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Psychoacoustic data confirm reduced hearing sensitivity in Hawaiian monk seals relative to Phocinae seals

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ABSTRACT: We presently have an incomplete understanding of hearing in Hawaiian monk seals *Neomonachus schauinslandi*. Their auditory biology is important from a conservation perspective and is especially intriguing given their long evolutionary isolation from related seal species. Available audiometric data for 2 individuals are conflicting, but suggest that monk seals have limited aquatic and terrestrial hearing abilities compared to the more well-studied species in the Phocinae subfamily of seals. To resolve representative amphibious hearing profiles for Hawaiian monk seals, we describe auditory sensitivity for 1 additional seal trained to participate in a psychophysical task while submerged and on land. Detection thresholds were measured for narrowband signals across the frequency range of hearing under water and at select frequencies in air. This individual demonstrated poor sensitivity in both media, with notable insensitivity to high-frequency waterborne sounds and an overall decreased ability to detect airborne sounds. The range of functional hearing was wider in water (<0.1–40 kHz) than in air (0.1–33 kHz), with peak sensitivities of 73 dB re 1 μPa (at 18 kHz) and 42 dB re 20 μPa (at 3.2 kHz), respectively. These data confirm recently published behavioral audiograms as typical for the species. When considered with the limited available data for related species, these findings suggest that hearing within the Monachinae subfamily of seals differs from that of the highly sensitive Phocinae seals. This study advances knowledge of the evolution of hearing in amphibious marine mammals and supports conservation and management decisions for the endangered Hawaiian monk seal.

KEY WORDS: Marine mammal · Phocid · Audiogram · Endangered species

1. INTRODUCTION

True seals — the semi-aquatic carnivores of the family Phocidae — have evolved to utilize sound in 2 very different physical environments, with waterborne sounds traveling faster and attenuating less than airborne sounds of the same frequency content. The consequences of these medium-dependent characteristics of sound for different seal species can be considered relative to their phylogenetic relationships, anatomical adaptations, and specific hearing abilities. Our knowledge of hearing in seals has increased substantially in recent decades, but several questions and data gaps remain (see Southall et al. 2019). The most complete dataset describing amphibious hearing is for the Phocinae subfamily (polar and most temperate seals of the Northern Hemisphere). These data indicate that Phocinae seals have acute

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amphibious hearing abilities, with best sensitivities rivaling those of aquatic and terrestrial mammalian specialists in their respective media (Kastelein et al. 2009, Reichmuth et al. 2013, Sills et al. 2014, 2015, 2020). Conversely, there are few hearing data for seals from the Monachinae subfamily (the Southern Ocean seals as well as elephant and monk seals). Hearing profiles from 1 elephant seal and 2 monk seals suggest that Monachinae species have significantly reduced abilities in air and water relative to other true seals, with especially poor sensitivity to airborne sound (Thomas et al. 1990, Kastak & Schusterman 1999, Reichmuth et al. 2013, Ruscher et al. 2021, Sills et al. 2021). While the available audiometric data indicate potential subfamily-level differences in hearing, additional information is needed to improve our understanding of similarities and differences in auditory biology among true seals.

Of the Monachinae species, the monk seals are of particular interest due to their Vulnerable or Endangered conservation status (Littnan et al. 2015, Karamanlidis et al. 2023) and their long evolutionary and biogeographical isolation from other true seals (Rule et al. 2021). The auditory biology of extant monk seals *Monachus monachus* and *Neomonachus schauinslandi* remains incompletely understood, though some hearing data are available for 2 Hawaiian monk seals *N. schauinslandi* studied in zoological settings. An initial underwater audiogram by Thomas et al. (1990) suggested that a young male Hawaiian monk seal was insensitive to sounds below 10 kHz, indicating that hearing in this species could differ from that of other true seals. More recently, comprehensive audiometric measurements were obtained to describe amphibious hearing capabilities in another Hawaiian monk seal. Sills et al. (2021) reported a much broader range of hearing in water, more similar to that of Phocinae seals despite a somewhat lower high-frequency hearing limit and elevated thresholds overall. Ruscher et al. (2021) reported poor sensitivity to airborne sounds in the same individual, with an unusually flattened audiogram and peak sensitivity approximately 50 dB higher than that measured for Phocinae seals. While these data collectively suggest that monk seals have reduced hearing abilities both above and below the water's surface, the unexpectedly high thresholds in both media and the discrepancies between the 2 underwater studies at frequencies below 10 kHz make the available audiograms difficult to interpret. More data are needed from at least 1 additional individual to characterize typical auditory sensitivity in Hawaiian monk seals and to help inform higher-level questions about hearing in related species.

By obtaining comprehensive behavioral hearing measurements in air and in water with a third Hawaiian monk seal and comparing these results to those of Ruscher et al. (2021), Sills et al. (2021), and Thomas et al. (1990), we resolve inconsistencies in available auditory data and confirm typical amphibious hearing abilities for *N. schauinslandi*. These findings improve our understanding of the evolution of hearing within the phocid clade of carnivores and support conservation and management decisions involving anthropogenic noise for monk seals and possibly other Monachinae species.

2. MATERIALS AND METHODS

2.1. Subject

The subject was an adult male Hawaiian monk seal identified as KP2 (NOA0006753, also known as *Hoʻailona*). This seal was born in the wild but brought into permanent human care after his habituation to humans rendered him non-releasable (Williams 2012). KP2 participated in this auditory study at Long Marine Laboratory at the University of California (Santa Cruz, CA, USA) while on loan from the Waikīkī Aquarium (Honolulu, HI, USA). KP2 was 13 yr old at the start of testing and weighed approximately 170 kg. His curvilinear interaural distance was 24 cm measured dorsally, while the straight length between his meatal openings was 19 cm. He had no known ear pathologies or exposure to ototoxic medications other than a short course (7 d) of topical tobramycin eyedrops at age 5 yr, which was considered unlikely to be harmful to auditory structures (C. Field pers. comm.). However, this seal had bilateral hypermature cataracts and lens-induced uveitis, resulting in significant permanent visual impairment.

KP2 participated in 1 audiometric session per day, up to 5 d per week. He received one-third to one-half of his scheduled daily diet of thawed fish and squid during this session. His prescribed diet was established for optimal health and was not constrained for experimental purposes. This seal had experience with operant conditioning using positive (fish) reinforcement for behavioral management and cooperative physiological research (Williams et al. 2011, Williams 2012, Kienle et al. 2019, 2020, John et al. 2021); however, he had no prior experience with auditory testing and was gradually trained over a 6 mo period to respond to airborne and waterborne acoustic signals. Subsequent audiometric testing occurred in water from April 2022 to July 2023 and in air from January to August 2023.

Research was conducted with approval and oversight from the Institutional Animal Care and Use Committee at the University of California Santa Cruz, with authorization from the National Marine Fisheries Service of the United States under marine mammal research permits 24054 to T. Williams and 23554 to C. Reichmuth. Behavioral audiometry was conducted without harm, stress, or food deprivation using positively conditioned voluntary responses to tonal sounds.

2.2. Underwater hearing measurements

To provide direct comparative data, we replicated the underwater hearing study conducted previously with Hawaiian monk seal KE18 (NOA0006781; Sills et al. 2021), with minor adjustments. In the present study, auditory measurements for monk seal KP2 were obtained either in the same circular, partially in-ground, seawater-filled pool (1.8 m deep and 7.6 m diameter; test frequencies 0.8 kHz and above) or in an adjacent pool of the same size (0.4 kHz and below). The training methods, acoustic calibration protocols, testing apparatus, and environmental controls matched those used previously for monk seal KE18. The audiometric procedure was generally similar, with minor differences in threshold determination (see Text S1 and Table S1 in the Supplement at www.int-res.com/articles/suppl/n056p019_supp/ for a detailed comparison of threshold methodology). Several items in the equipment chain, including the underwater sound projector, were different (see Fig. S1 for a detailed equipment schematic).

Underwater hearing was evaluated using a behavioral 'go/no-go' psychoacoustic procedure (Stebbins 1970) at 14 frequencies spanning 0.1–60.9 kHz (Video S1 at www.int-res.com/articles/suppl/n056p019_supp/). Hearing thresholds were measured using an adaptive staircase procedure (Cornsweet 1962), where frequency was held constant and signal level was varied based on subject performance. In practice, this involved presenting the seal with 40–60 successive trials within a session, 50–70% of which contained a narrowband signal. Each session contained at least 3 transitions between trials in which the signal was successfully detected and those in which the subject failed to respond after the signal level was lowered by 2 dB (i.e. hit-to-miss transitions). Sessions were repeated until performance on signal-present and signal-absent trials was stable. Within a session, only the plateau of consecutive signal trials with hit-to-miss transitions within 6 dB of one another was used to calculate threshold. Final threshold was determined as the average of 15 hit-to-miss transitions across 3–4 sessions with a standard deviation <3 dB and with a pooled false alarm rate >0 and <0.30. False alarm rate for an individual session was defined as the proportion of signal-absent trials between the first and last hit-to-miss transitions on which KP2 incorrectly reported a signal detection[1]. Frequencies were tested in a pseudorandom order, with the first hearing threshold remeasured near the end of the experiment to evaluate the possibility of a practice effect. At each test frequency, threshold-to-noise offset was calculated as the difference between hearing threshold and ambient noise spectral density level.

Acoustic stimuli were 500 ms frequency modulated upsweeps with a 10% bandwidth (±5% from center frequency) and 5% rise and fall times. Signals were generated in LabVIEW (NI) using custom Hearing Test Program (HTP) software (Finneran 2003). They passed through an NI USB-6259 BNC M-series data acquisition module (500 kHz update rate), a Krohn-Hite 3364 bandpass digital filter, a Tucker-Davis Technologies PA5 digital attenuator, and in some cases a Behringer NX1000 power amplifier prior to reaching the designated speaker. Signals were projected from 1 of 3 speakers, depending on frequency: a Naval Undersea Warfare Center (NUWC) J-11 transducer for 0.1–0.4 kHz, a NUWC J-9 transducer for 0.8–6.4 kHz, or an International Transducer Corporation 1042 projecting hydrophone for 12.8–60.9 kHz. The transducers were suspended into the pool approximately 6 m behind the seal and decoupled from the subject's listening station. Exact speaker positions were determined by spatial mapping of the sound field to ensure acceptable variability of the test stimuli (±3 dB) within a 14 × 14 × 14 cm grid surrounding the location of the seal's head during testing. For sound field mapping and daily calibration, signals were received in the absence of the seal through a calibrated Reson TC4032 low-noise hydrophone (0.01–80 kHz, ±2.5 dB) with a Reson EC6076 active input module, passed through the same data acquisition board, and measured in HTP. The entire system was checked regularly with a GRAS 42AA pistonphone with an RA0046 adapter.

Sound field mapping and daily calibration ensured that the acoustic conditions replicated Sills et al. (2021). As in Sills et al. (2021), ambient noise conditions in the pool were measured in 1/3-octave bands

[1]Responses prior to signal presentation on signal-present trials were also considered false alarms.

prior to every session using the TC4032 hydrophone and a self-powered Brüel and Kjær 2270 sound level meter (sampling rate 48 kHz). The median of daily, 1 min unweighted 50th percentile measurements (L50) were converted to units of power spectral density. On a subset of days, ambient noise was recorded above 24 kHz with the hydrophone and a battery-powered Fostex FR-2 Field Memory Recorder (sampling rate 192 kHz). At the end of testing, thresholds and ambient noise levels were adjusted based on the frequency-specific sensitivity of the TC4032 hydrophone used.

2.3. In-air hearing measurements

Prior auditory testing with monk seal KE18 demonstrated poor sensitivity to airborne sounds, even when evaluated in the very quiet conditions of a hemi-anechoic acoustic chamber (Ruscher et al. 2021). Therefore, we elected to conduct testing more efficiently with KP2 in a semi-controlled outdoor environment. Test frequencies were chosen to ensure that expected thresholds were sufficiently elevated above background noise. The theoretical lowest thresholds measurable outdoors were predicted by adding actual or extrapolated monk seal critical ratios (Ruscher et al. 2021) to ambient noise spectral density levels at corresponding frequencies. KE18's thresholds were all higher than the lowest values that could be measured outdoors, indicating that KP2's auditory thresholds — if his hearing were similar — could be accurately measured in this environment. Specifically, we tested 6 frequencies with sufficient separation (5–48 dB) between theoretical lowest thresholds and KE18's measured thresholds to allow for typical individual variation in detection abilities. At these frequencies, thresholds measured outdoors for KP2 were ultimately compared to theoretical lowest thresholds to evaluate whether hearing was influenced by background noise. Measurements falling well above theoretical lowest thresholds reflected absolute hearing sensitivity. Conversely, any thresholds similar to or below theoretical lowest thresholds were likely constrained by noise. The latter would reveal that KP2's auditory sensitivity is more acute than KE18's, thus requiring further testing in quieter conditions.

Auditory measurements were obtained at 0.2, 3.2, 6.4, 12.8, 18.1, and 33.2 kHz in a semi-enclosed 4 × 3 m triangular holding area adjacent to the underwater testing pools (Video S1). This area was covered with a shade cloth, and had vertical walls of HDPE, plexiglass, or vinyl-coated chain link. The floor was composite decking material. A listening station was positioned so the monk seal rested comfortably in an open doorway at the front of the holding area with his ear openings 19 cm above the deck. A response target was located 13 cm to his left and the space behind it remained open to the adjacent pool. The speakers used to generate test signals were positioned in front of KP2 on axis with his midline. Padding was added between the listening station and speaker as needed to reduce variability in the sound field (characterized during spatial mapping of received signals) due to nearby reflective surfaces. Frequencies were tested in a pseudorandom order, with one hearing threshold remeasured near the end of the experiment to evaluate the possibility of a practice effect.

Acoustic stimuli had the same parameters as for in-water testing and were generated in the same manner using HTP software. Signals were passed through an NI USB-6251 data acquisition module (500 kHz update rate), a 0.1–250 kHz Krohn-Hite bandpass active filter module, and a Radial 2-channel Mix 2:1 passive mixer, before being projected through a Neumann KH 80 DSP powered studio monitor (0.057–21 kHz, ±3 dB). For testing at 33.2 kHz, filtered signals were passed from the data acquisition module straight to an Avisoft ultrasonic power amplifier, and were projected with an Avisoft Vifa ultrasonic dynamic speaker (1–120 kHz, ±12 dB). Speakers were positioned 0.8–1.3 m in front of the seal. Their exact locations were determined by spatial mapping of the received sound field in the absence of the seal to confirm acceptable variability (± 3 dB) of the test stimuli across 14 positions in a 4 × 4 × 4 cm grid surrounding the location of each of the seal's ears during testing. For spatial mapping and daily calibration at 0.2–18.1 kHz, signals were received by a Brüel and Kjær battery-powered 2250 sound level meter (sampling rate 48 kHz) with a free-field 4966 1/2-in microphone (0.005–20 kHz, ±2 dB), passed through the data acquisition board, and measured in HTP. For 33.2 kHz, signals were received by a Microtech Gefell MK301 microphone capsule (0.005–100 kHz, ±2 dB) with a Josephson C617 body and a Stewart Electronics BPS-1 power supply, passed through the same data acquisition board, and measured in HTP. The entire system was checked regularly with a RION NC-73 sound level calibrator.

Training procedures and test stimuli matched those used for monk seal KP2's underwater audiogram and for monk seal KE18 in air (Ruscher et al. 2021). Threshold determination followed the methodology used for KP2 in water and by Jones et al. (2023) for odobenid and otariid carnivores. Acoustic calibration protocols and most equipment (see Fig. S1 for a detailed equipment schematic) were consistent with those used by Jones et al. (2023). As in water, ambient noise was measured prior to each session in 1/3-octave bands and converted to power spectral density levels. Below 20 kHz, measurements were obtained with the 2250 sound level meter and the 4966 microphone. Ambient noise measurements were limited above 20 kHz by the self-noise of the Fostex FR-2 recording system that was used for high-frequency noise measurements in water.

3. RESULTS

Underwater and in-air thresholds, false alarm rates, ambient noise levels, and threshold-to-noise offsets at each frequency are provided for monk seal KP2 in Table 1. The associated underwater audiogram and in-air thresholds are plotted along with comparative auditory data (Fig. 1). Thresholds collected for KP2 fell within 4 dB of KE18's auditory data on average (maximum of 11 dB difference at 33.2 kHz in air).

KP2's underwater audiogram was relatively flat (7 dB range) from 0.8–25.6 kHz, with a peak sensitivity of 73 dB re 1 μPa at 18 kHz. The functional range of hearing (frequencies audible at 120 dB re 1 μPa, see Houser & Finneran 2006) extended from <0.1 kHz to approximately 40 kHz. The 20 dB range of best sensitivity — defined as the frequency range of thresholds within 20 dB of peak sensitivity (see Reichmuth et al. 2013) — spanned from approximately 0.16–36 kHz. Above this range, thresholds increased by about 30 dB within a half octave. Sensitivity decreased more slowly at the low-frequency end of the audiogram, with a slope of 7 dB per octave on the roll-off.

The 6 in-air hearing thresholds measured for KP2 suggest that he has a flattened audiogram similar to that of KE18, with a relatively shallow curve compared to the typical mammalian U-shape. Best sensitivity was 42 dB re 20 μPa at 3.2 kHz and, like KE18, KP2's data exhibited a distinct upward notch at 6.4 kHz. Overall, KP2's thresholds indicate that both the functional range of hearing — defined as frequencies audible at 60 dB re 20 μPa (see Heffner & Heffner 2007) — and the 20 dB band of best sensitivity would fall between approximately 0.1 and 33 kHz for this individual. KP2's high-frequency hearing appears to decrease in sensitivity earlier and at a steeper rate than KE18's, with a slope of approximately 22 dB per octave. All 6 thresholds measured in air were at least 8 dB above the theoretical lowest thresholds predicted for this outdoor testing environment.

Table 1. Amphibious hearing thresholds obtained for Hawaiian monk seal KP2 using psychophysical methods. Detection thresholds are provided for 14 frequencies under water and 6 frequencies in air, along with corresponding SDs, pooled false alarm rates (n = 17–44 signal-absent trials per frequency), ambient noise levels, and threshold-to-noise offsets. False alarm rate was defined as the proportion of signal-absent trials between the first and last hit-to-miss transitions of a session on which KP2 incorrectly reported a signal detection. Ambient noise was calculated from 1/3-octave band levels including each test frequency and is reported as median (L50) power spectral density levels of daily measurements obtained throughout testing. Threshold-to-noise offsets are calculated as the difference between the detection threshold and the noise power spectral density level at each test frequency

Frequency, kHz	In-water					In-air				
	Threshold, dB re 1 μPa	SD	False alarm rate	Ambient noise, dB re (1 μPa)^2/Hz	Threshold-to-noise offset, dB	Threshold, dB re 20 μPa	SD	False alarm rate	Ambient noise, dB re (20 μPa)^2/Hz	Threshold-to-noise offset, dB
0.1	100	2.4	0.19	70	30	–	–	–	–	–
0.2	90	2.6	0.18	61	29	57	1.2	0.25	30	28
0.4	87	2.1	0.05	55	33	–	–	–	–	–
0.8	79	2.3	0.27	46	33	–	–	–	–	–
1.6	79	1.4	0.19	40	39	–	–	–	–	–
3.2	78	2.3	0.09	34	45	42	1.7	0.06	6	36
6.4	80	1.4	0.05	29	51	58	2.2	0.23	−3	61
12.8	77	1.6	0.23	29	48	50	1.6	0.18	−15	65
18.0	73	2.2	0.08	26	46	–	–	–	–	–
18.1	–	–	–	–	–	51	2.0	0.08	−24	75
25.6	75	1.4	0.25	24	50	–	–	–	–	–
33.2	–	–	–	–	–	72	1.7	0.23	<0	>72
36.2	94	1.8	0.03	22	72	–	–	–	–	–
43.1	130	1.4	0.22	22	107	–	–	–	–	–
51.2	136	1.6	0.21	23	113	–	–	–	–	–
60.9	141	0.9	0.06	23	118	–	–	–	–	–

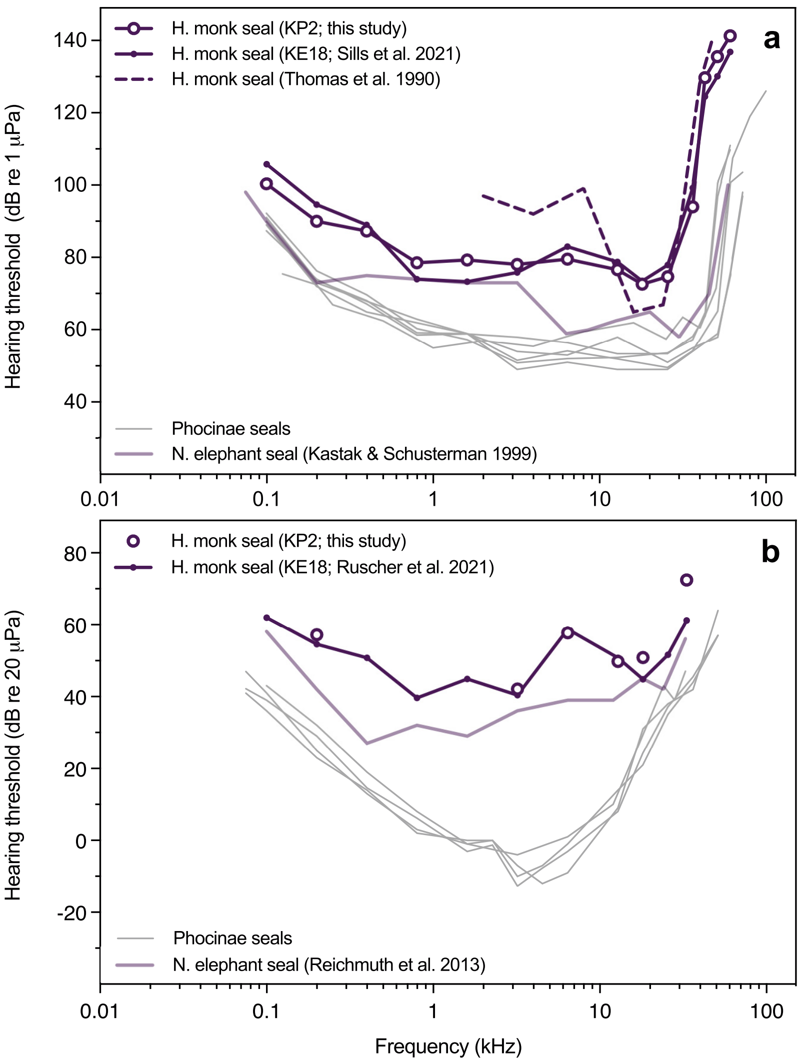

Fig. 1. Amphibious detection thresholds for 1 Hawaiian monk seal (KP2) obtained using psychophysical methods. For comparison, representative hearing data from each subfamily of true seals are provided. (a) Underwater audiogram for KP2. For the Monachinae subfamily, audiograms are included for other Hawaiian monk seals (n = 2, Thomas et al. 1990, Sills et al. 2021) and a northern elephant seal *Mirounga angustirostris* (n = 1, Kastak & Schusterman 1999). Data for the Phocinae subfamily include bearded *Erignathus barbatus* (n = 2, Sills et al. 2020), harbor *Phoca vitulina* (n = 2, Kastelein et al. 2009), ringed *Pusa hispida* (n = 1, Sills et al. 2015), and spotted seals *Phoca largha* (n = 2, Sills et al. 2014). (b) In-air hearing thresholds for KP2 at 6 frequencies tested in outdoor ambient conditions. Additional Monachinae hearing data are represented by another Hawaiian monk seal (n = 1, Ruscher et al. 2021) and a northern elephant seal (n = 1, Reichmuth et al. 2013). For Phocinae seals, audiograms are shown for harbor (n = 1, Reichmuth et al. 2013), ringed (n = 1, Sills et al. 2015), and spotted seals (n = 2, Sills et al. 2014). Associated hearing data and ambient noise values for this study are provided in Table 1

Repeated testing at 12.8 kHz in water and 18.1 kHz in air revealed differences of <3 dB, confirming the absence of a practice effect and demonstrating that KP2's performance on the task was reliable. Average response bias was similar in both testing environments, with a combined mean false alarm rate of 0.16 (range: 0.03–0.27); KP2 did not have an overly conservative response bias that could explain elevated thresholds. Additionally, threshold-to-noise offsets exceeded 28 dB in all cases, indicating that the auditory data were likely not masked by ambient noise and accurately reflect KP2's auditory capabilities in both media.

4. DISCUSSION

The underwater audiogram and in-air thresholds collected for Hawaiian monk seal KP2 closely follow the hearing curves collected previously with monk seal KE18 (Ruscher et al. 2021, Sills et al. 2021). These individuals were tested >2 yr apart, with some methodological differences across studies. These included minor changes in signal production and calibration equipment and methods of psychophysical threshold determination in both media. Most notably, the testing environment and associated noise conditions were different between the acoustic chamber used for monk seal KE18 and the outdoor testing conditions used for monk seal KP2 in air. Nevertheless, the detection thresholds measured for KP2 and KE18 fell within 6 dB of one another in nearly every case (19 out of 20 comparisons). This between-subject variation is similar to that of other seal species when tested in identical experimental configurations (e.g. Kastelein et al. 2009, Sills et al. 2014). Thus, we can now fully validate amphibious hearing profiles for Hawaiian monk seals, resolving the discrepancies in underwater hearing between Thomas et al. (1990) and Sills et al. (2021) and confirming the surprisingly poor terrestrial sensitivity described by Ruscher et al. (2021). The complete aquatic and terrestrial audiograms reported previously for monk seal KE18 are, in fact, representative of *Neomonachus schauinslandi*. We conclude that Hawaiian monk seals have auditory abilities and adaptations that are consistent with their evolutionary isolation within the Monachinae lineage of true seals.

The excellent agreement on the high-frequency portion of the 3 available underwater audiograms verifies that Hawaiian monk seals have a reduced high-frequency hearing ability, with a functional upper-frequency hearing limit near 40 kHz. Their hearing range is constrained even when compared to the more closely related northern elephant seal, which has an upper-frequency hearing limit extending to about 55 kHz (Kastak & Schusterman 1999) — similar to that of seals from the Phocinae lineage (Southall et al. 2019, Sills et al. 2020). This reduced sensitivity of monk seals at high frequencies may not be ecologically significant. However, it does suggest that the derived trait of expanded underwater high-frequency hearing occurred <15 million yr ago (Rule et al. 2021) and separately within each seal subfamily.

These validation data for Hawaiian monk seals show that auditory sensitivity in both media is most similar to that of the northern elephant seal from the Monachinae lineage. Auditory thresholds are higher than measured for 1 northern elephant seal and significantly elevated in comparison to 4 species of Phocinae seals (as illustrated in Fig. 1). Despite this, sound reception in water — particularly at the low frequencies — may be more important for monk seals than was previously concluded from the original Thomas et al. (1990) hearing curve. With respect to social communication, this validated audiogram combined with the recently described underwater vocal repertoire (Sills et al. 2021) collectively confirm that monk seals likely rely on acoustic communication underwater. Conversely, elevated in-air thresholds suggest that monk seal terrestrial communication is probably acoustically limited, likely occurring effectively over relatively short ranges and possibly including multimodal cues (i.e. acoustic, seismic, visual, or olfactory stimuli, as suggested by Miller & Job 1992). From an applied perspective, poor terrestrial hearing suggests that the use of acoustic deterrents — a common tool to mitigate marine mammal and human interactions — may not be very effective for this species.

This study, combined with Sills et al. (2021) and Ruscher et al. (2021), provides a core understanding of auditory biology in Hawaiian monk seals. The findings have implications for the conservation of Mediterranean monk seals *Monachus monachus* — a vulnerable species with no existing hearing data and a currently developing knowledge of vocal behavior (Muñoz et al. 2011, Charrier et al. 2017, 2023, Muñoz-Duque et al. 2024). While the results of the present study strongly indicate subfamily-level differences in hearing among true seals, additional Monachinae species need to be tested to confirm whether related species share similar auditory traits.

On the basis of the hearing data now available, we consider the functional grouping of all seals to be appropriate and conservative (for monk seals, northern elephant seals, and possibly the other 5 Monachinae seals) in terms of regulatory guidance on the effects of noise (see Southall et al. 2019). More applied bioacoustic research is needed to support the conservation of both extant monk seal species (e.g. passive acoustic monitoring, development of call detectors) and to resolve questions about the evolutionary biology of hearing among true seals, including Antarctic species.

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