

## Original Articles

# Passive acoustic monitoring and convolutional neural networks facilitate high-resolution and broadscale monitoring of a threatened species

Adam Duarte<sup>a,\*</sup>, Matthew J. Weldy<sup>b</sup>, Damon B. Lesmeister<sup>c</sup>, Zachary J. Ruff<sup>d</sup>,  
Julianna M.A. Jenkins<sup>c</sup>, Jonathon J. Valente<sup>e</sup>, Matthew G. Betts<sup>b</sup>

<sup>a</sup> U.S.D.A. Forest Service, Pacific Northwest Research Station, 3625 93rd Ave SW, Olympia, W.A. 98512, U.S.A

<sup>b</sup> Department of Forest Ecosystems and Society, 3180 SW Jefferson Way, Oregon State University, Corvallis, O.R. 97331, U.S.A

<sup>c</sup> U.S.D.A. Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, O.R. 98512, U.S.A

<sup>d</sup> Department of Fisheries, Wildlife, and Conservation Sciences, 2820 SW Campus Way, Oregon State University, Corvallis, O.R. 97331, U.S.A

<sup>e</sup> U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, College of Forestry, Wildlife and Environment, 602 Duncan Dr., Auburn University, Auburn, A.L. 36849, U.S.A

## ARTICLE INFO

## Keywords:

Bioacoustics

Convolutional neural network

*Brachyramphus marmoratus*

Machine learning

Passive acoustic monitoring

## ABSTRACT

Population monitoring is an essential component of biodiversity conservation and management, but low detection probabilities for rare and/or cryptic species makes estimating abundance and occupancy challenging. Passive acoustic monitoring combined with machine learning algorithms represents a potential path forward to effectively and efficiently monitor the occurrence of rare vocalizing species across entire forest landscapes. Our objectives were to develop and implement a convolutional neural network (PNW-Cnet) to identify vocalizations of a rare and threatened forest nesting bird species – the marbled murrelet (*Brachyramphus marmoratus*) – in the Pacific Northwest, U.S.A., 2018–2021. We used PNW-Cnet predictions from broadscale passive acoustic monitoring data to examine spatiotemporal patterns in the distribution of murrelets. PNW-Cnet showed sufficiently high prediction accuracy (overall precision > 0.9) to enable broadscale population monitoring. Spatiotemporal analysis showed that annual peak murrelet call abundance occurs in ordinal weeks 28–32 (late July–Mid August) but this varied by study area. The greatest number of detections typically occurred in the Olympic Peninsula and Oregon Coast Range where late-successional forest dominates and nearer to ocean habitats. We demonstrate that passive acoustic monitoring can be used to understand intensity of use across broad scales for a rare and cryptic species in addition to the typical detection/non-detection data that are often collected. Passive acoustic monitoring combined with PNW-Cnet offers considerable promise for species distribution modeling and long-term population monitoring for rare species.

## 1. Introduction

Population monitoring is an essential component of biodiversity conservation and management for providing the data and understanding needed for managers to make informed decisions. Although the resolution of data required depends on the context of the decision(s) (reviewed in Conroy and Peterson, 2013), it has become increasingly common to focus on species occurrence to examine population status and trends (Betts et al., 2007; Adams et al., 2013; Lesmeister et al., 2015; Duarte et al., 2021), quantify the effects of management actions on species (Bender et al., 2015; Fuller et al., 2016; Gaylord et al., 2023), and identify unoccupied land management project areas to avoid harm to

species of conservation concern (Evans Mack et al., 2003; Lindenmayer et al., 2017; Appel et al., 2023). Detecting rare species is a central problem in conservation biology because most species of conservation concern tend to be rare (Whittaker, 1965). Indeed, whether a species is detected within an occupied area depends on the number of individuals available for detection, the probability of detecting one or more of those individuals, and the sampling effort (Bayley and Peterson, 2001; Royle and Nichols, 2003). This complicates attempts to directly use monitoring data (particularly when sampling effort is relatively low) to estimate the occurrence of rare and/or cryptic species because they are, by definition, low in abundance and/or hard to detect. Thus, survey efforts that yield no detections for these species are largely considered absence

\* Corresponding author.

E-mail address: [adam.duarte@usda.gov](mailto:adam.duarte@usda.gov) (A. Duarte).

<https://doi.org/10.1016/j.ecolind.2024.112016>

Received 6 March 2024; Received in revised form 7 March 2024; Accepted 8 April 2024

Available online 13 April 2024

1470-160X/© 2024 Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

of evidence, rather than evidence of absence (MacKenzie, 2005).

The marbled murrelet (*Brachyramphus marmoratus*; hereafter murrelet) is a small seabird native to coastal environments along the Pacific Coast from California to the Aleutian Islands, U.S.A. (Nelson, 2020). Despite spending most of its time foraging in nearshore oceanic waters (Northrup et al., 2018; Nelson, 2020), murrelets typically nest in the late-successional, old-growth forests that are generally located within 80 km of the coastline (Whitworth et al., 2000; Hull et al., 2001; Baker et al., 2006; Barbaree et al., 2015; Wilk et al., 2016). Due to estimated declines in abundance at sea, murrelets are listed as threatened from California, U.S.A. to British Columbia, Canada (U.S. Fish and Wildlife Service, 1992; Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2012). Although the threats murrelets face are manifold (Raphael et al., 2002; Betts et al., 2020; Valente et al., 2023; Strong and Duarte, 2023), forest management practices in and adjacent to potential nesting habitat have long been a source of conflict in the Pacific Northwest, U.S.A. Indeed, murrelets were one of the major drivers behind the creation of the Northwest Forest Plan, which guides management on approximately 10 million ha of federally managed forestlands. Therefore, actions aimed at conserving murrelets and their habitats have direct effects on the people and economy of the region (reviewed in Raphael, 2006; Spies et al., 2019).

Murrelet monitoring across forest landscapes is currently conducted through two separate efforts. The first involves relating nest locations to remotely sensed habitat products to estimate status and trends in suitable nest habitat (Huff et al., 2006; Raphael et al., 2011; Raphael et al., 2016; Lorenz et al., 2021). Unfortunately, murrelet nest location data are extremely rare due to the cryptic nature of inland flights, the cost and difficulty of transmitter tagging and tracking birds to their nests, and the remote and rugged nature of the forests used for nest habitat. Moreover, habitat suitability is generally not a good indicator of species occurrence given the dynamic nature in which species use and/or occupy suitable habitats (reviewed in Royle et al., 2012).

The second, more common monitoring method uses audio-visual surveys to detect inland murrelet vocalizations and flight behavior indicative of nesting activity (Evans Mack et al., 2003). Audio-visual surveys involve navigating forested habitats during the pre-dawn period to begin surveys before sunrise in an attempt to hear or visually identify murrelets as they fly at high velocities above and through late-successional, old-growth forest stands with multilayered canopies and large limbs used for nesting (Evans Mack et al., 2003). Detection probabilities are typically low (Bigger et al., 2006; Valente et al., 2021) and most detections are auditory. Consequently, inferring absence with confidence necessitates a substantial number of surveys (Evans Mack et al., 2003).

Although human-based observations have been the standard for surveying murrelets in forests, the field of ecology is undergoing a rapid transformation due to the increasing availability of massive amounts of observational data made possible by technological advancements (reviewed in Tosa et al., 2021; Tuia et al., 2022). Improvements in passive acoustic monitoring with autonomous recording units (ARUs) constitute a promising approach to monitor vocalizing species (Gibb et al., 2018). They also represent a potentially effective alternative for monitoring rare species with low detectability, such as the murrelet. Unfortunately, processing and identifying target species vocalizations in passive acoustic monitoring data have traditionally required manual labeling, which can also be costly and time consuming (Rempel et al., 2019). However, concomitant computational advances have addressed many of the difficulties associated with working with acoustic data, including software packages available to store, manipulate, and document large volumes of data (Katz et al., 2016); analytical methods to streamline the processing of these data (Phillips et al., 2018); and the development of models to classify acoustic detections into species detections (Ruff et al., 2020; Ruff et al., 2021; Kahl et al., 2021). Machine learning algorithms (a form of artificial intelligence) via convolutional neural networks when paired with ARUs represent a potential path

forward to monitor the occurrence of rare vocalizing species effectively and efficiently across broad landscapes (Lesmeister et al., 2021). Our objectives were to conduct passive acoustic monitoring surveys and develop a convolutional neural network (PNW-Cnet) to semi-autonomously identify murrelet “keer” calls (Fig. 1) in large volumes of acoustic data (>1 million h and > 400 TB of acoustic data). Second, we used murrelet detections to examine spatiotemporal patterns in keer calling across two regions in the Pacific Northwest, U.S.A. Finally, we discuss proposed next steps for research and the implications of this work to inform conservation and management decision making for murrelets across forest landscapes.

## 2. Materials and methods

### 2.1. Study area

We conducted passive acoustic monitoring surveys in publicly owned forests managed by the Federal government in the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A. The passive acoustic monitoring program was designed to support northern spotted owl (*Strix occidentalis caurina*) population monitoring (Lesmeister et al., 2021) but objectives were expanded to include monitoring the distributional dynamics of other vocalizing wildlife species across long timespans (Lesmeister and Jenkins, 2022). These forests are comprised of forest stands that are considered to support among the best remaining murrelet nesting habitat in Oregon and Washington (Lorenz et al., 2021).

### 2.2. Data collection

We developed a 5 km<sup>2</sup> hexagon tessellation to form a sampling grid across study areas (Lesmeister et al., 2021). We randomly selected 120 sampling hexagons in each study area (approximately 20 % of available hexagons) that contained ≥ 50 % forest-capable lands and ≥ 25 % federal ownership. Forest-capable lands were lands with soil types, plant associations, and elevations capable of developing into forests (Davis and Lint, 2005). We also avoided sampling adjacent hexagons to minimize the odds of detecting the same individual northern spotted owl in multiple hexagons within a single field season (Lesmeister et al., 2021). Thus, survey hexagons were restricted from high elevation sites and were non-adjacent.

We used Song Meter 4 ARUs (Wildlife Acoustics, Maynard, MA) to conduct the passive acoustic monitoring. These units have a signal-to-noise ratio of approximately 80 dB at 1 kHz and were set to record at a 32 kHz sampling rate. We programmed ARUs to record during crepuscular diel periods from 1 h before sunset to 3 h after sunset and from 2 h before sunrise to 2 h after sunrise, producing 8 h of recordings per day. Within each sampling hexagon we randomly selected five survey station locations (600 survey stations per study area) that were at mid-to-upper slope positions; ≥50 m from roads, trails, and streams to reduce vandalism and excessive background noise; spaced ≥ 500 m

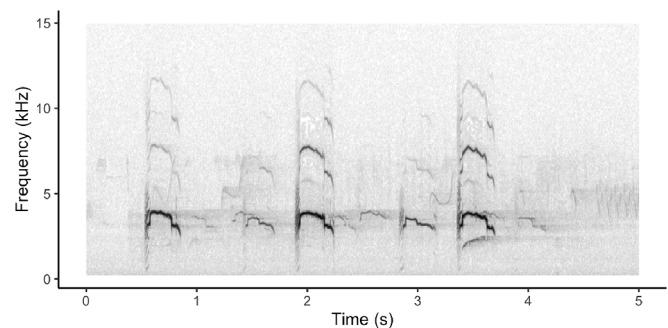


Fig. 1. Image of three “keer” calls, which are made by male and female marbled murrelets (*Brachyramphus marmoratus*).

apart; and located  $\geq 200$  m from the edge of a hexagon. At each survey station, we mounted the ARU to a tree with a diameter at breast height of 15–20 cm to allow the omni-directional microphones to extend past the bole for unobstructed recording ability. We deployed ARUs for a six-week period during March through August in each of the four years (2018–2021), which aligns with the breeding season for murrelets and most of the other forest birds (both resident and migrants) in the region. However, some ARUs remained deployed into October due to the scheduling of field logistics.

We attempted to monitor the same 240 hexagons (120 per study area) in each field season, but the number of hexagons monitored varied based on access and logistical limitations (Table 1). We made two sampling design changes between the 2018 and 2019 field seasons: 1) we reduced the number of survey stations to four (480 survey stations per study area) based on Duchac et al. (2020) that found cumulative detection probability for northern spotted owls exceeded 95 % with four units after six weeks of recording; and 2) we programmed ARUs to additionally record for the first 10 min of every hour (increasing total recording time to approximately 10 h of recording at each station per day) to allow for additional detections of diurnal and nocturnal species.

### 2.3. Convolutional neural network

Murrelet kee calls were detected using two different versions of PNW-Cnet, a deep convolutional neural network developed for semi-automated data processing and identification of multiple species in the passive acoustic recordings (Ruff et al., 2023; Lesmeister and Jenkins, 2022). The two versions used were version 3 (hereafter “PNW-Cnet v3”) and version 4 (“PNW-Cnet v4”), which were similar in structure to previous versions (Ruff et al., 2020; Ruff et al., 2021). However, they differed in the number of target classes recognized and in the training datasets and training procedures used.

PNW-Cnet was implemented in Python using the TensorFlow software library (Abadi et al., 2015) via the Keras functional API (Chollet, 2015; Ruff et al., 2023). Each version of PNW-Cnet consisted of one input layer, six convolutional layers, and two fully connected layers. The input layer accepted image data in the form of an array of pixel values in the range [0, 1]. The first and second convolutional layers each contained  $32 \times 5 \times 5$  filters, the third and fourth convolutional layers each contained  $64 \times 5 \times 5$  filters, and the fifth and sixth convolutional layers each contained  $128 \times 5 \times 5$  filters. All convolutional layers used rectified linear unit (“relu”) activation. During training, each convolutional layer was followed by  $2 \times 2$  max pooling to reduce the total number of trainable parameters and 20 % dropout to minimize overfitting, build redundancy, and reduce interdependence between nodes within each layer. Output from the sixth convolutional layer was flattened and passed to a fully connected layer with 256 nodes, which used relu

activation. Finally, the output layer was a fully connected layer using sigmoid activation, the values of which comprised the output of the model (i.e., the class scores). Sigmoid activation produces floating-point output in the range [0, 1] and is not normalized over the nodes of the output layer. Therefore, the class scores are nominally independent of one another, and each score can be treated as a binary classifier for the corresponding class. The class scores are loosely interpretable as the model’s degree of confidence that a given acoustic segment contains sounds matching a given class. The only structural difference between PNW-Cnet v3 and v4 was the number of nodes in the output layer, which defined the number of target classes recognized by the model. PNW-Cnet v3 had 37 output nodes, while PNW-Cnet v4 had 51 output nodes.

The datasets used to train PNW-Cnet v3 and v4 consisted of spectrograms representing 12-s recording segments (hereafter clips) of audio in the frequency range 0–4000 Hz. Spectrograms were generated as 8-bit grayscale Portable Network Graphic (PNG) image files with resolution  $1000 \times 257$ . Spectrograms were generated using SoX (Sound eXchange; <https://sourceforge.net/projects/sox/>) with the following parameters: Hann window with window length 2048, 50 % window overlap, and a 256-point DFT. The temporal and frequency scales were both linear, so each pixel in the resulting spectrograms covered 0.012 s of time and 15.6 Hz of frequency. Training images had a dynamic range of 0–90 dBFS. Spectrograms could contain signatures of zero or more target classes and were weakly labeled (i.e., the labels we provided to PNW-Cnet during training indicated which target classes were present in each image, but not where the acoustic signatures were located within the image). PNW-Cnet v3 was compiled and trained in August 2020 and was the first version to include the murrelet kee call as a target class. PNW-Cnet v3 was trained on a set of 194,524 images representing 37 target classes, including 1,363 images containing the murrelet kee call class. PNW-Cnet v4 was compiled and trained in May 2021. This version of the model was trained on a set of 426,605 images representing 51 target classes, including 5,757 images containing the murrelet kee call class. Training images for the murrelet class were drawn exclusively from the COA and OLY study areas. Within the PNW-Cnet v3 training dataset, 1,248 (91.6 %) of the images containing the murrelet class were from COA and 115 (8.4 %) were from OLY. Within the PNW-Cnet v4 training dataset, 3,173 (55.1 %) of the images containing the murrelet class were from COA and 2,584 (44.9 %) were from OLY. The large imbalance between COA and OLY in the PNW-Cnet v3 training dataset was not intentional and was due to data availability at the time, but may have affected performance of PNW-Cnet v3 in OLY (see results).

PNW-Cnet v3 and v4 were trained using the Adam optimizer (Kingma and Ba, 2014) with an initial learning rate of 0.001. We used binary cross-entropy as the loss function. During training, the model weights were saved only after epochs in which the validation loss decreased to prevent the model from overfitting to the training set.

**Table 1**

Summary of sampling and processing effort and estimated marbled murrelet (*Brachyramphus marmoratus*) detections in the Oregon Coast Range (COA) and Olympic Peninsula (OLY), 2018–2022. Data from 2020 were processed using PNW-Cnet v3 and data from 2018, 2019, 2021 and 2022 were processed using PNW-Cnet v4. Detections (naïve) for each year are the number of 12-s clips that PNW-Cnet assigned a score  $\geq 0.95$  for the murrelet kee call class. Detections (adjusted) are the number of 12-s clips that met the score threshold for murrelet kee call, multiplied by the precision of the corresponding version of PNW-Cnet for the murrelet class.

Study area	Year	Hexagons sampled	Survey stations	First recording date	Last recording date	Recording time (h)	Volume (TB)	Processing time (h)	Detections (naïve)	Detections (adjusted)
COA	2018	120	579	07 Mar	17 Sep	197,759	82.9	968.5*	53,259	48,072
	2019	106	413	04 Apr	11 Sep	155,222	32.5	461.8	13,920	11,831
	2020	120	471	03 Mar	20 Jul	186,406	39.1	587.9	7,828	4,908
	2021	120	476	03 Mar	04 Aug	217,292	45.5	530.6	17,633	14,370
	2022	117	466	02 Mar	22 Aug	258,513	54.2	635.6	23,337	19,121
OLY	2018	88	434	12 Mar	31 Aug	147,649	61.9	561.1	12,420	10,325
	2019	116	456	15 Apr	10 Sep	178,001	37.3	440.3	14,584	11,997
	2020	119	464	16 Apr	03 Oct	218,971	45.9	654.4	18,946	13,263
	2021	119	471	30 Mar	12 Sep	216,309	45.3	420.9	22,039	18,466
	2022	120	476	28 Mar	20 Sep	264,670	55.5	784.3	26,522	22,617

\*Processing time for the 2018 COA data is extrapolated from the 73% of these data that were processed using high-performance computers. The remaining 27% were processed using desktop computers, and we did not record total processing time for these data.

Additionally, we implemented a learning rate reduction callback, which halved the learning rate if the validation loss did not decrease for five consecutive epochs, with a cooldown period of five epochs. This was intended to allow the model to make finer adjustments as training progressed and the model approached an optimal configuration. PNW-Cnet v3 was trained for 40 epochs using an 80–20 training–validation split, and PNW-Cnet v4 was trained for 50 epochs using a 90–10 training–validation split.

The ARUs stored data in the form of waveform files with duration of either 1 h or 10 min as defined by the recording schedule. We uploaded the acoustic data to a central server and processed using high-performance computers at the Oregon State University Center for Quantitative Life Sciences. We used SoX to generate spectrograms representing non-overlapping 12-s clips of the acoustic data (i.e., 300 clips per hour) in the frequency range 0–4000 Hz, matching the preparation of the training data. We used PNW-Cnet v3 to process audio data from 2020 and used PNW-Cnet v4 to process audio data from 2018, 2019, and 2021. The data from 2018 to 2019 were initially processed using an earlier version of PNW-Cnet that did not identify murrelet kee calls; those data were reprocessed with PNW-Cnet v4 for this analysis. We considered clips with a score  $\geq 0.95$  for the murrelet class to be apparent detections. We computed precision by comparing the scores assigned to clips by each PNW-Cnet version with tags assigned to the same clips by trained human reviewers. At a given score threshold, precision is defined as the proportion of clips confirmed as containing murrelet kee calls (i.e., number of true positives) among clips with a class score meeting or exceeding the score threshold (i.e., number of apparent detections). We estimated the number of murrelet detections as the number of 12-s clips in the audio data to which PNW-Cnet assigned a score exceeding 0.95 for the murrelet class, multiplied by the estimated precision of the appropriate version of PNW-Cnet for the murrelet class in the specific study area (Table 2) rounded to the nearest integer. In addition to processing data with PNW-Cnet, we used the sound pressure level analysis feature in program Kaleidoscope to quantify the mean daily background noise levels at each survey station for each sampling week across seven frequency bands (250 through 1000 Hz), given background noise levels can influence our ability to detect species using ARUs (Appel et al., 2023; Weldon et al., 2023).

#### 2.4. Pnw-cnet performance

We calculated performance metrics for the murrelet class using two different test datasets from our two study areas. The first (2020) test dataset was intended to measure the overall performance of PNW-Cnet v3. This dataset was drawn from audio collected during the 2020 field season and consisted of 12-s clips for which PNW-Cnet v3 had assigned a score  $\geq 0.95$  for any of the 37 target classes. There were 48,876 clips

that met this threshold for the murrelet class in the 2020 data, of which we randomly selected 2,258 clips. All clips in this dataset were reviewed manually by human reviewers and were tagged according to whether they contained any of the target classes for PNW-Cnet v3. We also used the 2020 test dataset to assess overall performance for PNW-Cnet v4 after first removing any clips that had been included in the training dataset for PNW-Cnet v4.

The second (2022) test dataset was intended to measure PNW-Cnet v4's performance on the murrelet class specifically. We identified 12-s clips from the 2022 field season for which the class score assigned by PNW-Cnet v4 for the murrelet class was  $\geq 0.50$ . There were 96,139 clips that met this threshold in the 2022 data, of which we randomly selected 7,193 clips to review manually, tagging the murrelet class as well as any other species or call types that were present and identifiable.

#### 2.5. Spatiotemporal patterns in detection data

We used a hurdle model to quantify variation in murrelet detections, while also quantifying variation in the number of murrelet detections conditional on the survey station having at least one detection. Hurdle models are similar to widely used zero-inflated regression models except hurdle models completely separate zeros from the count process (Mullahy, 1986; Johnson et al., 2005). This approach fits two regression models to the count data simultaneously: a logistic regression model to model the detection/non-detection of the species to estimate habitat use, and a count-based zero-truncated regression model (e.g., Poisson, negative binomial) to model variation in the number of detections when the habitat is being used (i.e., the species was detected). We summed the number of kee call detections estimated for each sampling week and used a negative binomial distribution for the count process because the count data were overdispersed relative to a Poisson distribution. We incorporated covariates in both regression models to capture variability in factors we hypothesized would affect detections: covariates that were an artifact of our sampling were treated as fixed effects and other sources of variability not captured by these factors were treated as random effects. We modeled the detection/non-detection process as an additive function of study area and included year, hexagon, and station within hexagon random effects. Notably, this model describes the probability of absence rather than the probability of use that is generally more common in the ecological literature (Brooks et al., 2017). We modeled the count process as an additive function of study area, weekly average background noise, total survey effort (i.e., recording hours), and survey week, and again included year, hexagon, and station within hexagon random effects.

We then conducted a secondary analysis at the hexagon scale (combining detections from stations within a hexagon) to examine spatiotemporal variation in kee call patterns in relation to late-

**Table 2**

Performance metrics calculated for PNW-Cnet v3 and v4 based on the 2020 test dataset from the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A. PNW-Cnet v3 was tested on 101,403 12-s clips for which PNW-Cnet v3 had assigned a score  $\geq 0.95$  for any of the 37 target classes. PNW-Cnet v4 was tested on the same test dataset after removing clips that were included in its training dataset. Clips = total clips from each study area. Detections (naïve) are the number of 12-s clips that PNW-Cnet assigned a score  $\geq 0.95$  for the marbled murrelet (*Brachyrhamphus marmoratus*) kee call class. Positive Examples = total clips actually containing murrelet kee calls. TP = total clips that were true positives (i.e., clips that scored  $\geq 0.95$  for the murrelet class and contained murrelet calls). FP = total clips that were false positives (i.e., clips that scored  $\geq 0.95$  for the murrelet class and did not contain murrelet calls). TN = total clips that were true negatives (i.e., clips that scored  $< 0.95$  for the murrelet class and did not contain murrelet calls). FN = total clips that were false negatives (i.e., clips that scored  $< 0.95$  for the murrelet class and contained murrelet calls). Precision = TP / Detections (naïve). Recall = TP / Positive examples.

Model version	Study area	Clips	Detections (naïve)	Positive examples	TP	FP	TN	FN	Precision	Recall
PNW-Cnet v3	COA	69,841	1,432	1,457	1,373	59	68,325	84	0.959	0.942
	OLY	31,562	826	672	661	165	30,725	11	0.800	0.984
	Overall	101,403	2,258	2,129	2,034	224	99,050	98	0.901	0.955
PNW-Cnet v4	COA	60,369	1,245	1,380	1,232	13	58,976	148	0.990	0.893
	OLY	27,973	549	561	543	6	27,406	18	0.989	0.968
	Overall	88,342	1,794	1,941	1,775	19	86,382	166	0.989	0.914

successional (mature) forest availability and distance to ocean. We used the Old Growth Structure Index 80 (OGSI 80) for each year to quantify the amount of late-successional forest within each hexagon. The OGSI is a  $30 \times 30$  m resolution raster layer based on imputation of forest inventory and analysis (FIA) plot data onto Landsat imagery (Davis et al., 2022). The index is calculated using measures of old-growth structural elements such as density and diversity of large live trees, density of large snags, and percentage cover of down woody material. The OGSI 80 is derived from OGSI to describe the point (approximately 80 years) at which forests generally start to develop stand structures that represent late-successional forests in the Pacific Northwest. The OGSI 80 is a binary layer, where cells with a value of one are considered late-successional forest pixels and cells with a value of zero are not. We calculated the mean value of all pixels within each hexagon to estimate the proportion/amount of late-successional forest. We estimated distance to ocean as the minimum distance between the centroid of each hexagon and the Pacific Ocean and Salish Sea. We summed the number of kee call detections estimated for each sampling week for each hexagon and fit a negative binomial mixed model to these data. We modeled the count process as an additive function of OGSI 80, distance to ocean, study area, weekly average background noise, total survey effort (i.e., recording hours), survey week, and year, and included a hexagon-level random effect. We then used this model to predict kee call numbers across both study areas in all years to visually depict the intensity of habitat use across these landscapes.

We restricted both analyses to data collected from April through August to align with the period when murrelets typically nest and, by extension, undertake inland flights (Evans Mack et al., 2003). These models were fit in program R (R Core Team, 2020) using the *glmmTMB* package (Brooks et al., 2017). All random effects were assumed to be normally distributed with a mean of zero, and we standardized all continuous covariates to have a mean of zero and standard deviation of one prior to model fitting.

### 3. Results

Our annual sampling effort on each study area ranged from 106 to 120 hexagons (413–579 survey stations) in COA and 88–120 hexagons (434–476 survey stations) in OLY. We used PNW-Cnet v3 to process 405,377 h of audio (ca. 84.9 TB) from 935 survey stations across 239 unique hexagons in 2020, and we used PNW-Cnet v4 to process 1,112,232 h of audio (ca. 305.4 TB) recorded from 2,829 survey stations in 2018, 2019 and 2021 across 239 unique hexagons. We processed approximately 300–400 h of audio data per hour of processing time for a total of approximately 4,625 h of processing time, which is the equivalent to roughly six months of continuous processing over the four years of the study (Table 1).

The 2020 test dataset contained a total of 101,403 12-s clips. This included 2,258 clips for which PNW-Cnet v3 assigned a score  $\geq 0.95$  for the murrelet kee call class. Of the 2,258 apparent detections, manual review confirmed that 2,034 clips contained actual murrelet kee calls, giving an overall precision of 0.901 for PNW-Cnet v3 on the murrelet class (Table 2). When we ran PNW-Cnet v4 on the same test dataset, minus clips that had been included in the training dataset for PNW-Cnet v4 ( $n = 88,342$  clips), there were 1,794 apparent murrelet detections, of which 1,775 were confirmed to contain murrelet kee calls, giving an overall precision of 0.989 for PNW-Cnet v4 on the murrelet class (Table 2).

Model precision varied by study area and threshold (Table 2). Using a threshold of  $\geq 0.95$ , the 2020 test dataset contained 826 apparent murrelet detections from OLY, of which 661 were true positives (i.e., precision for OLY was 0.800). The 2020 test dataset contained 1,432 apparent murrelet detections from COA, of which 1,373 were true positives (i.e., precision for COA was 0.959). Clips in the 2020 test dataset that yielded false positives for the murrelet class often included olive-sided flycatcher (*Contopus cooperi*), nuthatch (*Sitta* spp.), hermit

thrush (*Catharus guttatus*), varied thrush (*Ixoreus naevius*), and “scream” calls from various raptors (Accipitridae).

Of the 7,193 clips in the 2022 test dataset, which all had class scores  $\geq 0.50$  for the murrelet kee call class, manual review confirmed that 5,665 clips actually contained murrelet kee calls. Hence, for the kee call class, overall precision was 0.788 at a score threshold of 0.50. Precision increased with increasing score threshold to a maximum of 0.979 at a score threshold of 0.99. Conversely, recall decreased with increasing score threshold. All 5,665 instances of kee calls in the 2022 test dataset were detected at a score threshold of 0.50, while 2,769 of these clips (48.9 %) were detected at a score threshold of 0.99. Detailed results for PNW-Cnet v4 on the 2022 test dataset are shown in Table 3.

The months in which ARUs were operational varied by year but spanned March through October. We used a 0.95 threshold and accounted for precision of PNW-Cnet for each study area and year for all subsequent findings. Although we had substantially fewer recording hours in September and October, as expected, we did not detect murrelet kee calls during these months (Fig. 2). We did, however, detect murrelet kee calls in March, albeit in lower numbers. Most of our call detections occurred from approximately July 9th to August 12th.

Results from our hurdle model indicate that murrelet habitat use did not differ based on study area (Table 4). Most of the unaccounted for variability (86.02 %) in habitat use was attributed to differences among hexagons, followed by stations within hexagons (12.33 %), and years (1.65 %). As expected, we found the number of call detections increased later in the season and with more recording hours but decreased as background noise increased (albeit the effect of background noise was not significant). When murrelets were present, we found there were significantly more calls in the COA study area compared to the OLY study area. Most of the unaccounted for variability (61.10 %) in call detection counts was attributed to differences among hexagons, followed by stations within hexagons (30.33 %), and years (8.56 %).

We had similar results when analyzing the data at the hexagon scale (Table 5). The number of detections increased with survey effort, decreased with increasing background noise, and was lower in the OLY study area. Although this analysis indicated call detection decreased later in the season, the effect size was relatively small and not statistically significant. Call detections were higher in 2018 when compared to the other sample years. Importantly and consistent with previous studies (e.g., Betts et al., 2020; Valente et al., 2023), we found call detections increased with increasing late-successional forest and decreased as the distance to ocean increased (Fig. 3).

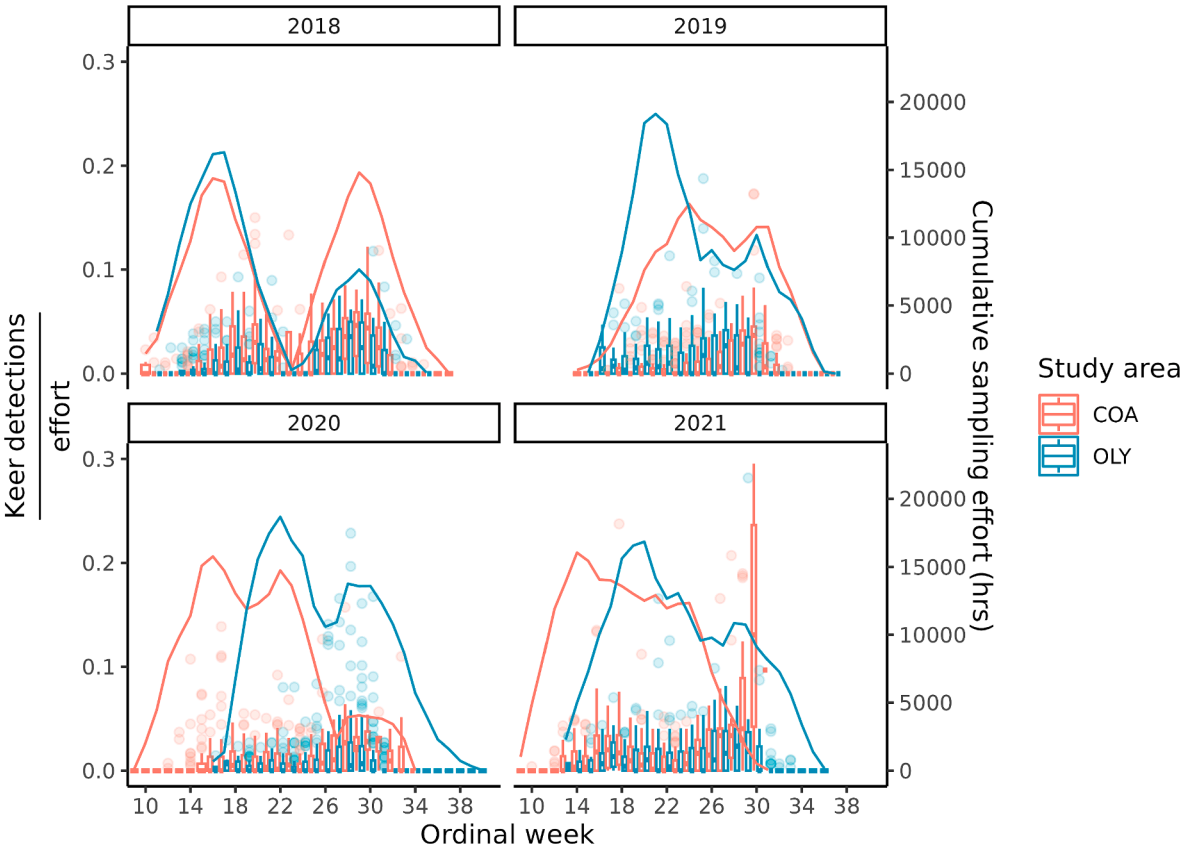
### 4. Discussion

We used data collected as part of a broader-scale passive acoustic monitoring program to conduct the first call phenology study for murrelets across two large regions in the Pacific Northwest, U.S.A. In doing so, we develop, apply, and evaluate a convolutional neural network (PNW-Cnet) that we used to accurately identify murrelet kee calls while processing large volumes of acoustic data in a relatively short time-frame. Overall, we found that PNW-Cnet provided a streamlined approach to find murrelet kee calls in our acoustic data. Our exploratory analysis of murrelet kee call patterns represents a shift in what is possible when quantifying murrelet distributional dynamics in forest habitats. Indeed, we demonstrated that passive acoustic monitoring is not limited to simply detection/non-detection data, and we can begin to understand intensity of use across broad scales for rare and/or cryptic species that vocalize. Coupling passive acoustic monitoring and machine learning models provides a powerful approach for new murrelet research and will undoubtedly open opportunities for broadscale inland monitoring of murrelet populations to inform natural resource management decisions.

There are numerous advantages to our semi-autonomous approach when compared to other currently implemented murrelet inland monitoring approaches, such as audio-visual surveys or nest searching.

**Table 3**  
Precision (Prec.) versus score threshold for PNW-Cnet v4 based on the 2022 test dataset from the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A. The dataset consisted of 7,193 12-s clips to which PNW-Cnet v4 assigned a score  $\geq 0.50$  for the marbled murrelet (*Brachyramphus marmoratus*) kee call class, randomly sampled from all clips ( $n = 96,139$ ) that met this criterion in the data collected in 2022. Det. (naïve) = total clips in the test dataset that met the score threshold. Det. (true) = total clips that met the score threshold and were confirmed to contain murrelet kee calls. Precision = True Positives / Det. (naïve).

Study area	Threshold = 0.50			Threshold = 0.75			Threshold = 0.90			Threshold = 0.95			Threshold = 0.99		
	Det. (naïve)	Det. (true)	Prec.	Det. (naïve)	Det. (true)	Prec.	Det. (naïve)	Det. (true)	Prec.	Det. (naïve)	Det. (true)	Prec.	Det. (naïve)	Det. (true)	Prec.
COA	3,251	2,679	0.824	2,576	2,310	0.897	2,082	1,961	0.942	1,802	1,731	0.961	1,263	1,245	0.986
OLY	3,942	2,986	0.757	2,977	2,580	0.867	2,419	2,210	0.914	2,093	1,972	0.942	1,506	1,466	0.973
Overall	7,193	5,665	0.788	5,553	4,890	0.881	4,501	4,171	0.927	3,895	3,703	0.951	2,769	2,711	0.979



**Fig. 2.** Depiction of relative kee call detections (boxplots) and survey effort (recording hours: lines) for marbled murrelet (*Brachyramphus marmoratus*) in the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A., 2018–2021. Relative kee call detections were estimated as the product of the number of kee calls detected for each hexagon and the processing model-specific precision divided by the hexagon specific recording effort. Note that variation in survey effort is related to field logistics and schedule, recording schedules, and equipment functionality (see Methods).

Foremost, collecting passive acoustic data is far less intrusive to the species than nest searching that involves catching, transmitter tagging, and tracking individual birds (Baker et al., 2006; Barbaree et al., 2014; Wilk et al., 2016). Secondly, our monitoring approach is also far less labor intensive than nest searching via telemetry, traditional ground-based nest searches (Baker et al., 2006; Hamer et al., 2021), and the audio-visual surveys protocols typically used (Evans Mack et al., 2003). Although comparative costs are difficult to quantify precisely, passive acoustic monitoring allows biologists to sample broader spatial areas at finer-temporal resolutions (i.e., across all times of the diel cycle) without a substantial increase in effort. Third, because ARUs can record continuously for vocalizations, our acoustic approach is likely to improve detectability compared to human-based audio-visual surveys which typically last only a couple of hours (e.g., Evans Mack et al., 2003). Fourth, because the acoustic recordings can be stored indefinitely, these data can be double-checked or revisited to answer additional questions regarding distributions of other vocalizing species,

phenology of murrelet call activity, or inter-specific effects on species distributions. Fifth, because longitudinal data on inland murrelet habitat use do not currently exist, establishment of permanent recording stations could help elucidate the relative role of local habitat characteristics, site fidelity, and climactic and at-sea conditions in driving changes in breeding distributions through time (Betts et al., 2020). Finally, with relatively small additions, sound broadcast functionality could be incorporated into the recording systems to investigate how environmental factors interact with social cues to shape murrelet distribution patterns (Valente et al., 2021).

Conversely, our automated approach to recording murrelet vocalizations does have a downside, in that it precludes visual observations. Traditional surveys rely on human-based observations of inland murrelets to document behaviors including overhead circling, sub-canopy flights, and landings in nest trees, which are assumed to be more reliable indicators of nesting activity than simple aural detections (Evans Mack et al., 2003). Preliminary evidence suggests that patterns in

**Table 4**

Parameter estimates from a mixed effects negative binomial hurdle model used to quantify variation in detected marbled murrelet (*Brachyramphus marmoratus*) kee calls at survey stations in the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A., 2018–2021.

Model	Parameter	Mean	SE	Z	p-value	Variance	SD
Zero-inflation	Intercept	1.015	0.215	4.731	<0.001		
	Study area: OLY	0.268	0.244	1.098	0.272		
	RE: Year					0.063	0.252
	RE: Hexagon					3.297	1.816
	RE: Station within hexagon					0.473	0.688
Count	Intercept	0.794	0.049	16.079	<0.001		
	Background noise	−0.007	0.012	−0.619	0.536		
	Julian week	0.114	0.012	9.615	<0.001		
	Study area: OLY	−0.010	0.029	−2.583	0.010		
	Survey effort	0.064	0.013	5.042	<0.001		
	RE: Year					0.007	0.082
	RE: Hexagon					0.048	0.219
	RE: Station within hexagon					0.024	0.154
	Dispersion	22.6					

**Table 5**

Parameter estimates from a mixed effects negative binomial model used to quantify variation in detected marbled murrelet (*Brachyramphus marmoratus*) kee calls at the hexagon scale in the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A., 2018–2021.

Parameter	Mean	SE	Z	p-value	Variance	SD
Intercept	0.869	0.110	7.906	<0.001		
Background noise	−0.137	0.021	−6.395	<0.001		
Distance to ocean	−1.001	0.077	−13.063	<0.001		
Julian week	−0.014	0.023	−0.620	0.535		
OGSI 80	0.549	0.077	7.102	<0.001		
Study area: OLY	−0.282	0.151	−1.875	0.061		
Survey effort	0.576	0.021	27.472	<0.001		
Year: 2019	−0.268	0.049	−5.535	<0.001		
Year: 2020	−0.669	0.049	−13.792	<0.001		
Year: 2021	−0.244	0.052	−4.724	<0.001		
RE: Hexagon					1.146	1.071
Dispersion	1.07					

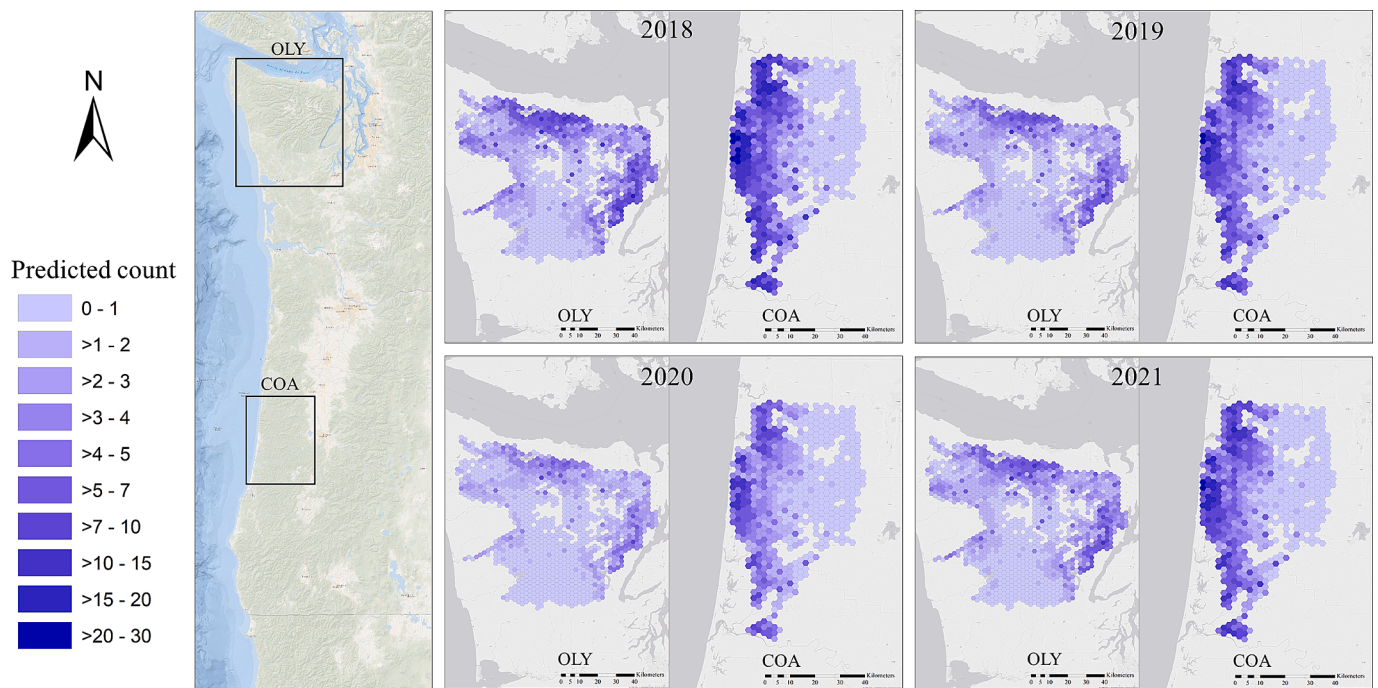
vocalizations could help distinguish areas of prospecting activity from those where indications of nesting activity have been confirmed (Adam Duarte, unpublished data), although further research is required. Yet regardless of whether breeding can be confirmed via audio recordings, passive acoustic monitoring can readily be applied to help managers identify potential nest sites, and thus prioritize areas that may require further investigation using more traditional survey methods (i.e., adaptive cluster sampling).

Overall, we found that both versions of the PNW-Cnet model (v3 and v4) were effective at detecting murrelet kee calls with relatively high precision in our study areas. Because the two versions of PNW-Cnet were structurally similar and because most clips used to train PNW-Cnet v3 were subsequently also used to train PNW-Cnet v4, we expected the two versions to behave similarly on classes that were included in both versions. The performance of PNW-Cnet v3 was less evenly distributed between study areas while PNW-Cnet v4 was more consistent. This may be attributable to the more balanced training dataset used for PNW-Cnet v4 and/or to the addition of new target classes for sounds that previously produced false positives for murrelets and that were not distributed evenly between different study areas. Measures of precision depend on the composition of the datasets on which they are based, and these measures can be difficult to generalize to real-world use. The relative abundance of positive examples (e.g., real murrelet calls) versus sounds likely to produce false positive detections has a strong influence on measured precision, but the array of sounds likely to produce false positives for a given class is difficult to characterize in advance. Once

identified, sources of false positives can be included as target classes in future versions of the model, allowing error rates to be reduced iteratively over time. The much lower incidence of false positive murrelet detections from PNW-Cnet v4 indicates that we succeeded in correcting at least some of the errors commonly made by PNW-Cnet v3. The apparent strong increase in precision of PNW-Cnet v4 over PNW-Cnet v3 based on the 2020 test dataset is also likely an artifact of how this test dataset was constructed. The 2020 test dataset consisted of clips that produced high-confidence detections of the PNW-Cnet v3 target classes, including murrelet kee calls. Hence, these clips had effectively been pre-screened by PNW-Cnet v3 before being processed using PNW-Cnet v4. The measured precision of PNW-Cnet v4 on the 2022 test dataset is likely more reflective of real-world performance, as these clips were randomly sampled from apparent murrelet detections in the 2022 data. PNW-Cnet will continue to be updated as more data become available, and we suggest that the latest version of PNW-Cnet be used by those interested in semi-automating murrelet detections.

The performance of PNW-Cnet v4 on the 2022 test dataset at varying thresholds illustrates the essential tradeoff between precision and recall as a function of score threshold. Setting a higher score threshold inevitably results in higher precision (i.e., fewer false positives) at the cost of lower recall (i.e., more false negatives or missed detections). The relative importance of precision and recall depends on project goals. For rare and/or elusive species, a low threshold can help to maximize species detectability and allow for the quantification of finer resolution call phenology studies (i.e., call patterns within a day). However, this may also necessitate considerable review to identify and omit false positive detections. Conversely, a high threshold can virtually eliminate false positive detections. This would allow for easy quantification of activity levels and comparisons across sites or years, but only if the target species vocalizes frequently enough and/or sampling effort is high enough that the lowered detectability is not an issue.

Our analysis of murrelet kee call patterns allowed us to decompose variability in these data related to our sampling design and to examine broad-scale ecological factors driving spatiotemporal distributions. The relationships uncovered between the number of call detections and background noise and survey effort are most certainly related to the detectability of the call within the audio data and not related to the ecology of the species. However, the effect of ordinal week on the number of call detections at survey stations is likely related to the breeding behavior of the species, where murrelets increase their propensity to undertake inland flights as they switch from finding suitable nesting habitat (i.e., prospecting) to incubating eggs to feeding young. Why the effect of ordinal week decreased as the scale of the analysis increased is unclear and warrants further investigation. Our multi-scale sampling design (i.e., stations within hexagon) allowed for the



**Fig. 3.** Mean predicted kee call counts for marbled murrelet (*Brachyramphus marmoratus*) in the Oregon Coast Range (COA) and Olympic Peninsula (OLY), U.S.A., 2018–2021. Predictions were made using the results from the hexagon scale analysis while assuming the mean value for weekly average background noise, total survey effort (i.e., recording hours), and survey week.

estimation of habitat use at multiple spatial scales. Still, a sample unit should represent a distinct unit that has relative homogeneity to accurately measure the response and covariates to be considered during analyses (Duarte and Peterson, 2021). The greater variability in call detections at a survey station among hexagons (relative to within hexagons) indicates that this scale is appropriate when modeling murrelet distribution dynamics across landscapes, which is similar to current northern spotted owl monitoring efforts (Appel et al., 2023; Weldy et al., 2023) and why we opted to subsequently analyze the data at the hexagon scale. Although the variability in call detections at survey stations attributed to year was relatively low, both analyses did find call detections varied by year. Some of this variability might be associated with the version of PNW-Cnet used each year; however, it is also reasonable to assume some of this variability is related to variation in nest habitat use and overall investment in nesting across years. Call detections increased with increasing late-successional forest and were higher in hexagons closer to foraging habitat (i.e., the Pacific Ocean and Salish Sea), suggesting our approach documents patterns that are in general agreement with the known breeding ecology of the species (Betts et al., 2020). However, the degree to which these patterns in kee call detections reflect murrelet prospecting vs. nesting activity requires further investigation.

The detection of kee calls is not currently considered an indication of murrelet nesting status, so call detections do not currently afford any protection status for the forest habitats they occur within nor sanction forest management practices to occur in stands that lack auditory detections. However, most murrelet detections using audio-visual surveys are auditory, and the recently released murrelet audio-visual survey protocol revision includes a survey option that only considers call detection information (Pacific Seabird Group, 2024). Therefore, call detections using ARUs, when paired with PNW-Cnet, may see near-term use for murrelet regulatory monitoring efforts across the region. Thus, it would be worthwhile to formally estimate detection probabilities of murrelets when using ARUs and PNW-Cnet across a range of conditions to quantify and compare the survey effort necessary to infer murrelet absence under different levels of certainty.

By integrating technological advances and computational advances, we were able to explore high-resolution patterns in call detections for a rare and highly cryptic seabird in remote forest habitats at a broad scale. This study represents the first broad-scale call phenology study for murrelets and the first in-depth exploration of the capabilities PNW-Cnet provides for murrelet monitoring. Importantly, PNW-Cnet is publicly available and can be used by managers as a tool to process large volumes of their own acoustic data in near real-time (Ruff et al., 2023), which lowers the barrier to adopting a passive survey approach to monitor murrelet populations. Collectively, this study highlights the potential use of passive acoustic monitoring in the next chapter of murrelet research and monitoring to inform conservation and management decisions for this rare and cryptic species across forest landscapes.

#### CRediT authorship contribution statement

**Adam Duarte:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Matthew J. Weldy:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Damon B. Lesmeister:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Zachary J. Ruff:** Visualization, Validation, Software, Methodology, Data curation, Writing – review & editing. **Julianna M.A. Jenkins:** Writing – review & editing, Data curation, Methodology. **Jonathon J. Valente:** Writing – review & editing. **Matthew G. Betts:** Writing – review & editing, Conceptualization.

#### Declaration of competing interest

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

## Data availability

Data will be made available on request.

## Acknowledgements

This work was funded by the U.S.D.A. Forest Service and the U.S.D.I. Bureau of Land Management and National Park Service. We would like to thank D. Culp, L. Duchac, S. Gremel, A. Thomas, and everyone else involved in collecting data and verifying detections. The neural network development and additional programming work were done with support from C. Sullivan and the Center for Quantitative Life Sciences at Oregon State University. This research was also partly supported by the College of Forestry at Oregon State University. We thank Z. Yang for his assistance in accessing the Old Growth Structure Index raster layers and B. Vernasco for his assistance in creating Fig. 1. The use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## References

- Abadi, M., Agarwal, A., Barham, P., Brevdo, E., Chen, Z., Citro, C., Corrado, G., Davis, A., Dean, J., Devin, M., Ghemawat, S., Goodfellow, I., Harp, A., Irving, G., Isard, M., Jia, Y., Jozefowicz, R., Kaiser, L., Kudler, M., Levenberg, J., Mané, D., Monga, R., Moore, S., Murray, D., Olah, C., Schuster, M., Shlens, J., Steiner, B., Sutskever, I., Talwar, K., Tucker, P., Vanhoucke, V., Vasudevan, V., Viégas, F., Vinyals, O., Warden, P., Wattenberg, M., Wicke, M., Yu, Y., Zheng, X., 2015. Tensorflow: Large-scale machine learning on heterogeneous systems. [online] URL: <https://www.tensorflow.org/>.
- Adams, M.J., Miller, D.A.W., Muths, E., Corn, P.S., Campbell Grant, E.H., Bailey, L.L., Fellers, G.M., Fisher, R.N., Sadinski, W.H., Waddle, H., Walls, S.C., 2013. Trends in amphibian occupancy in the United States. *PLoS ONE* 8, e64347.
- Appel, C.L., Lesmeister, D.B., Duarte, A., Davis, R.J., Weldy, M.J., Levi, T., 2023. Using passive acoustic monitoring to estimate northern spotted owl landscape use and pair occupancy. *Ecosphere* 14, e4421.
- Baker, L.M., Peery, M.Z., Burkett, E.E., Singer, S.W., Suddjian, D.L., Bessinger, S.R., 2006. Nesting habitat characteristics of the marbled murrelet in central California redwood forests. *The Journal of Wildlife Management* 70, 939–946.
- Barbaree, B.A., Nelson, S.K., Dugger, B.D., Roby, D.D., Carter, H.R., Whitworth, D.L., Newman, S.H., 2014. Nesting ecology of marbled murrelets at a remote mainland fjord in southeast Alaska. *The Condor* 116, 173–184.
- Barbaree, B.A., Nelson, S.K., Dugger, B.D., 2015. Marine space use by marbled murrelets *Brachyramphus marmoratus* at a mainland fjord system in southeast Alaska. *Marine Ornithology* 43, 1–10.
- Bayley, P.B., Peterson, J.T., 2001. An approach to estimate probability of presence and richness of fish species. *Transactions of the American Fisheries Society* 130, 620–633.
- Bender, M.J., Castleberry, S.B., Miller, D.A., Wigley, T.B., 2015. Site occupancy of foraging bats on landscapes of managed pine forest. *Forest Ecology and Management* 336, 1–10.
- Betts, M.G., Forbes, G.J., Diamond, A.W., 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* 21, 1046–1058.
- Betts, M.G., Northrup, J.M., Guerrero, J.A.B., Adrean, L.J., Nelson, S.K., Fisher, J.L., Gerber, B.D., Garcia-Heras, M.-S., Yang, Z., Roby, D.D., Rivers, J.W., 2020. Squeezed by a habitat split: Warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. *Conservation Letters* 13, e12745.
- Bigger, D., Peery, M.Z., Chinnici, S., Courtney, S.P., 2006. Efficacy of audiovisual and radar surveys for studying marbled murrelets in inland habitats. *The Journal of Wildlife Management* 70, 505–516.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. *glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9, 378–400.
- Chollet, F., 2015. Keras. [Online] <https://keras.io>.
- Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2012. COSEWIC assessment and status report on the marbled murrelet *Brachyramphus marmoratus* in Canada. COSEWIC, Ottawa, Canada.
- Conroy, M.J., Peterson, J.T., 2013. *Decision Making in Natural Resource Management: A Structured Approach*. John Wiley and Sons, Hoboken, New Jersey, U.S.A. Adaptive Approach.
- Davis, R.J., Lint, J., 2005. Habitat status and trends. Pages 21–82 in J. Lint, editor. Status and trends of northern spotted owl populations and habitat. PNW-GTR-648. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
- Davis, R.J., Bell, D.M., Gregory, M.J., Yang, Z., Gray, A.N., Healey, S.P., Stratton, A.E., 2022. Northwest Forest Plan—the first 25 years (1994–2018): Status and trends of late-successional and old-growth forests. Gen. Tech. Rep. PNW-GTR-1004. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 82 p.
- Duarte, A., Pearl, C.A., McCreary, B., Rowe, J.C., Adams, M.J., 2021. An updated assessment of status and trend in the distribution of the Cascades frog (*Rana cascadae*) in Oregon, U.S.A. *Herpetological Conservation and Biology* 16, 361–373.
- Duarte, A., Peterson, J.T., 2021. Space-for-time is not necessarily a substitution when monitoring the distribution of pelagic fishes in the San Francisco Bay-Delta. *Ecology and Evolution* 11, 16727–16744.
- Duchac, L.S., Lesmeister, D.B., Dugger, K.M., Ruff, Z.J., Davis, R.J., 2020. Passive acoustic monitoring effectively detects northern spotted owls and barred owls over a range of forest conditions. *The Condor* 122, 1–22.
- Evans Mack, D., Ritchie, W.P., Nelson, S.K., Kuo-Harrison, E., Harrison, P., Hamer, T.E., 2003. Methods for surveying marbled murrelets in forests: A revised protocol for land management and research. Pacific Seabird Group.
- Fuller, A.K., Linden, D.W., Royle, J.A., 2016. Management decision making for fisher populations informed by occupancy modeling. *The Journal of Wildlife Management* 80, 794–802.
- Gaylord, M.A., Duarte, A., McComb, B.C., Ratliff, J., 2023. Passive acoustic recorders increase white-headed woodpecker detectability in the Blue Mountains. *Journal of Field Ornithology* 94 in press.
- Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution* 10, 169–185.
- Hamer, T.E., Nelson, S.K., Jones, J., Verschuyll, J., 2021. Marbled murrelet nest site selection at three fine spatial scales. *Avian Conservation and Ecology* 16, 4.
- Huff, M.H., Raphael, M.G., Miller, S.L., Nelson, S.K., Baldwin, J., 2006. Northwest Forest Plan the first 10 years (1994–2003): Status and trends of populations and nesting habitat for the marbled murrelet. Gen. Tech. Rep. PNW-GTR-650. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 149 p.
- Hull, C.L., Kaiser, G.W., Loughheed, C., Loughheed, L., Boyd, S., Cooke, F., Danchin, E., 2001. Intraspecific variation in commuting distance of marbled murrelet (*Brachyramphus marmoratus*): Ecological and energetic consequences of nesting further inland. *The Auk* 118, 1036–1046.
- Johnson, N.L., Kemp, A.W., Kotz, S., 2005. *Univariate Discrete Distributions*, Third edition. John Wiley and Sons, Hoboken, New Jersey, U.S.A.
- Kahl, S., Wood, C.M., Eibl, M., Klinck, H., 2021. Birdnet: A deep learning solution for avian diversity monitoring. *Ecological Informatics* 61, 101236.
- Katz, J., Hafner, S.D., Donovan, T., 2016. Tools for automated acoustic monitoring within the R package *monitoR*. *Bioacoustics* 25, 197–210.
- Kingma, D.P., Ba, J.L., 2014. Adam: A method for stochastic optimization. International Conference on Learning Representation 2015, San Diego, California, U.S.A.
- Lesmeister, D.B., Appel, C.L., Davis, R.J., Yackulic, C.B., Ruff, Z.J., 2021. Simulating the effort necessary to detect changes in northern spotted owl (*Strix occidentalis caurina*) populations using passive acoustic monitoring. Res. Pap. PNW-RP-618. Volume PNW-RP-618. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
- Lesmeister, D.B., Jenkins, J.M.A., 2022. Integrating new technologies to broaden the scope of northern spotted owl monitoring and linkage with USDA forest inventory data. *Frontiers in Forests and Global Change* 5, 966978.
- Lesmeister, D.B., Nielsen, C.K., Schaubert, E.M., Helligren, E.C., 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. *Wildlife Monographs* 191, 1–61.
- Lindenmayer, D.B., Crane, M., Evans, M.C., Maron, M., Gibbons, P., Bekessy, S., Blanchard, W., 2017. The anatomy of a failed offset. *Biological Conservation* 210, 286–292.
- Lorenz, T.J., Raphael, M.G., Young, R.D., Lynch, D., Nelson, S.K., McIver, W.R., 2021. Status and trend of nesting habitat for the marbled murrelet under the Northwest Forest Plan, 1993 to 2017. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p. 64.
- MacKenzie, D.I., 2005. What are the issues with presence-absence data for wildlife managers? *The Journal of Wildlife Management* 69, 849–860.
- Mullahy, J., 1986. Specification and testing in some modified count data models. *Journal of Econometrics* 33, 341–365.
- Nelson, S.K., 2020. Marbled Murrelet (*brachyramphus marmoratus*), Version 1.0. in *Birds of the World* (a.f. Cornell Lab of Ornithology, Ithaca, NY, USA).
- Northrup, J.M., Rivers, J.W., Nelson, S.K., Roby, D.D., Betts, M.G., 2018. Assessing the utility of satellite transmitters for identifying nest locations and foraging behavior of the threatened marbled murrelet *Brachyramphus marmoratus*. *Marine Ornithology* 46, 47–55.
- Pacific Seabird Group, 2024. A revised protocol for Marbled Murrelets in forests. Pacific Seabird Group Technical Publication Number 6. Available from <https://pacificseabirdgroup.org/psg-publications/technical-publications/>.
- Phillips, Y.F., Towsey, M., Roe, P., 2018. Revealing the ecological content of long-duration audio-recordings of the environment through clustering and visualisation. *PLOS ONE* 13, e0193345.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raphael, M.G., 2006. Conservation of the marbled murrelet under the Northwest Forest Plan. *Conservation Biology* 20, 297–305.
- Raphael, M.G., Falxa, G.A., Dugger, K.M., Galleher, B.M., Lynch, D., Miller, S.L., Nelson, S.K., Young, R.D., 2011. Northwest Forest Plan the first 15 years (1994–2008): Status and trend of nesting habitat for the marbled murrelet. Gen. Tech. Rep. PNW-GTR-848. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.
- Raphael, M.G., Falxa, G.A., Lynch, D., Nelson, S.K., Pearson, S.F., Shirk, A.J., Young, R. D., 2016. Status and trend of nesting habitat for the marbled murrelet under the Northwest Forest Plan. In: G.A. Falxa and M.G. Raphael, tech. coords. Northwest Forest Plan—the first 20 years (1994–2013): Status and trend of marbled murrelet populations and nesting habitat. Gen. Tech. Rep. PNW-GTR-933. Portland, OR: U.S.

- Department of Agriculture, Forest Service, Pacific Northwest Research Station: 37–94.
- Raphael, M.G., Evans Mack, D., Marzluff, J.M., Luginbuhl, J.M., 2002. Effects of forest fragmentation on populations of the marbled murrelet. *Studies in Avian Biology* 25, 221–235.
- Rempel, R.S., Jackson, J.M., Van Wilgenburg, S.L., Rodgers, J.A., 2019. A multiple detection state occupancy model using autonomous recordings facilitates correction of false positive and false negative observation errors. *Avian Conservation and Ecology* 14, 1.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777–790.
- Royle, J.A., Chandler, R.B., Yackulic, C., Nichols, J.D., 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution* 3, 545–554.
- Ruff, Z.J., Lesmeister, D.B., Duchac, L.S., Padmaraju, B.K., Sullivan, C.M., 2020. Automated identification of avian vocalizations with deep convolutional neural networks. *Remote Sensing in Ecology and Conservation* 6, 79–92.
- Ruff, Z.J., Lesmeister, D.B., Appel, C.L., Sullivan, C.M., 2021. Workflow and convolutional neural network for automated identification of animal sounds. *Ecological Indicators* 124, 107419.
- Ruff, Z.J., Lesmeister, D.B., Jenkins, J.M.A., Sullivan, C.M., 2023. PNW-Cnet v4: Automated species identification for passive acoustic monitoring. *SoftwareX* 23, 101473.
- Spies, T.A., Long, J.W., Charnley, S., Hessburg, P.F., Marcot, B.G., Reeves, G.H., Lesmeister, D.B., Reilly, M.J., Ceveny, L.K., Stine, P.A., Raphael, M.G., 2019. Twenty-five years of the Northwest Forest Plan: What have we learned? *Frontiers in Ecology and the Environment* 17, 511–520.
- Strong, C.S., Duarte, A., 2023. Reproductive indices of common murre *Uria aalge* and marbled murrelets *Brachyramphus marmoratus* indicate murrelets are more resilient during poor years. *Marine Ornithology* 51, 187–194.
- Tosa, M.I., Dziedzic, E.H., Appel, C.L., Urbina, J., Massey, A., Ruprecht, J., Eriksson, C.E., Dolliver, J.E., Lesmeister, D.B., Betts, M.G., Peres, C.A., Levi, T., 2021. The rapid rise of next-generation natural history. *Frontiers in Ecology and Evolution* 9, 698131.
- Tuia, D., Kellenberger, B., Beery, S., Costelloe, B.R., Zuffi, S., Risse, B., Mathis, A., Mathis, M.W., van Langevelde, F., Burghardt, T., Kays, R., Klinck, H., Wikelski, M., Couzin, I.D., van Horn, G., Crofoot, M.C., Stewart, C.V., Berger-Wolf, T., 2022. Perspectives in machine learning for wildlife conservation. *Nature Communications* 13, 792.
- U.S. Fish and Wildlife Service, 1992. Determination of the threatened status for the Washington, Oregon, and California population of the marbled murrelet. *Federal Register* 57, 45328–45337.
- Valente, J.J., Nelson, S.K., Rivers, J.W., Roby, D.D., Betts, M.G., 2021. Experimental evidence that social information affects habitat selection in marbled murrelets. *Ornithology* 138, ukaa086.
- Valente, J.J., Rivers, J.W., Yang, Z., Nelson, S.K., Northrup, J.M., Roby, D.D., Meyer, C. B., Betts, M.G., 2023. Fragmentation effects on an endangered species across a gradient from the interior to edge of its range. *Conservation Biology* e14091.
- Weldy, M.J., Lesmeister, D.B., Yackulic, C.B., Appel, C.L., McCafferty, C., Wiens, J.D., 2023. Long-term monitoring in transition: Resolving spatial mismatch and integrating multistate occupancy data. *Ecological Indicators* 146, 109815.
- Whittaker, R.H., 1965. Dominance and diversity in land plant communities: Numerical relations of species express the importance of competition in community function and evolution. *Science* 147, 250–260.
- Whitworth, D.L., Nelson, S.K., Newman, S.J., Van Vliet, G.B., Smith, W.P., 2000. Foraging distances of radio-marked marbled murrelets from inland areas in southeast Alaska. *The Condor* 102, 452–456.
- Wilk, R.J., Raphael, M.G., Bloxton Jr, T.D., 2016. Nesting habitat characteristics of marbled murrelets occurring in near-shore waters of the Olympic Peninsula, Washington. *Journal of Field Ornithology* 87, 162–175.