaged weekly at each station; NOISE = measure of average weekly background noise between 200 and 1,000 Hz; NSO-LOC = distance to nearest known Spotted Owl nest or activity center; NSO-NEST = distance to nearest known Spotted Owl nest; NSO-PAIR-HEX = highest pair status of historical Spotted Owl territory overlapping ARU hexagon; NSO-IN-HEX = binary whether nearest known Northern Spotted owl nest or activity center was within (1) or outside (0) of survey hexagon; BO-ADJ = number of Barred Owl broadcast surveys in 6 adjacent hexagons within a survey week; BO-HEX = binary, 1 if Barred Owl broadcast survey occurred within ARU hexagon in a survey week; BO-ANY = binary, 1 if Barred Owl broadcast survey occurred in ARU hexagon or 6 adjacent hexagons in a survey week; WEEK = numbered week of the survey season (1–18).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020

APPENDIX TABLE 6. Two-species co-occurrence detection models. Model selection results including −2 log likelihood (−2LogL), number of parameters (*k*), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c; adjusted for small sample size), and Akaike weights (w_i) from co-occurrence detection probability (*p*) and use (ψ) models for Northern Spotted Owls and Barred Owls from 150 autonomous recording unit (ARU) stations surveyed at 18 1-week intervals from March to July, 2017. ARU stations were clustered in groups of 5 within 30 500-ha hexagons in 3 study areas in western Oregon and Washington. We included a limited set of species-specific effects on ψ.

	Model [a]	ΔAIC_c	w_i	*k*	−2LogL
1	ψ (SP + INT + AREA), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC + NOISE + SP * NOISE)	0	1	12	3,746.08
2	ψ (SP + INT), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC + NOISE + SP * NOISE)	36.86	0	10	3,787.63
3	ψ (SP + INT + AREA), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC + AREA + SP * AREA)	172.53	0	14	3,913.78
4	ψ (SP + INT), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC + AREA + SP * AREA)	217.32	0	12	3,963.4
5	ψ (SP + INT + AREA + SP * AREA), *p*(SP + INT_OCC + INT_DET)	315.32	0	11	4,063.77
6	ψ (SP + INT + AREA + SP * AREA), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC)	317.06	0	12	4,063.15
7	ψ (SP + INT + AREA), *p*(SP + INT_OCC + INT_DET)	318.78	0	9	4,071.85
8	ψ (SP + INT), *p*(SP + INT_OCC + INT_DET)	368.52	0	7	4,126.1
9	ψ (SP + INT), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC)	370.16	0	8	4,125.5
10	ψ (SP), *p*(SP + INT_OCC + INT_DET + SP * INT_OCC)	377.19	0	7	4,134.76
11	ψ (SP + INT), *p*(SP)	405.57	0	5	4,167.51
12	ψ (SP), *p*(SP)	412.65	0	4	4,176.73

[a]SP = Species; INT = occupancy interaction between species; INT_OCC = detection interaction between species depending on presence of other species; INT_DET = detection interaction between species depending on detection of other species; AREA = study area; NOISE = weekly background noise level (dBFS).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duaa017/5825670 by DigiTop USDA's Digital Desktop Library user on 28 April 2020