



# Aerial hearing thresholds and ecoacoustics of a threatened pursuit-diving seabird, the marbled murrelet *Brachyramphus marmoratus*

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**ABSTRACT:** As humans increasingly utilize sensitive coastal areas, diving seabirds like the marbled murrelet *Brachyramphus marmoratus* face a unique combination of exposure to pervasive anthropogenic sound and acoustically mediated disturbances in terrestrial and marine environments. Despite its threatened status, the sound sensitivities and sensory ecology of this species are unknown, limiting any predictions of the frequencies or sound levels that may induce acoustic impacts. In this study, we measured electrophysiological aerial hearing thresholds for 10 wild individuals captured, sedated, examined inside a field-deployed anechoic chamber and subsequently released. Auditory responses were detected across a 0.5 to 6 kHz frequency range. The median auditory threshold was lowest at 2 kHz (33 dB), while hearing was generally sensitive between 0.75 and 3.8 kHz. *B. marmoratus* thresholds were elevated compared to other studied alcid species. In-air sensitivities were used to provide an initial prediction of underwater hearing thresholds. To further explore the auditory sensory ecology of this solitary-nesting species, hearing data were also compared to short-term recordings (5 d) of the aerial soundscape of a marbled murrelet nesting habitat. The soundscape contained both abiotic and biotic sounds that contributed to broadband sound levels of 46–55 dB re: 20 µPa rms (0.2–10 kHz). This comparatively quiet habitat enabled relatively frequent detection of anthropogenic sounds within the soundscape. Energy from this acoustic pollution consistently overlapped marbled murrelet sound sensitivities, indicating that the species is susceptible to disturbance from a range of noise types.

**KEY WORDS:** Hearing · Noise · Soundscape · Seabird · Sensory ecology · Endangered species

## 1. INTRODUCTION

Marbled murrelets *Brachyramphus marmoratus* are long-lived seabirds of the family Alcidae, spending most of their life in the marine environment but nesting inland in the mature forests of western North America along the Northeast Pacific Coastal Zone (Ralph et al. 1995, Piatt et al. 2007, Nelson 2020). The

species has experienced downward population trends throughout much of its range (Bertram et al. 2015, Betts et al. 2020, McIver et al. 2021), which are thought to be the result of reduced availability of nesting habitat and increased variability in marine conditions, particularly in the Pacific Northwest USA. Consequently, the species is federally listed as threatened under the US Endangered Species Act in

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Washington, Oregon and California, and under the Species at Risk Act in Canada.

As a diving seabird that pursues prey underwater and nests solitarily on land, the marbled murrelet faces a unique combination of exposure to pervasive anthropogenic sound in both terrestrial and marine environments (Mooney et al. 2019b). Anthropogenic noise accompanies nearly all human-induced environmental changes and is pervasive across both marine and terrestrial environments, with few habitats unaffected by altered acoustics (Buxton et al. 2017b). Extensive scientific literature has documented numerous auditory and behavioral effects of noise on terrestrial birds and other animal taxa (for reviews, see Erbe et al. 2018, Halfwerk et al. 2018, Hawkins & Popper 2018, Simmons & Narins 2018, Slabbekoorn et al. 2018). Although less extensive, there are also indications that seabird species are susceptible to disturbance from low-level noise, a point particularly concerning given seabirds' often imperiled status (e.g. Croxall et al. 2012, Lascelles et al. 2016). Gunshots, passing aircraft and vessels are all known to elicit varying degrees of behavioral changes or flushing in nesting murrelets *Uria aalge* and *U. lomvia* at distances ranging from 50 m out to 5 km (Rojek et al. 2007, Labansen et al. 2021). Additionally, the sounds of off-road vehicles and pedestrians decrease adult attendance of nests and hatchling survival in American oystercatchers *Haematopus palliatus* (Borneman et al. 2016) and Brandt's cormorants *Urile penicillatus* (Buxton et al. 2017a).

The potential for behavioral or physical effects of anthropogenic noise in threatened species such as the marbled murrelet is cause for concern. For example, underwater and airborne sounds from pile driving and pier construction have the potential to impact murrelets by changing important behaviors, causing stress or causing temporary or permanent hearing loss (US Navy 2013, 2015). It is notable that exposure to even low-level anthropogenic noise caused behavioral responses in colonial nesting murrelets and cormorants (Rojek et al. 2007, Buxton et al. 2017a, Labansen et al. 2021), despite their raucous nests being located on cliffside habitats which can already have an elevated background noise environment (A. B. Smith et al. unpubl.). It might be assumed that under such naturally noisy conditions, intruding anthropogenic noise would be largely masked, or animals would be more habituated to noise and thus less likely to respond. Yet critical nesting disturbances still occurred. This raises concerns for species such as the marbled murrelet which nest solitarily in mature forests of the Pacific Northwest, a habitat which likely has lower am-

bient noise levels than seaside cliffs (Hebert & Golightly 2006, Golightly et al. 2009, Lee & MacDonald 2016, Kuehne & Olden 2020) and thus potentially increased opportunities for noise disturbance.

While there is general awareness that anthropogenic noise may negatively impact seabirds such as the marbled murrelet, addressing sound sensitivities is often an overlooked priority (but see European Parliament Directive 2002/49/EC, <https://eur-lex.europa.eu/legalcontent/EN/TXT/?uri=celex:32002L0049>). Thus, no basic data on the hearing of marbled murrelets exist, in part because the species does not thrive in captivity (Carter & Kuletz 1995). This limits predictions of the frequencies and sound levels that would induce impacts. It also hinders the development of the appropriate criterion for evaluating acute disturbance thresholds in the marbled murrelet such as the onset of hearing loss (temporary or permanent), injury or lower-level disturbance thresholds like the detectability of noise and onset of behavioral changes. Key to understanding, predicting, and mitigating noise effects is establishing hearing thresholds and levels of sound detectability, which underpin all subsequent assessment of acoustic effects, potential injury and/or hearing loss, estimates of auditory masking and other noise impact criteria (Southall et al. 2019).

An emerging way to measure the hearing abilities of wild birds is field applications of auditory evoked potential (AEP) techniques (Mooney et al. 2019a). Empirical measurements of bird hearing have traditionally been collected using psychophysical testing paradigms, a method that can provide important perceptual sensitivity information, but is time consuming, expensive and challenging for many species. Alternatively, electrophysiological hearing tests involve the measurement of time-averaged AEPs elicited by the presentation of acoustic stimuli. They are a relatively rapid way to measure a subject's overall hearing sensitivity and audible frequency range and allow for measuring untrained and even wild animals. Although behavioral metrics may provide lower, more sensitive thresholds compared to AEP methods (Brittan-Powell et al. 2002), the frequency response of AEP audiograms in birds is similar to that of behavioral audiograms and low signal-to-noise AEP data can produce sensitive thresholds that are considered comparable to psychophysical methods. These AEP methods have been applied to birds in the laboratory (Brittan-Powell et al. 2002) and used for other taxa (often odontocetes) in the field for nearly 2 decades. However, field AEP methods have only recently been applied to wild birds, provided they can be safely caught, sedated, tested

and released (Mooney et al. 2019a, 2020). While such studies are not trivial, particularly in regards to sedation, they are nonetheless a minimally invasive method for auditory measurements with individuals of untested species that can be successfully released within several hours of capture.

Here, we applied field-based AEP methods to measure the hearing of 10 marbled murrelets, safely caught and released from Auke Bay, Alaska, USA (58° 21.413' N, 134° 43.733' W). Although the species is listed as threatened across most of its range, it is considered to have a comparatively robust population in Alaska (Piatt et al. 2007). Our primary goal was to define the in-air hearing sensitivities and audible frequency range of the marbled murrelet. Given that local environments may influence sound detection and noise disturbance thresholds, we also sought to place the auditory data into the context of local soundscape measurements, predicted underwater hearing abilities and potential sensitivity to anthropogenic noise.

## 2. MATERIALS AND METHODS

### 2.1. Study site and animal capture

Experiments took place nightly from 20:00 to 06:00 h in the waters of Auke Bay, Alaska, USA, between May 3 and 13, 2021. Animals were temporarily captured and sedated before undergoing auditory tests. We captured birds using the night-lighting capture method, wherein birds were located on the water at night using a spotlight from a small inflatable boat, quickly approached, and netted using a salmon dipnet (Whitworth et al. 1997). Following capture, birds were carefully extracted from the net, placed in a padded water-resistant box, and returned to the dock within 20 min, where they were immediately weighed (mean body weight 230 g) and administered midazolam (5 mg kg<sup>-1</sup>, intranasal) to provide mild sedation. At the testing site (15–20 min following administration of midazolam), the birds received an intramuscular injection of ketamine (10 mg kg<sup>-1</sup>) and xylazine (2.5–5.0 mg kg<sup>-1</sup>), which provided adequate sedation (responsive with minimal muscle movement) within 5 to 10 min. Vital parameters (body temperature, heart rate, respiratory rate) were monitored and recorded every 15 min during the hearing tests using a stethoscope and a continuous digital thermometer probe placed in the cloaca (DataTherm II, model 501501). Body temperatures were maintained between 37.1 and 41°C by adding damp towels, or heat or ice packs.

Heart rates were ca. 200 beats min<sup>-1</sup>; respiration rates were 10 to 40 breaths min<sup>-1</sup>. Upon completion of testing, the birds received an intramuscular injection of flumazenil (0.1 mg kg<sup>-1</sup>) and atipamezole (0.25–0.5 mg kg<sup>-1</sup>) to reverse the effects of midazolam and xylazine, respectively. Afterwards, individuals were examined for appropriate mentation, vital signs (temperature, respiratory rate) and ambulation prior to release. Subjects were banded and released on the bay where they were originally captured. Total mean holding time from capture to release was 4 h 50 min (minimum: 3 h 21 min; maximum: 6 h 36 min).

### 2.2. Evoked potential recording and stimulus presentation

Once birds were properly sedated, we conducted hearing tests in a portable semi-anechoic chamber lined with 4 cm thick sound-absorbing foam. Each bird was positioned near the chamber door with its head slightly elevated and facing toward the speaker at the far end of the chamber. We then inserted three 30 gauge stainless steel electrodes just underneath the skin. An active (non-inverting) electrode was placed just above the auditory meatus (typically left ear). A reference electrode was placed on the vertex of the head just off the midline (1–2 mm to the right side or opposite the active electrode), and in-line with the meatus. A third electrode (grounding) was placed dorsally on the back. The AEP system also was grounded to the soil using a long copper wire inserted directly into the nearby terrain. The electrodes were connected to a custom-made differential amplifier (Aarhus University) that amplified all responses 10 000× and bandpass filtered them from 300 to 3000 Hz. A second 8-pole Krohn-Hite DC-powered single channel filter (300–3000 Hz, FMB300) further conditioned the signals. The biopotential amplifier was connected to a BNC Breakout Box (2110, National Instruments) and a PCMCIA-6062E data acquisition card implemented in a semi-rugged Toughbook computer. Using a custom LabView program (National Instruments), the data acquisition card converted the analog signal to a digital record at a 16 kHz sampling rate. All data were stored on the laptop computer.

Stimuli were presented between 750 and 1000 times for each sound level, with concurrent AEP responses averaged and stored for later data analyses. The summed average evoked response waveform was monitored at each sound level and stimuli were decreased in steps of 5–10 dB using an HP 350D 5W

600 $\Omega$  DC attenuator until evoked responses were no longer visually detectable for 2 to 3 trials. If no response was detected relative to the background noise, we increased the sound level. Decibel step size was based on the amplitude of the signal and the animal's neurological response. Audiometric sounds were generated by a self-contained, battery-powered speaker and amplifier (a Nagra DSM speaker, functional range: 60–15 000 Hz  $\pm$  4 dB) located at the far end of the hearing test chamber 70 cm from the bird's beak. This distance varied by  $\pm$ 5 cm across experiments due to occasional movements by the birds while in the chamber.

Acoustic stimuli were created using the same custom LabView program, laptop and data acquisition card. Outgoing signals were produced at a 256 kHz update rate and presented at a rate of 10 s<sup>-1</sup>. Examinations began with a broadband 'click' stimulus consisting of 6 cycles of a 2 kHz sine wave (3 ms duration) with a 1.5 ms symmetrical ramp up and ramp down. We then examined the auditory frequency range using tone pips of the following frequencies: 0.5, 0.75, 1, 2, 3, 4 and 6 kHz. The tones were 10 ms in duration except for the 0.5 kHz tones, which were 20 ms in duration. Tone pips were ramped up to limit spectral spreading using a sine envelope; thus, the maximum amplitude was found at the middle 2 stimulus waves depending on the signal duration.

### 2.3. Acoustic calibration and AEP threshold calculation

During experiments, we made acoustic recordings within the chamber via a Type-4189 microphone attached to a Type-2250 hand-held analyzer (Brüel & Kjær) placed adjacent to the birds' auditory meatus. These recordings were made using an Olympus LS-12 Linear PCM recorder attached to the line output of the analyzer. Recordings were made of each projected test tone, as well as the ambient background noise within the chamber. Recordings were calibrated against a 94 dB SPL tone at 1 kHz from a calibrated pistonphone recorded prior to the start of data collection for each bird.

Final threshold calculations were made offline in Matlab (Mathworks). Thresholds for each stimulus were estimated by plotting the AEP peak-to-peak magnitudes as a function of the calibrated stimulus received level and fitting a linear regression to points with clearly visible response waves. A threshold estimate was taken as the intersection of the linear regression with the zero-magnitude level. Potential dif-

ferences in final thresholds between males and females were examined by running a generalized linear mixed model (GLMM) with Gamma error structure using sex as a fixed effect and frequency and individual variation as random effects.

Preliminary analysis revealed that some AEPs recorded here exhibited differing onset latencies over the course of the hearing tests. Such differences likely reflect differing neuronal generation sites of the responses (Colon & Visser 1990), and for this reason, AEPs are commonly subdivided according to their latency (e.g. in humans: short latency (0–12 ms), middle latency (10–100 ms) and long latency (50–1000 ms); see Colon & Visser 1990). For the purposes of differentiation specifically within this study, we labeled response types according to the latency of the dominant AEP wave elicited by the highest tested stimulus level for each threshold. Responses with a dominant wave latency before 8 ms were labeled as short latency, and responses with onsets after 8 ms were simply labeled as longer latency, reflecting a bimodal latency distribution (see Fig. 1).

### 2.4. Soundscape recording and analysis

We made passive acoustic recordings to document environmental acoustic conditions that may be experienced by marbled murrelets at or near their nests. While most murrelets nest on large limbs of dominant trees within mature forests, they also occasionally nest on cliffs and on the ground (e.g. Simons 1980, Nelson 2020). Thus, we recorded the ambient soundscape within a murrelet nesting habitat (58° 17.675' N, 134° 27.204' W) approximately 500 m from a known murrelet ground nest from previous years (Willson et al. 2010). The nest was unreachable due to ground conditions, but the habitat was similar between the locations. Recordings were made continuously from May 8 to 13, 2021 using a SongMeter SM4 recorder (Wildlife Acoustics) with an omni-directional A2 microphone (8 dB gain, 24 kHz sample rate) placed on a tree 2.5 m above ground. Recordings were saved as .WAV files on an SD card for offline analysis. We manually calibrated the microphone before and after deployment with a 94 dB SPL 1 kHz tone from a calibrated pistonphone.

Sound levels were measured from the recordings in 1 s intervals. The median and 10–90<sup>th</sup> percentile sound levels were calculated for multiple spectral bands across 5 min bins of the data. These sound levels were compared to spectral data visualized as a long-term spectral average (L TSA) and compared to

environmental parameters of interest such as rainfall and windspeed, which were retrieved from publicly available datasets from a weather station in Juneau, Alaska (US National Centers for Environmental Information). The occurrence of anthropogenic, biophonic and geophonic sound source contributions to the soundscape were investigated qualitatively via a combination of viewing the LTSA, spectrograms and listening to the complete recordings via Raven Pro software.

### 3. RESULTS

#### 3.1. AEP responses and audiograms

We captured and administered anesthesia to 12 marbled murrelets, and of these, AEPs were measured from 10 individuals (4 females, 6 males). Nominal sedation was not achieved in 2 individuals, which were therefore not tested. Most *B. marmoratus* AEPs exhibited a series of positive and negative wave deflections that began approximately 4 ms after stimulus projection and lasted approximately 4–8 ms after AEP onset ('short-latency' AEPs, Fig. 1a,b). Among birds, there was variation in the number of waves visible and their amplitudes relative to one another, which is likely explained by slight variability in electrode placements for each bird. Notably, the onset of some AEP responses in many birds occurred at greater latencies after the stimulus projection ('longer-latency' AEPs, ca. 9–16 ms, Fig. 1c,d). The amplitudes of both response types decreased and wave latencies increased as a function of decreasing stimulus intensity (Fig. 1b,d). Thus, auditory thresholds were estimated regardless of which AEP response type was generated (Fig. 1e).

Full or partial audiograms were measured from the 10 tested individuals (Fig. 2a). Lowest thresholds for all individuals occurred between 1.0 and 3.5 kHz, while the lowest threshold from any bird was 17 dB re: 20  $\mu$ Pa rms at 1.5 kHz. Thresholds generally increased above 3.5 kHz until AEPs were no longer detected (above 6 kHz). Similarly, thresholds increased below 1.5 kHz but became progressively more difficult to obtain. At 0.75 kHz, thresholds were obtained for 8 of 10 tested birds, but stimulus artifact often contaminated the generally lower AEP response levels when projecting sounds at 0.5 kHz. As a result, while 7 individuals were tested at 0.5 kHz, only 2 of those exhibited sufficiently clear responses to estimate a threshold. A largely frequency-dependent pattern arose regarding the occurrence of short- or longer-latency AEPs during the tests (Fig. 2b). Short-

latency AEP responses were largely elicited at or below 2 kHz, while the longer-latency AEPs became more prevalent at or above 3 kHz.

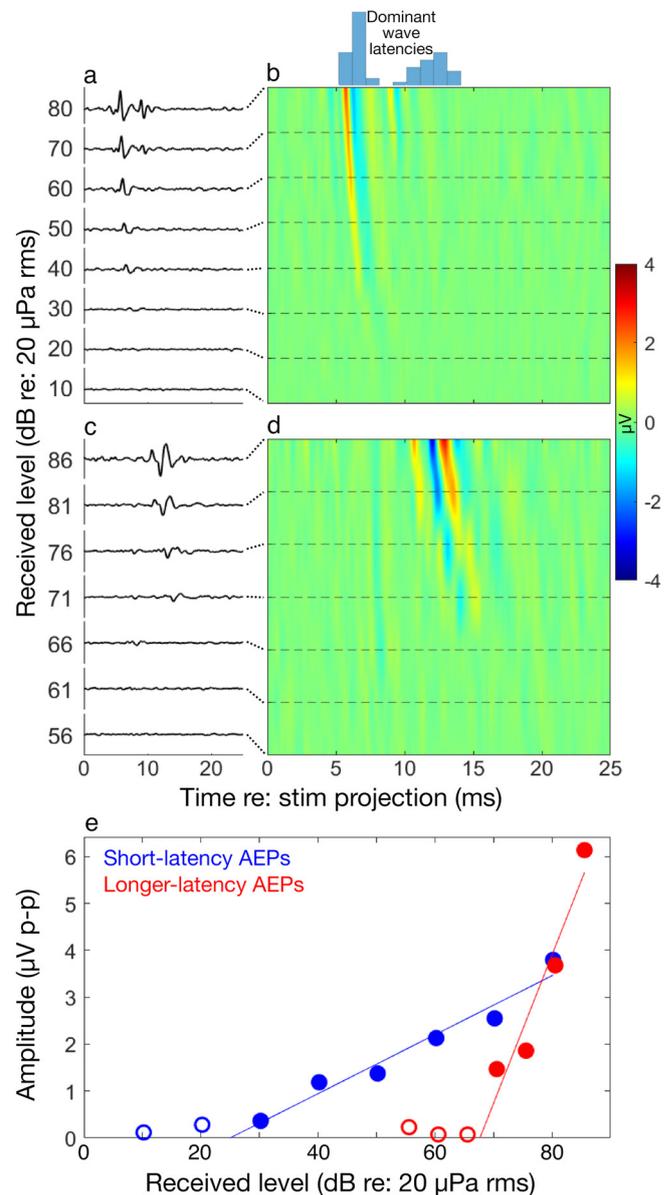


Fig. 1. Marbled murrelet (a,b) short-latency auditory evoked potential (AEP) responses to broadband clicks and (c,d) longer-latency AEP responses to 2 kHz tone pips. Panels (a) and (c) show example AEP waveforms elicited by the stimuli presented at decreasing received levels. Panels (b) and (d) show the corresponding AEP wave latency delays as a function of stimulus received level. The histogram above (b) shows the latency distribution of the dominant AEP wave from the highest tested stimulus level for each threshold measured in this study. Panel (e) shows threshold calculations from the corresponding waveform amplitudes in (a) and (c). Filled circles represent averaged waveforms with detectable AEP responses used for the linear regression threshold estimation, while outlined circles reflect averaged waveforms where no AEP response was detected

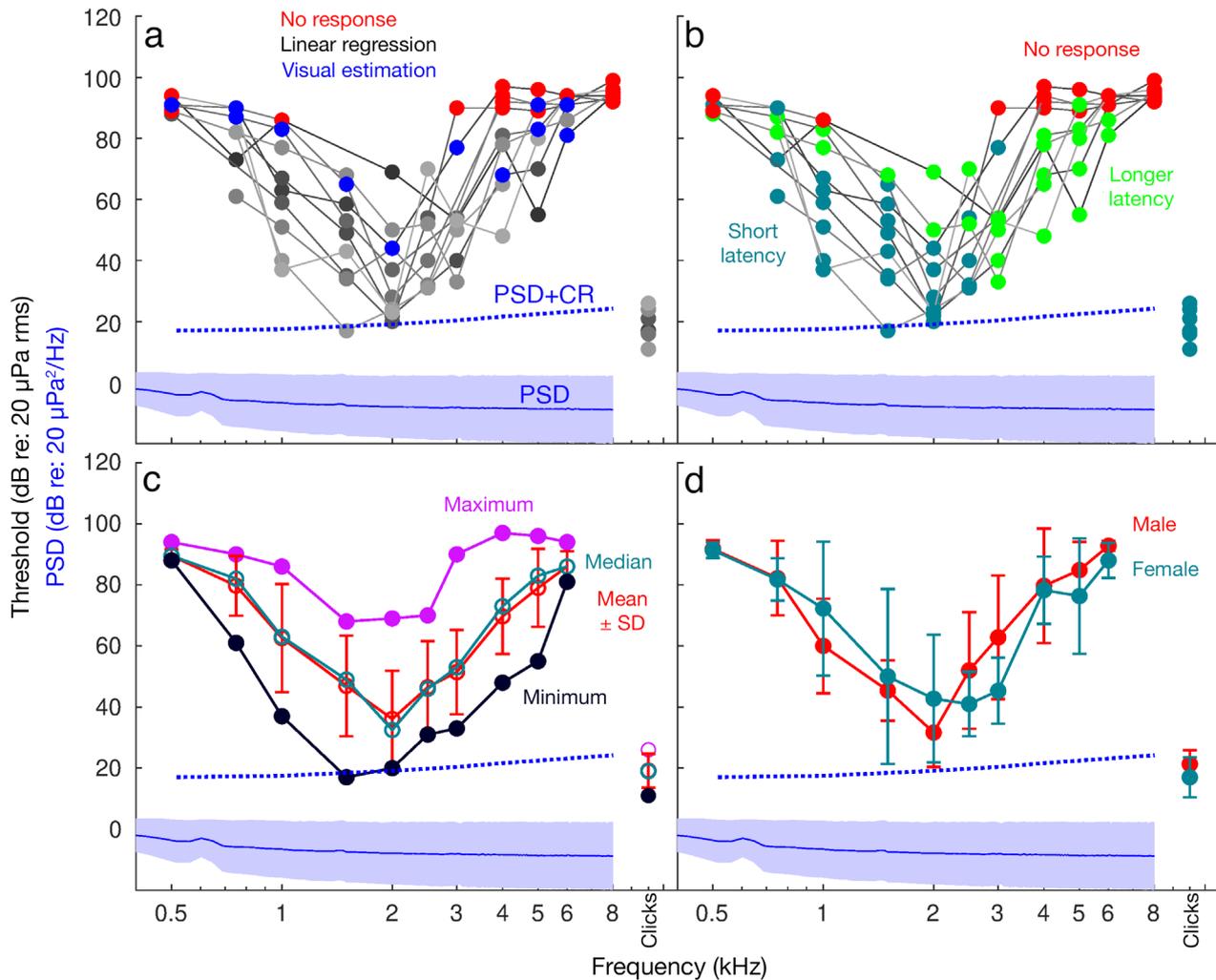


Fig. 2. Hearing threshold curves for the marbled murrelet: (a,b) individual audiograms and threshold characteristics of 10 individuals, (c) audiograms calculated from the mean, median, maximum and minimum thresholds across all individuals and (d) mean audiograms of male and female birds. In all panels, audiogram data is plotted against the mean (solid blue line) and standard deviation (blue shaded area) of the background noise power spectral density (PSD) in the experimental acoustic chamber. The dotted blue line indicates an estimated level of masking by adding mean avian critical ratios (Dooling 2002) to the mean chamber PSD

Composite audiograms calculated across all birds using measures of central tendency (median, mean  $\pm$  st.dev) showed a lowest threshold of 33 and 36 dB at 2 kHz (Fig. 2c). The dominant bandwidth as measured by thresholds within 30 dB of the lowest threshold was 3 kHz, extending from 0.8 to 3.8 kHz. At frequencies both above and below 2 kHz, thresholds increased sharply at a rate ca. 20–25 dB per octave. There was variation in auditory threshold estimates between individuals for a given stimulus frequency. Within the dominant bandwidth, thresholds differed by between 39 and 57 dB, which was the maximum inter-individual difference and occurred at 3 kHz (Fig. 2c). We did not find a significant difference in

thresholds between sexes (GLMM,  $t = -0.169$ ,  $p = 0.866$ , Fig. 2d). Ignoring the 2 thresholds at 0.5 of 0.75 kHz, threshold variability was lower at higher frequencies (Fig. 3).

### 3.2. Nesting soundscape characteristics

The aerial soundscape was continuously recorded for 118 h and contained both biotic and abiotic signals, corresponding to geophonic, biophonic and anthropogenic sources (Fig. 4). The biophony consisted of bird vocalizations, which were most prominent at frequencies between 2 and 8 kHz. Lower-frequency

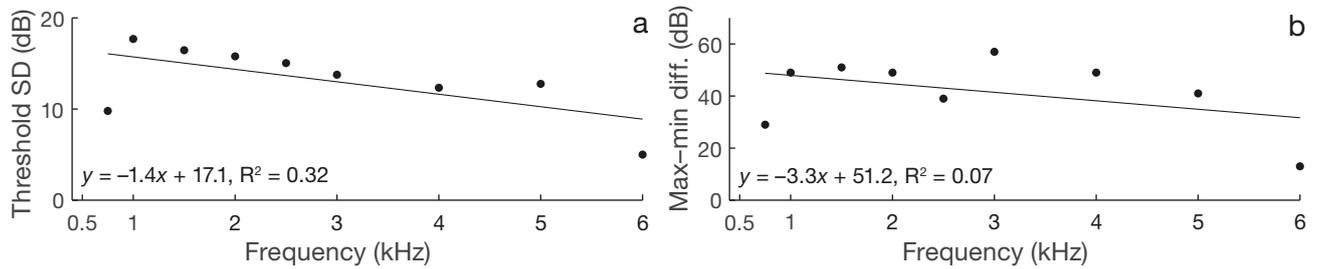


Fig. 3. Threshold variability between marbled murrelet individuals. The (a) standard deviation and (b) maximum–minimum threshold difference of thresholds between individuals tended to decrease with increasing stimulus frequency

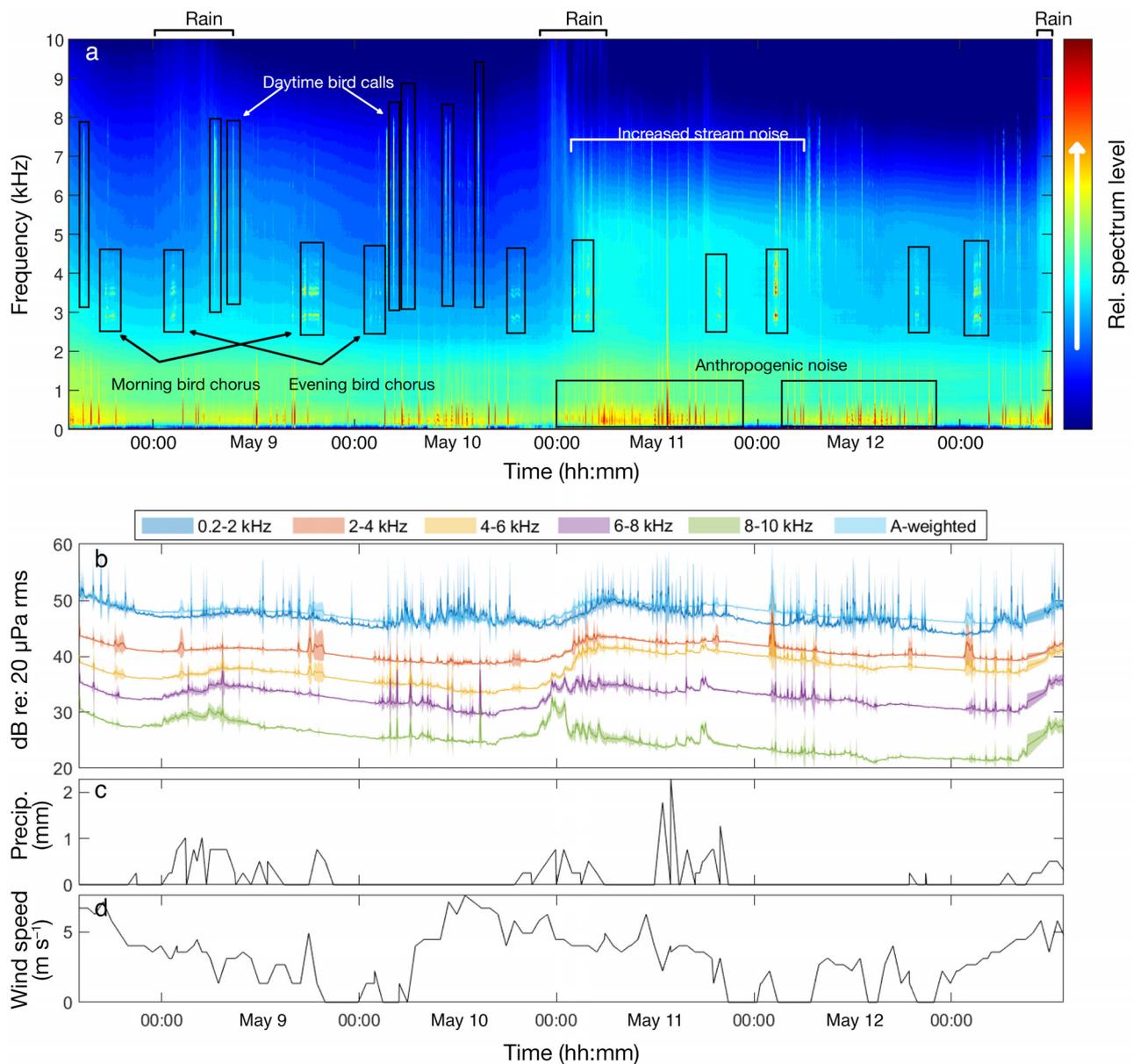


Fig. 4. Comparison of short-term soundscape and environmental patterns of marbled murrelet nesting habitat, May 8–13, 2021. (a) long-term spectral average (LTSA) of the nesting soundscape, with bounding boxes around examples of identifiable sound sources, including bird calls, rain, stream noise, and anthropogenic noise. (b) comparison of environmental sound level dynamics across multiple frequency bandwidths temporally aligned with data on (c) precipitation, and (d) wind speed

corvid calls were also present but less prominent in the LTSA. The geophony consisted of the sounds of a nearby stream (broadband across the recording bandwidth from 0.2 to 10 kHz) and rainfall (most spectrographically salient from 7 to 10 kHz). The sound of wind through the trees was almost certainly an additional contributor to the geophony but was not spectrally differentiable in the recordings from the similar, yet more dominant, broadband noise of the stream. Anthropogenic contributions included sounds from automobiles and aircraft, which were common at frequencies primarily below 1 kHz, but spectral energy occasionally extended up to 2 kHz.

Sound levels encompassing frequencies from 0.2 to 10 kHz varied temporally at the recording site within this short timeframe (Fig. 4a,b). The maximum and minimum mean levels across any 5 min epoch within the recording period were 55 and 46 dB re: 20  $\mu$ Pa rms, respectively. The maximum and minimum A-weighted sound levels were 53 and 46 dBA rms. Although the soundscape recordings covered a brief time span, we observed multiple diel sound patterns. A general increase in sound level variability occurred across all frequency bands within the hours of daylight each day, which reflected daylight-dependent activity patterns of both humans and birds. Some bird vocalizations showed a strong presence twice a day, corresponding to a morning and evening vocalization chorus by those species, while other bird sounds occurred primarily during a broader timespan across the daylight hours. Notably, the highest mean sound levels within each 24 h period occurred during the daylight hours at low frequencies between 0.2 and 2 kHz and were generated by anthropogenic sources.

## 4. DISCUSSION

### 4.1. Marbled murrelet audiogram

We successfully elicited AEPs from all marbled murrelets tested, and the threshold-derived audiograms show the species is most sensitive to in-air sound at frequencies from 1.5 to 3 kHz, with progressively poorer sound sensitivity outside this range, and a high frequency limit around 6 kHz. As a general comparison, this frequency-dependent pattern is similar to other bird species studied to date, with the exception of auditory specialists like many owls, whose most sensitive frequency and upper-frequency cutoff are shifted to higher frequencies (e.g. Van Dijk 1972, Dyson et al. 1998, Brittan-Powell et al. 2005,

Beatini et al. 2018). Below 1 kHz, the steeply increased thresholds (ca. 20 dB per octave) might be partially attributable to inherent technical difficulties associated with eliciting AEPs using low-frequency stimuli and doing so in a field-based context. For example, low-frequency stimulus contamination within the response waveform precluded viable threshold measurement in many individuals tested. Thus, while the elevated low-frequency thresholds may indeed reflect the marbled murrelet's auditory characteristics, they should be considered cautiously. Lowest mean and median thresholds of 33 and 36 dB, combined with lowest thresholds between 11 and 20 dB in some individuals, indicate the marbled murrelet has generally sensitive aerial hearing that is comparable to many non-auditory specialist terrestrial birds (Fig. 5a). Moreover, since electrophysiological methods typically underestimate absolute hearing sensitivities, absolute perceptual thresholds of the marbled murrelet may be even lower, especially across its most sensitive bandwidth (Brittan-Powell et al. 2002, 2005, Crowell et al. 2016).

Aerial hearing comparable to some terrestrial birds is notable due to the marbled murrelet's amphibious lifestyle. As pursuit-diving seabirds, they dive from the surface of the water and pursue prey in water depths up to 45 m (Strachan et al. 1995), but nest on land and communicate vocally in air. Recent anatomical research has shown the evolution of changes in the middle ear structures of aquatic birds compared to their fully terrestrial counterparts, including reduced input areas of the tympanic membrane, as well as reduced volume and interconnectivity of cranial air cavities (Zeyl et al. 2022). These structural changes are most pronounced in deep pursuit-diving species (like the murrelet) and may have evolved as an adaptation for baroprotection during dives (Zeyl et al. 2022). However, the impact of these structural adaptations on the hearing and sensory ecology of aquatic and diving species is an open question. In addition to the marbled murrelet, aerial hearing has also been measured in 13 other species of diving bird using AEP methods (Crowell et al. 2015, Mooney et al. 2019a, 2020, Larsen et al. 2020), including 2 additional alcids (common murre and Atlantic puffin *Fratrercula arctica*). Across these species, lowest mean AEP thresholds range between 16 dB for the pursuit-diving puffin and 68 dB for the plunge-diving northern gannet *Morus bassanus* and are therefore highly variable in comparison to the lowest AEP thresholds of many terrestrial birds. Thus, while some clearly elevated diving bird audiograms may hint at reduced aerial hearing sensitivity, it is clearly not ubiquitous

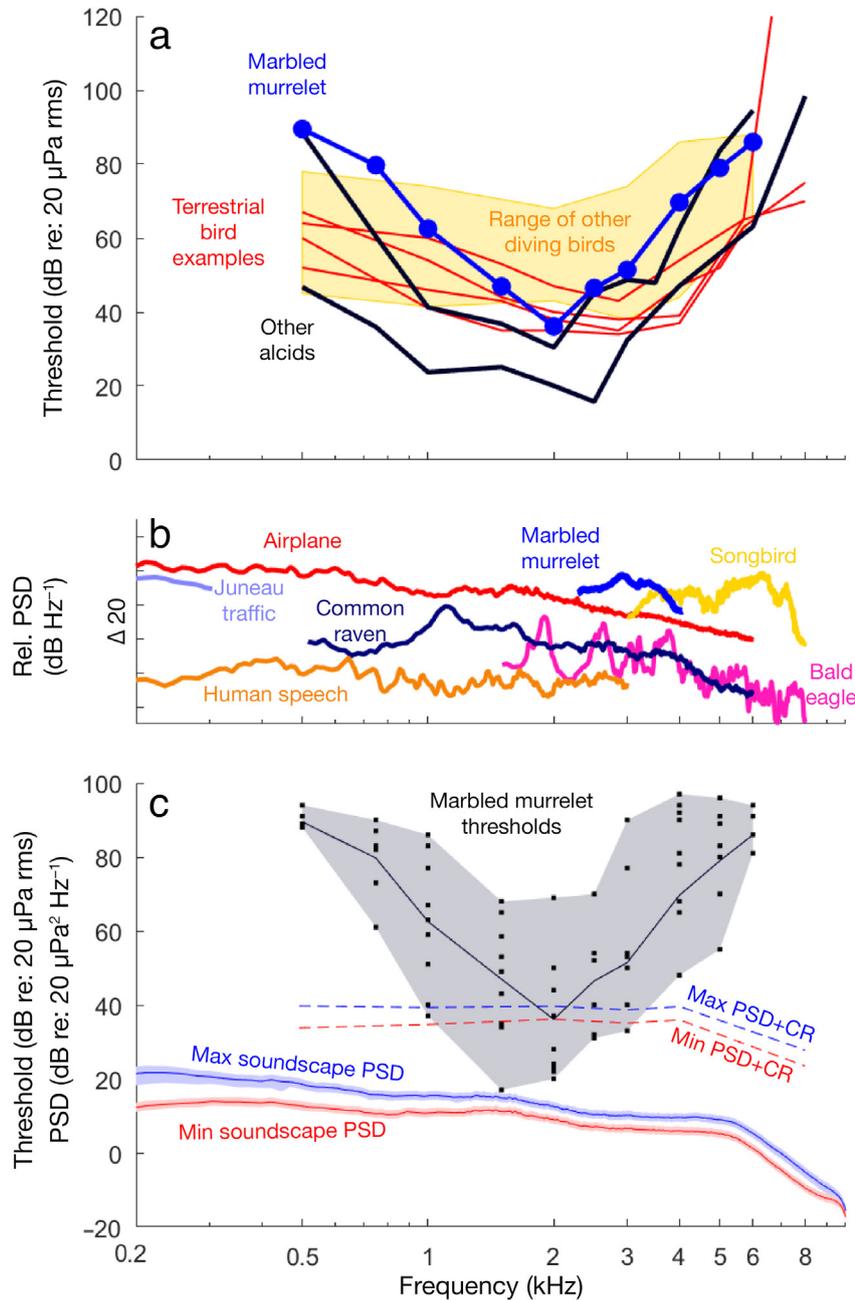


Fig. 5. (a) Mean auditory evoked potential (AEP) audiograms of the marbled murrelet and select bird species, including terrestrial species in red (canary *Serinus canaria*, Brittan-Powell et al. 2010; woodpeckers [average of multiple species], Lohr et al. 2013; budgerigar *Melopsittacus undulatus*, Brittan-Powell et al. 2002; zebra finch *Taeniopygia guttata*, DeAngelo 2008) and other alcids in black (Atlantic puffin, Mooney et al. 2020; common murre, A. B. Smith et al. unpubl.). The tan-shaded region encompasses the mean AEP audiograms of other non-alcid diving birds measured to date (Crowell et al. 2015). (b) Relative power spectral density (PSD) profile of various sound sources within the nesting environmental soundscape. Sounds overlapping the marbled murrelet audiograms in frequency are potentially audible to individuals depending on the source distance. All example spectra originated from recordings made by the authors, except common raven *Corvus corax* and bald eagle *Haliaeetus leucocephalus* vocalizations, which were downloaded from [www.xeno-canto.org](http://www.xeno-canto.org). (c) Comparison of marbled murrelet auditory thresholds to the soundscape PSD (mean  $\pm$  SD) corresponding to the maximum and minimum environmental sound levels recorded over the brief recording period (May 8–13, 2021). Dashed lines denote simple estimated levels of auditory masking by adding mean avian critical ratios (CR) to the PSD. CR values are taken from Dooling (2002)

to diving birds in general. It is also noteworthy that the 3 alcids fall on the lower end of this range, despite being among the deepest diving seabirds tested so far (up to 150 m; e.g. Piatt & Nettleship 1985, Burger & Simpson 1986, Bonnet-Lebrun et al. 2021) and having high degrees of structural modification to the middle ear (Zeyl et al. 2022). Thus, the marbled murrelet audiograms here further suggest that auditory adaptations for baroprotection during deep diving have not led to noticeably reduced aerial hearing sensitivity in studied alcids (Mooney et al. 2020).

#### 4.2. AEP response type and morphology

Notably, both short latency and longer latency AEPs were observed in this study, with onset latencies of approximately 4 and 9 ms, respectively. The different latencies suggest different origins of recorded responses within the auditory reception and processing neural pathways. Short latency AEPs within a few ms of signal reception are generally accepted as being generated by neural components along the auditory periphery, while the longer

latency AEPs observed here likely originated from more central auditory structures (e.g. Colon & Visser 1990). Short-latency AEPs are typically targeted for auditory threshold measurements across taxa, as was the case in this study. Yet since the longer latency AEP magnitudes were sound-level dependent and occurred in 7 of the 10 individuals tested, they were considered suitable for threshold measurement in this field-based context when short latency AEPs were not observed.

It is unclear what factors ultimately determined which type of AEP responses were elicited. There was a frequency-dependent pattern to which AEP type was elicited by which stimulus, but there were deviations to this trend (see Fig. 2b), and in some cases, both response types appeared concurrently within a single averaged AEP waveform. Variations in electrode placement, within or between individuals, are possibly a contributing factor. Electrodes were consistently placed at conventional locations following previous avian AEP studies (e.g. Brittan-Powell et al. 2002, Lohr et al. 2013, Crowell et al. 2015, 2016), with the meatus providing a particularly clear landmark for active electrode placement in contrast to the vertex electrode. However, the influence of electrode placement on avian AEPs has not been studied systematically and small variations were unavoidable due to the field-based environment, the small size of the animals' heads relative to electrode needle length, and the safe sedation protocols required to maintain the health and safety of these sensitive birds. For instance, we largely avoided manipulation of the test subjects after hearing trials began since such interaction counteracted the effectiveness of sedation and could be counterproductive from an animal care perspective. The trade-off to this approach was that potentially small shifts in an animal's head position could leave the electrode attachment locations the same but cause undetected changes in the needle electrode orientation under the skin, which then went uncorrected. Notably, both response types were often recorded within individuals despite no clearly observed change in electrode position. Combined, these various possibilities make it difficult to draw conclusions. At minimum, both types of responses were elicited by neuronal auditory structures, but which response was elicited may have been influenced by either unknown experimental factors or unknown biological factors such as how sound is transmitted through the ear or how responses are generated in the basilar papillae.

#### 4.3. Ecoacoustics and anthropogenic noise considerations

Although the soundscape measurements reported here cover a short timescale, they provide a valuable quantitative characterization of the acoustic environment, sound levels and sound sources at a known nesting site of the relatively healthy marbled murrelet population in Alaska. Notably, most of the discrete sound cues in the environment have spectral components that overlap with the murrelet auditory range (Fig. 5b) and are likely detectable to individuals depending on the sound source distance. This includes biophonic sounds such as hetero- or conspecific avian vocalizations, as well as anthropogenic sounds such as passing aircraft, traffic noise and human speech. Marbled murrelets are a cryptic, solitary nesting alcid, but they vocalize regularly in flight and on the water using a broad vocal repertoire (Dechesne 1998, Nelson 2020) that can convey important social information that influences breeding site selection (Major & Jones 2011, Valente et al. 2021). Sensitive aerial hearing is thus likely important for the detection of these important conspecific calls as well as potential nest predators, and anthropogenic sounds have the capacity to mask such acoustic cues. There is also a growing body of evidence that detection of even low-level anthropogenic noise can impact wildlife physiology and behavior (for reviews, see Erbe et al. 2018, Halfwerk et al. 2018, Hawkins & Popper 2018, Simmons & Narins 2018, Slabbekoorn et al. 2018). Marbled murrelets are clearly capable of detecting such signals and are susceptible to similar negative effects, though it is unknown if such effects would result in demographic or population level impacts.

Marbled murrelets nest in what could be considered a fairly quiet habitat when excluding anthropogenic disturbances. Lowest sound levels of 46 dB re: 20  $\mu$ Pa rms recorded here during a period of calm but occasionally rainy weather likely reflect a naturally occurring lower bound at this site (i.e. a mature forest near a stream). This lower bound is perhaps slightly elevated compared to sites that are not proximal to sound sources like a stream and city, but is generally comparable to natural ambient levels documented at other murrelet nesting sites in California and Washington (see Hebert & Golightly 2006, Golightly et al. 2009, Lee & MacDonald 2016, Kuehne & Olden 2020). Under these baseline conditions, a typical nesting marbled murrelet with average hearing likely encounters low levels of masking of potentially relevant bioacoustics cues (Fig. 5c). It is noteworthy that despite the proximity to a noisy stream and urban

area, these environmental sounds levels are 10 dB lower than the colonial, cliff-nesting soundscape levels of the common murre (A. B. Smith et al. unpubl.). Although the timespan of the presented soundscapes for the 2 related species is brief and would benefit from longer recording datasets, the environmental sound levels appear to be quite different, which may be relevant when designing species specific noise-impact criteria.

The relatively quiet habitat of the marbled murrelet may ease the incursion of anthropogenic noise pollution and encroachment and heighten the potential for disturbance in nesting individuals. Such noise encroachment and disturbance is a problem seen across many wildlife habitats (e.g. Buxton et al. 2019) and can occur even at sound levels as low as 45–50 dBA (e.g. Buxton et al. 2017a) which are akin to those measured here. However, the onset of acoustic disturbance in the murrelet may not be only related to overall sound levels, but also the different acoustic characteristics of a sound source. For example, anthropogenic sounds could cause increases in the overall ambient sound level equivalent to the flowing stream, but still disturb nesting individuals due to clear differences in frequency emphasis, impulsiveness (kurtosis), or onset time.

Given the murrelet's amphibious lifestyle, noise pollution concerns extend to underwater sound as well. It is currently unknown to what general extent pursuit-diving seabirds utilize acoustics underwater, and there is a growing need to understand how their acoustic biology may be adapted for underwater use. Specifically, the empirical measurement of underwater auditory thresholds is essential for the assessment of impact thresholds due to underwater anthropogenic noise exposure. Increasing levels of anthropogenic noise in coastal marine waters are making such data and assessments an increasingly important conservation tool (Elmer et al. 2021). Although underwater auditory data was not collected for this study, the detection of underwater sound has so far been documented in 4 species of aquatic or seabirds: common murre (Hansen et al. 2020), long-tailed duck *Clangula hyemalis* (Therrien 2014), gentoo penguin *Pygoscelis papua* (Sørensen et al. 2020), and great cormorant *Phalacrocorax carbo* (Johansen et al. 2016, Hansen et al. 2017, Larsen et al. 2020). Of these, empirical underwater auditory thresholds have been measured from only the long-tailed duck (Therrien 2014) and great cormorant (Larsen et al. 2020).

In particular, the study by Larsen et al. (2020) provided a robust comparison of in-air and underwater hearing thresholds in the cormorant using AEP

methodologies. Their results indicated that mean hearing thresholds across all individuals were similar between the 2 media when compared in terms of the stimulus acoustic pressure. If the assumption is made that this aerial–underwater threshold relationship is similar across other diving seabirds, then marbled murrelets are predicted to have a pressure-equivalent mean underwater threshold around 62 dB re: 1  $\mu$ Pa at 2 kHz. The lowest individual aerial threshold of 17 dB re: 20  $\mu$ Pa also leads to the lowest underwater threshold prediction of 43 dB re: 1  $\mu$ Pa. These predictions suggest marbled murrelets may have sensitive hearing underwater, with thresholds comparable to some pinnipeds (Reichmuth et al. 2013). While these predictions represent an oversimplified extrapolation and therefore should be interpreted with great caution, such extrapolative predictions are nonetheless valuable in the absence of more direct data. There would be great benefit from future studies to establish and compare aerial and underwater auditory thresholds across additional diving bird species.

## 5. CONCLUSIONS

In this study, we applied electrophysiological auditory methods in the field to measure hearing thresholds of 10 wild marbled murrelets using a temporary capture and release paradigm. The data reported here are the first empirical measurements of sound sensitivity for this threatened species. We conclude marbled murrelets exhibit generally sensitive aerial hearing despite their amphibious lifestyle. Moreover, short-term acoustic recordings indicate this solitary and inland nesting seabird nests in a relatively quiet environment which may permit heightened incursion of nearby anthropogenic sounds. These data provide an important addition to our understanding of the acoustic biology of the species. They also constitute a valuable baseline that will benefit future assessments of noise exposure impact thresholds and the design and implementation of acoustic mitigation and conservation guidelines for the threatened marbled murrelet (Dooling et al. 2019, Southall et al. 2019, Hawkins et al. 2020).

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