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RESEARCH ARTICLE

A field study of auditory sensitivity of the Atlantic puffin, *Fratercula arctica*

T. Aran Mooney^{1,*}, Adam Smith^{1,2}, Ole Næsbye Larsen², Kirstin Anderson Hansen² and Marianne Rasmussen³

ABSTRACT

Hearing is vital for birds as they rely on acoustic communication with parents, mates, chicks and conspecifics. Amphibious seabirds face many ecological pressures, having to sense cues in air and underwater. Natural noise conditions have helped shape this sensory modality but anthropogenic noise is increasingly impacting seabirds. Surprisingly little is known about their hearing, despite their imperiled status. Understanding sound sensitivity is vital when we seek to manage the impacts of man-made noise. We measured the auditory sensitivity of nine wild Atlantic puffins, *Fratercula arctica*, in a capture-and-release setting in an effort to define their audiogram and compare these data with the hearing of other birds and natural rookery noise. Auditory sensitivity was tested using auditory evoked potential (AEP) methods. Responses were detected from 0.5 to 6 kHz. Mean thresholds were below 40 dB re. 20 μ Pa from 0.75 to 3 kHz, indicating that these were the most sensitive auditory frequencies, similar to other seabirds. Thresholds in the 'middle' frequency range 1–2.5 kHz were often down to 10–20 dB re. 20 μ Pa. The lowest thresholds were typically at 2.5 kHz. These are the first in-air auditory sensitivity data from multiple wild-caught individuals of a deep-diving alcid seabird. The audiogram was comparable to that of other birds of similar size, thereby indicating that puffins have fully functioning aerial hearing despite the constraints of their deep-diving, amphibious lifestyles. There was some variation in thresholds, yet animals generally had sensitive ears, suggesting aerial hearing is an important sensory modality for this taxon.

KEY WORDS: Hearing, Evoked potentials, Masking, Noise, Soundscape

INTRODUCTION

Birds have long been studied for their acoustic capabilities. The call structure, development and communication of songbirds, and the often impressive hearing abilities in taxa such as owls, has received substantial attention (Konishi, 1973; Naguib and Riebel, 2014). The study of avian acoustic ecology has become increasingly vital as many bird populations decline. There has been increasing attention on how the noise in a bird's habitat may influence a range of behaviors and the overall population (Habib et al., 2007; Proppe et al., 2013; Quinn et al., 2006; Slabbekoorn and Ripmeester, 2008). Hearing data provide insight into how birds may use an acoustic

habitat as well as support estimations of the frequencies and sound levels that may negatively impact a taxon (Dooling and Blumenrath, 2013; Dooling et al., 2000), and are therefore critical for determining habitat conservation and management needs.

Acoustic cues play an important role in the sensory biology of birds, including seabirds, which live at the interface of marine and terrestrial habitats. Many studies have focused on their calls and communication abilities, perhaps because of their often raucous colonies (Aubin and Jouventin, 1998). Species such as Adélie (*Pygoscelis adeliae*), king (*Aptenodytes patagonicus*) and gentoo penguins (*P. papua*) use their calls to facilitate mate and chick identification as parents or partners return to the noisy colonies. Individuality can be conveyed through certain parameters including call duration, amplitude modulation rates, spectrum bandwidth and distribution of energy among harmonics (Humphries et al., 2016; Jouventin et al., 1999; Kriesell et al., 2018; Ligout et al., 2016; Mathevon, 1997). In Wilson's storm-petrels (*Oceanites oceanicus*) and several auk species, chicks in poorer condition emit higher frequency calls, and these higher pitched calls also result in the chick receiving increased care, including larger meals (Gladbach et al., 2009; Klenova, 2015).

Research on seabird acoustic communication has led to a small but increasing body of evidence that noise may also impact this group of animals. Early work examining the behavior of herring gulls (*Larus argentatus*), crested terns (*Thalasseus bergii*) or mixed-species colonies showed the effects of intense aircraft noise and jet sonic booms on nesting animals, quantifying the sound levels of exposure and dose-based responses (Bowles et al., 1991; Brown, 1990; Burger, 1981; Dunnet, 1977). More recent studies have examined the impacts of noise from off-road vehicles, pedestrians and human presence on American oystercatchers (*Haematopus palliatus*) and Brandt's cormorants (*Phalacrocorax penicillatus*). These observations showed that although more distant aircraft noise had minimal effects, the noise from nearby human presence resulted in birds spending less time on their nests, and decreased survival of their hatchlings (Borneman et al., 2016; Buxton et al., 2017). Consequently, there is an increasing realization that even low-amplitude noise can have reproductive and population-level impacts, underscoring the need for audiograms and data on sound sensitivities for species of concern.

Indeed, to understand acoustic ecology and predict noise impacts, hearing data are vital. Hearing studies allow for the evaluation of baseline sound sensitivity, the audibility of calls and cues, as well as potential predictions of behavioral disturbance, and physiological or anatomical noise-induced damage. Yet we have few hearing data for the vast majority of seabird taxa. Initial work used both psychophysical and neurophysiological (cochlear potentials) methods to address hearing abilities of the mallard duck (*Anas platyrhynchos*; Trainer, 1946) and the black-footed penguin (*Spheniscus demersus*; Wever et al., 1969). Recent laboratory efforts with the great cormorant (*Phalacrocorax carbo*) have

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produced audiograms using both psychophysical and auditory evoked potential (AEP) methods (Hansen et al., 2017; Larsen et al., 2020; Maxwell et al., 2017). The AEP recording method has been used as a rapid, physiological technique to measure auditory sensitivity in many taxa including various bird species and groups such as owls, canaries, aquatic taxa and, as noted, cormorants (Beatini et al., 2018; Brittan-Powell et al., 2002, 2005; Crowell et al., 2015; Henry and Lucas, 2010; Lohr et al., 2013; Maxwell et al., 2016). The method involves measuring the neurological responses from components of the auditory system, including the auditory nerve and brainstem nuclei, to controlled sounds (Burkhard et al., 2007; Mooney et al., 2019b). Additional physiological studies have measured cochlear action potentials (Chen et al., 1993; Gleich et al., 1995; Gummer et al., 1987; Köppl and Gleich, 2007; Patuzzi and Bull, 1991; Saunders et al., 1973; Sun et al., 2000). These data sets have been invaluable, often providing hearing sensitivity estimates of species for which there were few or no hearing data. Notably, these physiological methods are generally considered to be only an estimate of psychophysically derived thresholds and typically provide hearing approximations that are less sensitive than behavioral audiograms (Brittan-Powell et al., 2002; Houser and Finneran, 2006a; Yuen et al., 2005).

Despite these advancements in hearing measurements, seabird audiogram data are few and preliminary. Initial results from the common murre (*Uria aalge*) and the Atlantic puffin (*Fratercula arctica*), both a sample size of one, showed hearing thresholds at multiple frequencies seemingly elevated by 40–80 dB compared with some other bird species measured with comparable methods (Mooney et al., 2019a,b). Aerial AEP data of the greater cormorant and northern gannet also show relatively high hearing thresholds (Crowell et al., 2015; Larsen et al., 2020). Perhaps, given the low sample size for the auk data, the measurements should be repeated. These data together suggest that some seabirds may not hear well in air. This may be particularly true for birds that must make adaptive compromises as a result of pressures from their aquatic niche.

Auks (Alcidae family) are amphibious seabirds, spending most of their lives at sea, where they routinely forage, avoid predators, communicate and navigate underwater. The dive depths of puffins and common murres can routinely reach >150 m (Piatt and Nettleship, 1985). Thus, it is conceivable that the air-filled sinuses and auditory abilities are modified in auks, perhaps to withstand deep dives or enable underwater hearing. Such adaptations are noted in other amphibious taxa such as the elephant seal (*Mirounga angustirostris*), which hears a broader range of frequencies and is comparatively more sensitive underwater than in air (Kastak and Schusterman, 1999), and in the hippopotamus (*Hippopotamus amphibius*), which is thought to use bone conduction to hear sounds underwater (Barklow, 2004). The generalist diving cormorant is suggested to have particular adaptations for underwater hearing, a trade-off that seems to limit their in-air auditory thresholds (Cosolo et al., 2010; Larsen et al., 2020). If the pressures of deeper diving, or an underwater foraging lifestyle, do influence aerial hearing in multiple seabird species, we might expect similar, or perhaps poorer, aerial sensitivity, for deep-diving auks. New, in-air hearing measurements for an auk species would shed light upon whether these taxa can hear well in air, and thus provide insight into their sensory ecology and communication.

Like other seabirds, auks face many challenges, largely from climate-associated habitat changes and disturbance, habitat loss due to human development, and other anthropogenically induced pressures (Lascelles et al., 2016). At least one auk species, the great auk (*Pinguinus impennis*), was driven to extinction (Bengtson,

1984), and populations of several other species are listed as Threatened or Endangered. This includes the marbled murrelet (*Brachyramphus marmoratus*) and the Atlantic puffin (BirdLife International, 2018a,b). Given their conservation status and that airborne noise is a key pollutant affecting seabird behavior, hearing data are particularly valuable for the auk family. Further, Atlantic puffins are a major tourist attraction in many areas. This certainly exposes them to potential acoustic stressors including human (often tourist) presence. Having an improved understanding of their hearing abilities would allow us to better evaluate noise as a stressor.

Here, we measured the audiograms of nine wild Atlantic puffins. Our goals included addressing how well these seabirds heard in air and examining whether the puffin AEP audiograms were similar to AEP auditory sensitivity data of other birds to address whether their aerial hearing was comparatively limited given the constraints of the amphibious lifestyle. Finally, once we defined their audiogram, we sought to consider whether aerial anthropogenic noise is a potential threat to this taxon. The animals were captured, carefully anesthetized, and placed in a semi-anechoic chamber where AEP measurements were performed. Afterwards, the birds were allowed to recover from sedation and then released at the capture site.

MATERIALS AND METHODS

Animals and study sites

We measured the auditory sensitivity of nine wild Atlantic puffins [*Fratercula arctica* (Linnaeus 1758)] using AEP recording methods. The field-based AEP audiogram study was conducted in May 2018 and methods were nearly identical to a pilot study the prior year measuring the hearing of one Atlantic puffin and one common murre (Mooney et al., 2019b). The puffins were caught using a 10×1.5 m mesh net (10-cm diameter eye size) strung across multiple burrows at a rookery near Tjörnes, northern Iceland. As an animal exited the burrow, it became lightly entangled within the net. It was quickly removed (<2 min) by hand and placed in a soft, black bird bag. The bird was then transported to the hearing test site, a local farm shed, ca. 1 min drive away. The aluminum shed provided some shelter from potentially inclement Icelandic weather conditions.

Once at the hearing test site, the birds were immediately weighed and sedated with an intramuscular injection of a Ketamine hydrochloride:Xylazine hydrochloride 2:1 mixture. The initial dose was 20 and 10 mg kg⁻¹ body mass for Ketamine and Xylazine, respectively. The animals' heart rates were monitored with a stethoscope and body temperature was continuously observed with a veterinary continuous digital anal monitor and probe (DataTherm II, USA). Rates and temperatures were recorded every 5 min. Body temperatures were kept between 40.5 and 41.5°C while heart rates were ca. 200 beats min⁻¹. Animals were ready for the hearing tests 15–20 min post-injection, as noted by a stable temperature, heart rate, respiration rate, minimal movement and closure of the eyes. Work was conducted under a research permit from the Icelandic Environmental Agency and approved by the WHOI IACUC (no. BI21798.01).

Acoustics and evoked potentials

Auditory sensitivity tests were conducted in a portable semi-anechoic chamber built from a large wire-frame dog kennel (118×84×77 cm) that was insulated on all inner sides with 4 cm of soft bedding foam. The door was removed and replaced with an insulated foam flap that could be closed during the hearing tests. A self-contained, battery-powered speaker and amplifier (Nagra DSM speaker, functional range: 60–15,000 Hz ±4 dB; Switzerland)

placed at the far end of the kennel was used to produce the stimuli. The bird was placed on a bed liner near the kennel door with its head aligned toward the speaker during the hearing tests. This allowed easy access to monitor the animal's health status during the hearing test. The distance from a given bird's beak tip to the speaker was 68–70 cm, allowing the animals to be out of the near-field for all but the very lowest frequencies.

Full calibrations, including background noise measurements and stimulus tones, were made both before and after the hearing tests, and stimuli and noise were monitored and recorded during each hearing test. The calibrations and sound level measurements were conducted by playing each stimulus at a constant attenuation level and recording the received sound pressure level using a precision sound level meter (type 2235, flat spectrum setting, Brüel & Kjær, Nærum, Denmark) with its microphone (type 4176) placed at the location of the bird's head. The sound level of each stimulus was controlled by the dB increase or decrease of the attenuator relative to this initial calibrated start value. The received tones were also measured during the hearing tests using the sound level meter, and attenuations and received levels were as expected. To ensure proper spectral content of the stimuli, signals were digitally recorded using an M-Audio Microtrack II recorder (Irwindale, CA, USA) connected to the AC output of the sound level meter. Background noise measurements were similarly made using the sound level meter and saved on the Microtrack recorder. These data and the accuracy of the sound level meter were assessed relative to a 94-dB calibration tone (1 kHz, 1 Pa) from the calibrator of the sound level meter (type 4230, Brüel & Kjær).

The AEP methods used to test hearing thresholds were generally similar to those used in prior AEP studies in birds (Beatini et al., 2018; Brittan-Powell et al., 2002, 2005; Crowell et al., 2015; Henry and Lucas, 2010; Lohr et al., 2013; Maxwell et al., 2016). Hearing test tones and the evoked potentials were recorded using a custom-built LabVIEW (National Instruments, Austin, TX, USA) data acquisition program and a National Instruments PCMCIA-6062E data acquisition card implemented in a semi-ruggedized Panasonic Toughbook laptop computer. We started each examination with a broadband pulse constructed using six cycles of a 2 kHz signal (1.5 ms rise time until the peak, and a corresponding 1.5 ms fall time). The resulting 'click' was relatively broadband with -10 dB energy from 4–12 kHz (see Fig. S1 for spectra) owing to the short duration and rapid onset of the signal. We decreased the tone burst sound levels and measured the thresholds of the click-based responses. The auditory frequency range was then examined using tone bursts of the following frequencies: 0.125, 0.25, 0.5, 1, 1.5, 2, 2.5, 3, 4, 6 and 8 kHz (for further details on experimental birds, see Table S1). The tone presentation order was prioritized, starting with 2 kHz (a frequency generally heard well in birds and showing clear responses in the 2017 pilot tests; Maxwell et al., 2017; Mooney et al., 2019b). We collected what was expected to be a clear response and threshold at 2 kHz, then a general audiogram (i.e. select frequencies), and as time allowed, additional frequencies for greater audiogram detail. Test tones were 10 ms in duration except for the 0.25 and 0.5 kHz tones, which were 20 ms in duration. Each test signal was created using a 256 kHz sample rate and presented at a rate of 10 s^{-1} . The tone bursts were created using a sine envelope, which allowed us to ramp up, reach a maximum and immediately ramp down. With this design, spectral spreading owing to signal onset or offset was limited (Fig. S1). An individual tone burst ramped up over 5 ms (10 ms for the longer duration tones at 0.25 and 0.5 kHz); the ramp down took the same amount of time. The maximum amplitude was found at 5 or 10 ms, depending on tone

duration. In spite of this, the modulation of the brief tones created some minor sidebands (see Fig. S1), but these were 40 dB lower than the center frequency, and thus minimal at low amplitudes (near thresholds) and were not expected to impact auditory sensitivity estimates (Supin and Popov, 2007).

Once the animal was sedated and stable, three 30 gauge, uncoated, stainless steel needle, evoked potential recording electrodes were inserted just under and parallel to the surface of the skin. The active electrode was placed just below the meatus of the anesthetized bird. The reference (inverting) electrode was attached at the vertex of the bird's head. A third 'ground' electrode was inserted dorsally on the animal's back. The AEP system was then grounded to the soil using a long copper wire attached to a 20 cm carbon-fiber rod inserted into the earth outside the shed.

The electrodes were connected to a bandpass filter (300–3000 Hz) and amplifier (CP511, Grass Technologies, Warwick, RI, USA), which amplified all responses 10,000-fold. A second 8-pole Krohn-Hite DC-powered single channel filter (FMB300, Brockton, MA, USA) (passband 300–3000 Hz) further conditioned the signals. The AEP data were finally recorded using the custom laptop program. Responses were sampled at 16 kHz with records beginning coincident with stimulus presentation. Stimuli were presented 1000 times for each sound level and 1000 corresponding AEP responses were averaged and stored for later data analyses. The averaged evoked response waveforms were monitored in real time at each sound level and stimuli were decreased in 5–10 dB steps using an HP 350D 5 W 600 Ω DC attenuator until evoked responses were no longer visually detectable for two to three trials. If no response was discernible relative to the background noise, the SPL was increased by 20–30 dB for the last record of the frequency (confirming a response could still be obtained), after which the next frequency was tested.

Audiogram thresholds were calculated offline. Records were first examined in the time domain (Fig. 1). To extract the AEP waveform from the background noise, cross-correlation functions (CCFs) between the evaluated record and a standard AEP waveform were computed, using an AEP record from a high-amplitude stimulus as the standard. The CCF peak was SPL and response dependent, with its delay lengthening and amplitude decreasing with each stimulus SPL decrease. To determine AEP hearing thresholds, the CCF peak magnitudes were plotted as a function of stimulus SPL expressed in

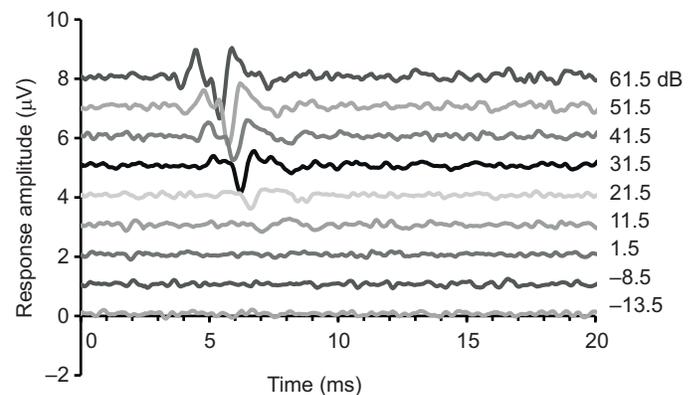


Fig. 1. Evoked potential waveforms of an Atlantic puffin from a stimulus pulse centered at 2 kHz. Acoustic signals, not shown, started at 0 ms. Responses were latency dependent with earliest responses starting at ca. 3 ms after the pulse onset. Received levels (re. 20 μPa) are plotted to the right of the wave form.

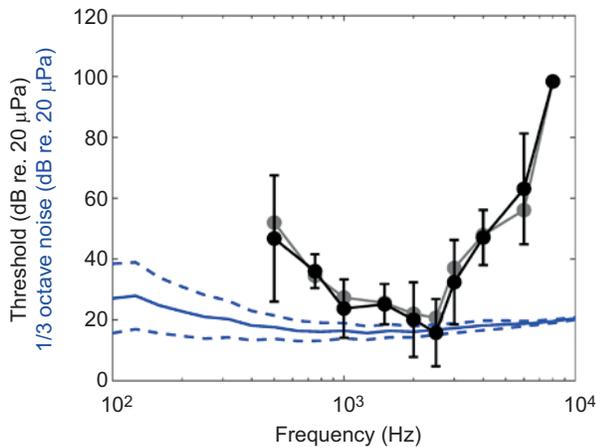


Fig. 2. Mean and median puffin audiograms. Data shown are the mean \pm s.d. (black) and medians (gray) of all puffins. The ambient noise profile (blue; mean \pm s.d.) of the hearing test chamber is also shown.

dB re. 20 μ Pa (further details shown in Mooney et al., 2019b). Intersection of the regression line with the zero-magnitude level was accepted as a threshold estimate (Nachtigall et al., 2007; Supin and Popov, 2007). Data were initially viewed via the custom LabVIEW software and EXCEL (Microsoft, USA). Subsequent analyses including calculating CCFs and regression-based thresholds were conducted using MATLAB (MathWorks, Natick, MA, USA) code. All threshold values are presented in dB re. 20 μ Pa unless otherwise stated.

Background noise measurements

For comparison with the threshold results, background noise measurements were made within the hearing test chamber during experimentation and at the puffin rookery where the test subjects were captured. Background noise within the test chamber was recorded continuously for 3–5 min during experimentation with seven of the nine birds using an Olympus LS-12 Linear PCM recorder connected to the output channel of the Brüel & Kjaer sound level meter (sample rate: 44.1 kHz). Background noise at the puffin rookery was recorded in 1-min segments over 48 h (3–6 June 2018) using an SMM-A2 microphone attached to a Song Meter SM4 Acoustic Recorder (Wildlife Acoustics, Maynard, MA, USA) on a

25% duty cycle at a sampling rate of 24 kHz. Analyses were conducted using custom MATLAB code.

RESULTS

Puffin evoked potentials were clearly observed in response to tones and broadband pulses during both data collection and *post hoc* analyses. Like for many other taxa, responses in puffins were SPL dependent, with response amplitude decreasing with received levels (Fig. 1).

Responses were observable, and thus thresholds could be determined, from 0.5 to 6 kHz. Only one animal showed responses to 8 kHz (Figs 2 and 3A). Individual mean and median thresholds were generally similar and varied between 6 and 19 dB (the range of s.d. values across the thresholds), depending on the frequency tested (Fig. 2). Mean thresholds were below 40 dB re. 20 μ Pa from 0.75 to 3 kHz, reflecting these as the most sensitive frequencies. Mean thresholds and AEP waveform responses to ‘middle’ frequencies of 1–2.5 kHz reached ca. 10–20 dB re. 20 μ Pa. The lowest mean thresholds were observed at 2.5 kHz (16 dB re. 20 μ Pa), although only four animals were measured at this frequency (owing to time constraints of the sedation). At 2 kHz, a frequency tested in all animals, thresholds were 20 ± 12 dB (mean \pm s.d.) and ranged from -4 to 37 dB re. 20 μ Pa. Above 2.5 kHz, hearing thresholds increased steeply. Below 2.5 kHz, thresholds increased more gradually, roughly 12 dB per octave between 2 kHz and 500 Hz. The most sensitive thresholds approached the average background noise levels of the test chamber, reflecting high auditory sensitivity at these ‘best’ puffin frequencies. The test chamber was relatively quiet within the frequency range of the hearing measurements (ca. 20 dB re. 20 μ Pa), ensuring a quiet study environment (Fig. 2).

There was some variability between the animals’ audiograms (Fig. 3). These differences were examined in several ways to provide insight into the variability that exists in the wild and to provide options for assessing sound sensitivity. Thresholds from all birds were presented together, showing the range within and between individuals. Some individual puffins exhibited more variability. For example, birds 2018_05, 2018_07 and 2018_09 showed particularly low thresholds at 1, 2 and 2.5 kHz, respectively (Fig. 3, Fig. S2, Table S1). The audiograms for animals 2018_04 and 2018_06 showed more consistency between frequencies. Most animals had very high auditory sensitivity; two

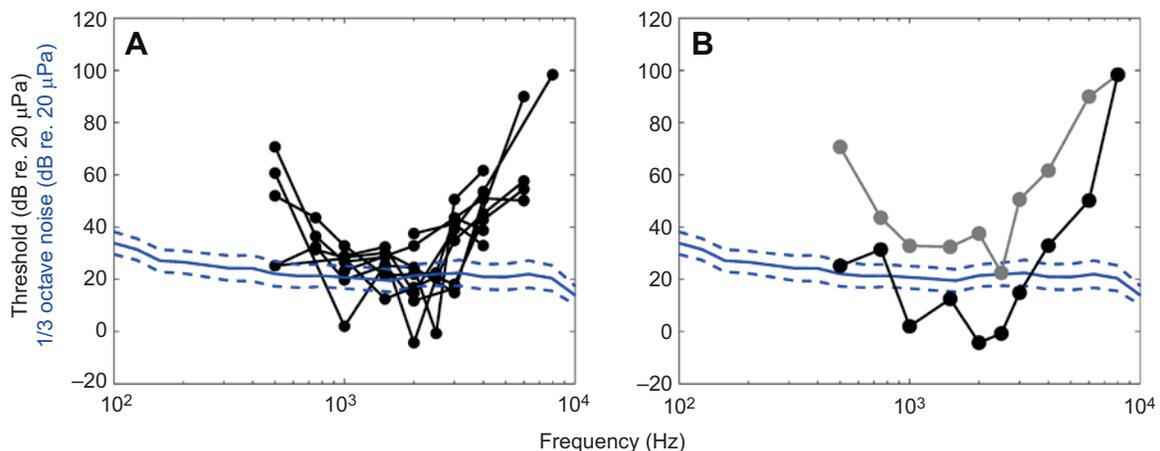


Fig. 3. Addressing audiogram variability. (A) Combined audiograms of nine Atlantic puffins. (B) Audiograms representing the highest (i.e. poorest sensitivity) and lowest thresholds (i.e. greatest sensitivity) for all Atlantic puffins. The noise profiles in both subplots (blue; mean \pm s.d.) show the ambient, third-octave noise levels from the rookery where the puffins were caught and released.

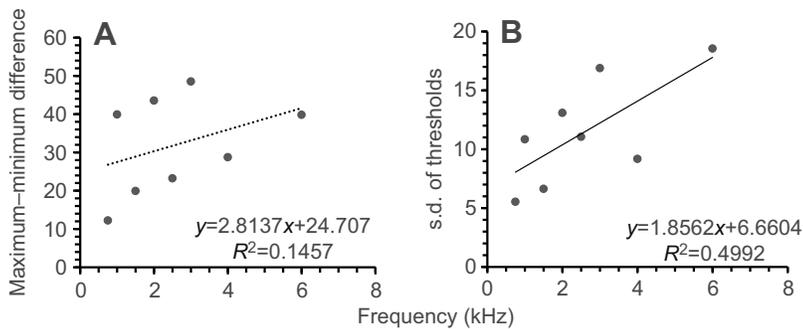


Fig. 4. How variation compares across hearing thresholds. (A) Difference between the maximum and minimum thresholds (dB re. 20 μ Pa) for each hearing test frequency. The maximum–minimum difference showed a general linear increase, albeit a weak relationship, with frequency tested, except for the lowest frequency (0.5 kHz, not shown). (B) Standard deviation of the thresholds relative to the frequencies tested. This variation also increased with frequency, showing the greatest variation as hearing threshold increased (except again for 0.5 kHz).

even had thresholds below 0 dB re. 20 μ Pa. Three animals had thresholds, at their most sensitive frequencies, that were within 2 dB of 0 dB re. 20 μ Pa.

The auditory abilities of many of the puffins tested were approximately the same sound level as the mean background noise levels of the birds' cliffside nesting habitats. Yet the most sensitive thresholds (measured in a very quiet, semi-anechoic chamber) were below these ambient noise conditions. This suggests that at times, the natural soundscape of the cliffside habitat would mask these animals' hearing abilities (but see Discussion). Of course, puffins nest in burrows with long entrance tunnels (0.5–1 m), and these tunnels may act like lowpass filters, substantially reducing ambient noise, and quiet places for puffins to acoustically communicate their low-amplitude signals.

Composite maximum and minimum thresholds were plotted for each frequency (Fig. 3B), illustrating an empirically based assessment of both the most and least sensitive thresholds. This maximum–minimum assessment illustrates how much thresholds can vary at a particular frequency (Figs 3 and 4). This variation range could reach 40–50 dB for the more disparate thresholds (0.5, 2 and 3 kHz), but was as low as 10–20 dB (0.75, 1.5 and 2.5 kHz). The mean difference between maximum and minimum thresholds at each individual frequency for all nine puffins was 32 dB. The difference between maximum and minimum thresholds increased with frequency, although this relationship was weak ($R^2=0.15$; Fig. 4A). Furthermore, there was a positive correlative relationship of threshold variation (measured in s.d.) with hearing test frequency, showing that auditory variation increased with frequency ($R^2=0.50$). However, this relationship was true only when not considering 0.5 kHz, for which thresholds varied by 17 dB (the value of 1 s.d. at 0.5 kHz 1 s.d.).

DISCUSSION

The puffin audiogram

Our AEP measurements resulted in audiograms of nine puffins, thereby rendering the first in-air hearing data on multiple wild-caught individuals of an alcid species. The audiogram was comparable to that of other birds of similar size, indicating that these puffins have fully functioning aerial hearing. The upper frequency limit of auditory sensitivity in one animal was slightly higher than the rest (8 versus 6 kHz). There was some variation in thresholds; the average standard deviation across frequencies was ± 12 dB (6–18 dB range). However, this variation might be considered minor, compared with intra-species differences noted in the audiograms of other wild taxa (e.g. humans, fishes and odontocetes) (Amoser and Ladich, 2005; Corso, 1959; Houser and Finneran, 2006b; Mooney et al., 2018). The frequency of greatest sensitivity (2.5 kHz) matched well with the data and predictions of Gleich et al. (2005), who predicted hearing abilities based on body mass. Overall, the animals had generally sensitive ears, suggesting

aerial hearing is an important sensory modality for this taxon. Although puffin sounds are not well described, one would expect acoustic communication to play a key role in their ecology.

How to assess a wild population's 'average' auditory sensitivity remains to be fully defined. Population assessments often summarize the audiogram using mean and median thresholds (Amoser and Ladich, 2005; Brittan-Powell et al., 2002; Houser and Finneran, 2006b; Sysueva et al., 2018), thereby creating a type of general or 'representative' audiogram for the group of test subjects. These traditional methods are 'standard' and allow for comparisons to many prior studies. Yet, these assessments can lead to potential biases when (i) a frequency with a small number of observations (from only a few animals) contains potential outlier data, or (ii) not all frequencies have the same number of data points (Branstetter et al., 2017). The latter can easily occur when limited by field constraints, sedation, other veterinary concerns, and health of the animal.

An alternate method, used in cetaceans (Branstetter et al., 2017; Finneran, 2016; Mooney et al., 2018; Popov et al., 2007) and birds (Gleich et al., 1995), examines the auditory thresholds of multiple animals together using a polynomial line to address all animals' threshold values (Fig. 5). This polynomial interpolation can more

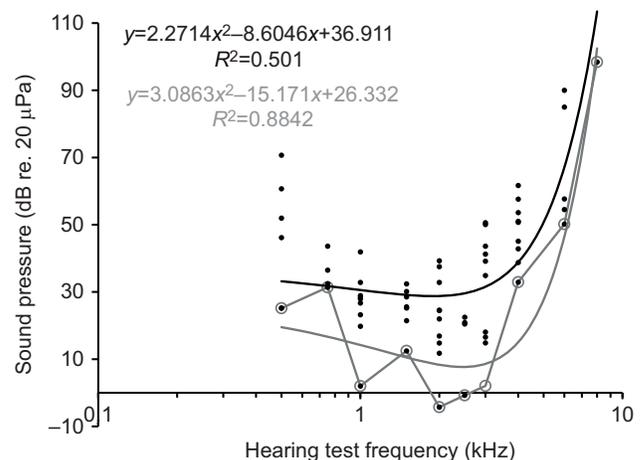


Fig. 5. Responses of all puffins plotted using three curves that might be used to address population sound sensitivity. The solid black curve is a best-fit second-degree polynomial line addressing all the measured hearing thresholds. The smooth gray curve is a best-fit second-degree polynomial that addresses just the lowest, most sensitive, hearing points noted by the gray circles. This curve reflects the most sensitive approximation of hearing. The equations and R^2 for the polynomial lines are listed on the graph. The somewhat jagged gray line directly addresses the most sensitive hearing thresholds for each frequency. Note that the gray polynomial line often falls above the hearing threshold points at the most sensitive, mid-frequencies.

robustly address sensitivity curves without major influences by certain data points and individuals (Branstetter et al., 2017).

In some cases, however, a standard or average audiogram of a species may not be the most appropriate or desired metric. For example, when assessing potential impacts of anthropogenic noise, particularly for endangered or threatened species, a conservative estimate of auditory sensitivity may be desired. We therefore calculated a separate polynomial line to address only the lowest, most sensitive, thresholds (gray line, Fig. 5).

The composite minimum thresholds (Fig. 3B) presented the ‘most sensitive’ auditory abilities measured and provided an important way to address the near-limit of auditory sensitivity in these birds. This conservative method of addressing the population’s auditory sensitivity is vital when considering anthropogenic noise impacts. Recent studies of noise influences on birds have shown that lower level noise from nearby human presence (talking, off-road vehicles, tourists), resulted in birds spending less time on their nests, and decreased survival of those hatchlings (Borneman et al., 2016; Buxton et al., 2017). These studies underscore the need for integrating the lower thresholds into management to limit acoustic disturbances. The methods outlined here provide managers with options in how they choose to evaluate a population’s sound-sensitivity and protect a population from anthropogenic noise.

Comparative hearing

To put these threshold values into context, we compared the lowest and the mean puffin audiograms measured here with a number of other avian audiograms measured using AEP methods (Fig. 6). This included audiograms from the screech owl, northern saw-whet owl, budgerigar, cormorant, northern gannet and lesser scaup (Beatini et al., 2018; Brittan-Powell et al., 2002, 2005; Crowell et al., 2015; Larsen et al., 2020). Many of these audiograms were averages compiled in their respective papers. Yet there were some methodological differences between papers. For example, we averaged 1000 records (similar to Brittan-Powell et al., 2002, 2005), whereas other researchers used fewer tone presentations and averages [Crowell et al. (2015) used 600 for several species, Beatini et al. (2018) for the northern saw-whet owl used 800, and Larsen et al. (2020) used 400 in the cormorant]. Bandpass filter ranges were

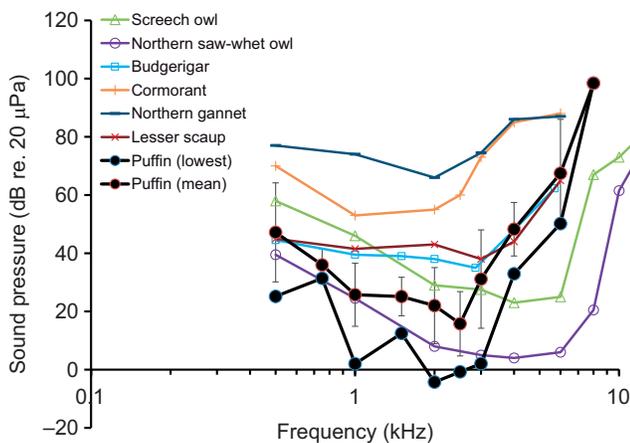


Fig. 6. Lowest and mean auditory evoked potential (AEP) audiogram thresholds compared with six other bird species also measured using AEP methods. Audiograms from other studies include those from Beatini et al. (2018), Brittan-Powell et al. (2002, 2005), Crowell et al. (2015) and Larsen et al. (2020).

similar, but AEP amplifications differed between studies. The 10 ms tone durations used here were slightly longer than some of the tones in aforementioned previous research [except Larsen et al. (2020), who used 25 ms]. We found that the 10 ms tone duration used in the present study was a good balance of creating an onset response, typical and necessary for obtaining clear AEPs, and generating a fairly narrow-band tone (Fig. S1). The free-field is not easily obtained in sedated animals that must rest on a surface, and the exact distance from animal to speaker also varied. It is difficult to determine the combined effects of these various differences; thus, the comparisons should be considered preliminary.

The thresholds for the puffins in this study were lower than those measured for a single puffin and common murre in 2017 (Mooney et al., 2019b). Although this could be due to species or population differences, we suggest the elevated thresholds in 2017 were likely the result of greater physiological noise in the data collected that year. The 2017 root mean square (rms) AEP noise levels for the puffin and murre were $1.9 \pm 0.11 \mu\text{V}$ ($n=5$ samples) and $5.3 \pm 0.28 \mu\text{V}$ ($n=5$ samples), respectively. In comparison, the AEP noise levels from all birds in 2018 were much lower, with a mean of $0.89 \pm 0.15 \mu\text{V}$ rms (5 samples per bird). This may have been in part due to myogenic movement; the murre was snoring and moving subtly every 1–2 min throughout the examination, causing spikes in physiological noise. Such events, if rare, may be averaged out or the record can be repeated; however, if such movement occurs regularly, it will increase noise levels. Such an issue is difficult to reduce in the field with limited recording time on a sedated animal. We were able to avoid these issues in 2018 with slightly lighter sedation and improved grounding at the puffin field site. Notably, we would suggest that AEP noise similarly affects thresholds in other studies as well. Crowell et al. (2015) and Larsen et al. (2020) provide the most comprehensive summary of AEP audiograms in aquatic birds. The animals with the highest thresholds also seem to have the highest levels of physiological noise.

In the range 0.5–2.5 kHz, the mean puffin audiogram was typically lower (more sensitive) than all other birds noted except the northern saw-whet owl (Fig. 5, Fig. S3). Notably, the saw-whet owl study used tone bursts that were relatively short duration and likely somewhat broadband. This would have stimulated a greater proportion of the basilar papillae and likely resulted in lowered thresholds compared with the more tonal stimuli used for other birds. At 3 kHz and above, the mean puffin audiogram was on par with the other birds’ audiograms, suggesting that hearing abilities at these frequencies were quite similar. The hearing range cut-off of the puffins was 6–8 kHz, also like non-owl birds; only the owls showed thresholds at higher frequencies. Further, the mean puffin audiogram was usually below (more sensitive than) that of the other seabirds (the lesser scaup, northern gannet and cormorant). Overall, this suggests that the puffin auditory sensitivity in air was good and perhaps more sensitive than many other terrestrial and aquatic birds. This is despite having to cope with the constraints of pressure from diving down to great depths. Put another way, the ears have not overcompensated for diving adaptations and constraints by limiting in-air hearing. We do not know how well auks hear underwater, but initial tests suggest they do at least hear and respond to underwater sounds (Hansen et al., in press).

Sensory ecology and considering noise

The lowest thresholds (1–2.5 kHz) approached the levels of background noise measured in one-third octave bands of the test chamber, with some thresholds falling below the mean noise level. Although some evidence suggests that the thresholds may have been

masked, this may not be the case. Strictly speaking, it is the critical ratio (CR; e.g. the acoustic power in the tone over the spectrum level of noise) that is the relevant measure. CRs have been measured in approximately 16 species of birds and on average are approximately 25 dB around 2–3 kHz (Dooling et al., 2000, 1986). In the present study, the spectrum levels of the background noise from 1 to 3 kHz (data not shown) were ca. –10 to –20 dB re. $1 \mu\text{Pa}^2 \text{Hz}^{-1}$. Adding the average bird CR to these spectrum levels provides values of 5 to 15 dB, or less than the mean thresholds measured here (and nearly all thresholds), suggesting that the present audiograms were unmasked. The situation may be even better when it is considered that these spectrum levels are constant averages, but ambient noise is temporally structured, so there would likely be co-modulated masking release and further unmasking of the thresholds (e.g. see Klump, 1996).

A similar unmasked scenario is evident for the ‘quiet’ sound levels of the rookery where the puffins were caught and released, indicating that at quiet times, the puffin hearing is unmasked at the rookery. However, the rookery ambient noise data were selected to be when the wave and wind noise were low; as weather-induced noise increases, the masking by the cliff habitat is likely to increase. Yet, we might expect that inside the puffins’ burrows, and perhaps out at sea, conditions might be quieter and masking there reduced as well.

The puffins’ relatively high low-frequency auditory sensitivity is intriguing. Low frequencies tend to transmit with less attenuation in a constant media and can propagate well through *terra firma*. Puffins nest in underground burrows on the edge of cliffs. They might use low-frequency sounds to hear cues of predators walking above the burrows. Puffin vocalizations are also low frequency and not very high amplitude (unpublished observations, T.A.M. and A.B.S.; Mooney et al., 2019a). Their auditory sensitivity likely facilitates hearing of conspecific calls, and perhaps nest, pair and young recognition.

The understanding of puffin hearing is complicated by their amphibious and subterranean nature. In some taxa with habitats spanning two media (often air and ground), hearing abilities are limited or adapted to a particular medium [i.e. some ants or snakes detect substrate borne sounds and hear airborne sound poorly (Roces and Tautz, 2001), and elephant seals hear well underwater but seemingly not as well in air (Kastak and Schusterman, 1999)]. Yet some amphibious species, such as spotted seals, ringed seals and cormorants, hear well in both air and water (Sills et al., 2014, 2015). At this point, we can conclude that puffins can hear well in air. Like many other seabirds, this suggests that increasing human encroachment and airborne noise is a concern for this taxon.

Overall, this field-based audiometry represents a new step in bird acoustic ecology by enabling fast and flexible auditory measurements in more taxa and individuals of target species. Future studies could combine these hearing measurements with additional studies such as demography, genetics or health measurements, including potential influences of hormones, parasites and contaminants (Mooney et al., 2018; Norman et al., 2012), to assess how hearing abilities may be associated with certain habitats, individual condition, relatedness and chronic stress. By combining auditory sensitivity data with the acoustic environment around the birds and the frequency content and amplitudes of their communication sounds, we can address how changes in background noise levels may lead to masking and shorter communication ranges. Indeed, the low aerial thresholds suggest that these animals will easily detect anthropogenic noise. Given the influence of human encroachment on bird colonies (Buxton et al., 2017), the sensitive hearing of these animals, and the fact that puffins are a

major tourist attraction in many countries, we suggest that human disturbance noise, even low-level sounds from hikers and visitors, have the potential to disturb puffins. This may be true for other auks as well. Although seabird colonies may now be tourist destinations, many species have long been hunted. Human presence likely carries this evolutionary threat, particularly during nesting season, when puffins have been traditionally hunted from their burrows. These data show that puffins can have low auditory thresholds, illustrating the importance of this sensory modality for this taxon. These hearing abilities and accompanying acoustic communication are subsequently at risk of being impacted by anthropogenic noise. The rates of noise encroachment and the importance of preserving quiet or natural acoustic habitat conditions are topics deserving greater attention in the future. The ability to measure bird auditory sensitivity in the field allows us to rapidly examine hearing abilities in a range of different seabirds and perhaps other avian taxa, providing a broader understanding of the acoustic ecology of many taxa and the increasing encroachment of anthropogenic noise.

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Competing interests

The authors declare no competing financial interests.

Author contributions

Conceptualization: T.A.M., M.R.; Methodology: T.A.M., A.B.S., O.N.L., K.A.H., M.R.; Software: T.A.M.; Validation: T.A.M., O.N.L.; Formal analysis: T.A.M., A.B.S.; Investigation: T.A.M., A.B.S., O.N.L., K.A.H., M.R.; Resources: T.M., M.R.; Data curation: T.A.M.; Writing - original draft: T.A.M.; Writing - review & editing: T.A.M., A.B.S., O.N.L., K.A.H.; Visualization: T.A.M., A.B.S.; Supervision: T.A.M.; Project administration: T.A.M., M.R.; Funding acquisition: T.A.M., M.R.

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Supplementary information

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