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Research Paper

Exploring auditory thresholds for Reindeer, *Rangifer tarandus*

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ABSTRACT

Current and proposed human development throughout high northern latitudes must assess and try to mitigate impacts on caribou and reindeer (*Rangifer tarandus*) herds. Sound created by development can be far-reaching, and determining the potential impacts of noise on wildlife can inform landscape use. To advance our understanding of *Rangifer*'s potential response to anthropogenic noise, we must first understand what they can hear. Using domestic reindeer from the Large Animal Research Station at the University of Alaska Fairbanks, we performed a Brainstem Auditory Evoked Response to estimate auditory thresholds of the species. We assessed the central auditory response and tested the sensitivity in 6 female reindeer of various ages. Prior to our work, the lowest audible frequency for the species was reported to be 63 Hz in previous studies. We identified an auditory threshold lower limit of 30 Hz in our study subjects and quantified reindeer sensitivity thresholds (dB peSPL) to frequencies ranging from 30 to 16,000 Hz. Our results indicate that anthropogenic sounds previously thought to be beyond the hearing range of *Rangifer*—such as seismic exploration—are likely to be audible to the species, and therefore have the potential to affect their soundscape. We compared our findings on *Rangifer* hearing with new measurements of anthropogenic sounds recorded on passive acoustic monitors distributed throughout northern Alaska, as well as biological sounds produced by the *Rangifer* themselves (e.g., vocalizations and sesamoid clicks produced by the ankles). All classes of anthropogenic sound fall within the threshold range that we identified for *Rangifer*. Our findings have important implications for the assessment of environmental impacts within *Rangifer* range and will inform future soundscape ecology research.

Introduction

The effects of human development on caribou and reindeer (*Rangifer tarandus; hereafter Rangifer*) populations is an unresolved concern throughout the Arctic. Several studies have investigated how *Rangifer* distribution and movement are impacted by industrial infrastructure (e.g., roads, pipelines, oil pads) or aircraft overflights (Calef et al., 1976; Smith et al., 1994; Johnson and Russell, 2014; Johnson et al., 2019). Arthur and Vecchio (2009) have described lower calf weights from calves born closer to infrastructure in the Central Arctic Herd (CAH) of Alaska, and Luick et al.'s (1996) noted that an increase in noise exposure could reduce the probability of pregnancy for *Rangifer* females. Wilson et al. (2016) found that the strength of a *Rangifer*'s response to roads differed between individuals and, most recently, Johnson et al. (2019) found that there is little evidence of habituation to human infrastructure in the CAH. Altogether, this supports the idea that human development has a real, albeit sometimes variable, impact on *Rangifer*.

Few studies have evaluated *Rangifer*'s auditory range, with the exception of Flydal et al. (2001) and Flydal and Kilda (2003), who presented an important advancement in understanding the auditory capabilities of the species. Inconsistencies between their work and the ethology of the species remain unexplained, specifically: the average frequency of a vocalizing bull was reported to be 55 Hz (Frey et al., 2007), but Flydal et al. (2001) reported that the lower limit of *Rangifer* hearing was 63 Hz. If the lower limit they found for *Rangifer* hearing is true, then *Rangifer* may have a limited capacity to hear their own vocalizations used during reproduction.

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From an evolutionary perspective, this is unlikely and warrants further evaluation (Charlton et al., 2019).

To corroborate or expand on Flydal et al.'s (2001) work, we used a Brainstem Auditory-evoked Response (BAER) threshold. The BAER test is not a true measure of hearing, like pure tone audiometry, but rather a test of hearing threshold, i.e., the lowest sound level at which the ear (specifically the auditory cortex) is still able to detect a sound. BAER threshold estimates are determined by the repeatable waves of an electroencephalogram (EEG), and give close approximation of the auditory acuity of an animal at a given time (Erwin and Husain, 2003), and don't require animal training so it is easier to test a greater number and variety of individuals (Wolski et al., 2003). However, this test can underestimate the lower frequency sensitivities when compared with behavioral studies (Gorga et al., 1988), and cross-referencing behavioral and electrophysiological results, as we are doing here, may help overcome this challenge. For this reason, the sound stimuli we used were similar to Flydal et al. (2001), with the expectation that our BAER threshold estimations would show some consistencies with the results of the behavioral experiments.

Rangifer's auditory acuity is of conservation concern because anthrophony (sound made by humans) will increase with expanding infrastructure across the Arctic, and has the potential to alter movement, elevate stress, reduce reproductive rates and disrupt an organism's communication (Barber et al., 2010; Halfwerk et al., 2011; Iglesias-Merchan et al., 2018). Indigenous communities have already expressed concern about how sound disturbance is affecting their hunting practices (Stinchcomb et al., 2020). Our objective is to develop a better understanding of what sounds *Rangifer* are sensitive to by comparing the results of our BAER test to the behavioral results of Flydal et al. (2001). An updated understanding of *Rangifer*'s auditory sensitivities will help inform efforts that mitigate such disturbances, and ensure a predictable and sustainable harvest for the human communities that are nutritionally and culturally reliant on the species (Parlee et al., 2018).

Materials and methods

Audiology study space and conditions

We conducted our research during December, 2019 at the Large Animal Research Station (LARS) at the University of Alaska, Fairbanks (UAF). A sound booth was constructed within a barn onsite made of 1.9 cm sound board and rubber flooring to minimize the noise floor (i.e. the ambient sound level) during testing. Booth dimensions were 2.3 m wide x 5.0 m long x 2.2 m tall. Domesticated reindeer research subjects were brought into the booth where they were held into position by a halter for testing. The reindeer were habituated to the space over several weeks prior to testing; they were brought into the booth 3 times a week for 5 weeks, and were held for gradually increasingly periods of time (up to 45 min). During habituation and during the experiment they were kept in pairs to minimize stress.

Six female reindeer were tested for hearing threshold estimation using a standardized BAER threshold estimation test technique (D'angelo et al., 2007). Male subjects were unavailable for testing. Animals ranged in age from yearling to 8 years. All animals were kept and cared for by UAF LARS staff. This research was conducted under Animal Care and Use (IACUC) protocol number 1508780-1.

Audiological methods

BAER tests were run using an Intelligent Hearing Systems (IHS) hardware system and Smart EP software (Intelligent Hearing Systems, Miami Florida). Prior to testing, system output levels and frequencies were measured using a Bruel & Kjaer 2270 sound level meter (Naerum, Denmark) and by running a power spectrum analysis using Spectra Plus software (Pioneer Hill software LLC, Paulsbo, Washington). This was performed to ensure that the system was taking accurate measurements before the experiment began. No veterinary history on our subject's acoustic acuity was available, but gross ear inspection and response to stimuli were indicative of no occlusion to the ears tested, and repeatable waveform morphology was present (Figure 1) indicating that there was a response to stimulus.

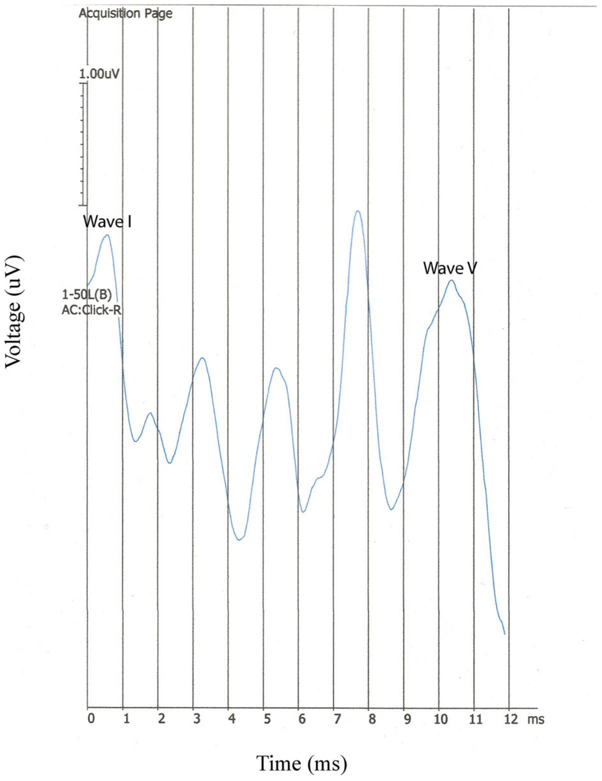

Figure 1. An example of the waveform produced during a BAER (Brainstem Auditory Evoked Response) test given to a reindeer subject; the 5 visible peaks in this waveform represent the reindeer auditory system's clear response to a 30 Hz stimulus.

Prior to conducting each BAER test, the ambient sound level was taken using a Bruel & Kjaer model 2270 sound level meter taking the equivalent continuous sound level (LAeq) for five (5) minutes (Table 1). No sedative was administered to reindeer prior to testing. A lidocaine analgesic topical cream was rubbed onto the sites of the reindeer's head where Rhythmlink^{TM} bent-needle subdermal electrodes would be placed for the BAER test. Three electrodes were inserted to the head of the reindeer (Figure 2), with the test ear (negative electrode) at the dorsal border of the zygomatic arch, vertex (positive electrode) and opposite ear (ground electrode) at the dorsal border of the zygomatic arch. This corresponds to the similar electrode montage used for testing other mammals and humans as per the International 10-20 System (Homan, 1988).

Auditory stimuli were selected as gated tone bursts with 5msec rise/fall with 5 msec duration for the low frequencies. The use of tone bursts allowed us to differentiate the brain's response to the signal from its response to other sounds in the environment. Stimuli were gated using a Blackman filter and were delivered at a rate of 29.1 per second to an insert that is both an ER-2 and Etymotic ear inserts. Etymotic ear inserts perform down to 20Hz (Personal

Table 1
The hearing thresholds determined from BAER (Brainstem Auditory Evoked Response) tests conducted on 6 female reindeer at the Large Animal Research Station at the University of Alaska Fairbanks; these thresholds are presented in dB peSPL, a decibel scale based on sound pressure levels alone, and dB NHL, a decibel scale based on the normalized hearing levels of humans. Values were originally recorded in dB NHL and then converted to dB peSPL. The reported values used to produce the audiogram are the lowest thresholds found for the individuals tested at a given frequency, in order to represent the full auditory capabilities of the species. The mean thresholds are shown in cases where N $\geq$ 2, but generally these reflect the variation within our research subjects as opposed to the true auditory range of the species.

Frequency (Hz)	Lowest Threshold (dB peSPL)	Threshold Range (dB peSPL)	Mean (dB peSPL)	N	Lowest Threshold (dB NHL)
30	30	30-60	43.3	3	10
60	40	40-60	NA	2	30
125	50	50-60	55.0	4	30
500	40	40-70	55.0	4	20
1000	35	35-45	41.6	3	20
3000	20	20-30	25.0	3	-10
3800	38	38-78	NA	2	20
4000	30	30-60	NA	2	10
8000	30	30-50	38.3	3	10
16,000	25	25-50	43.0	5	5

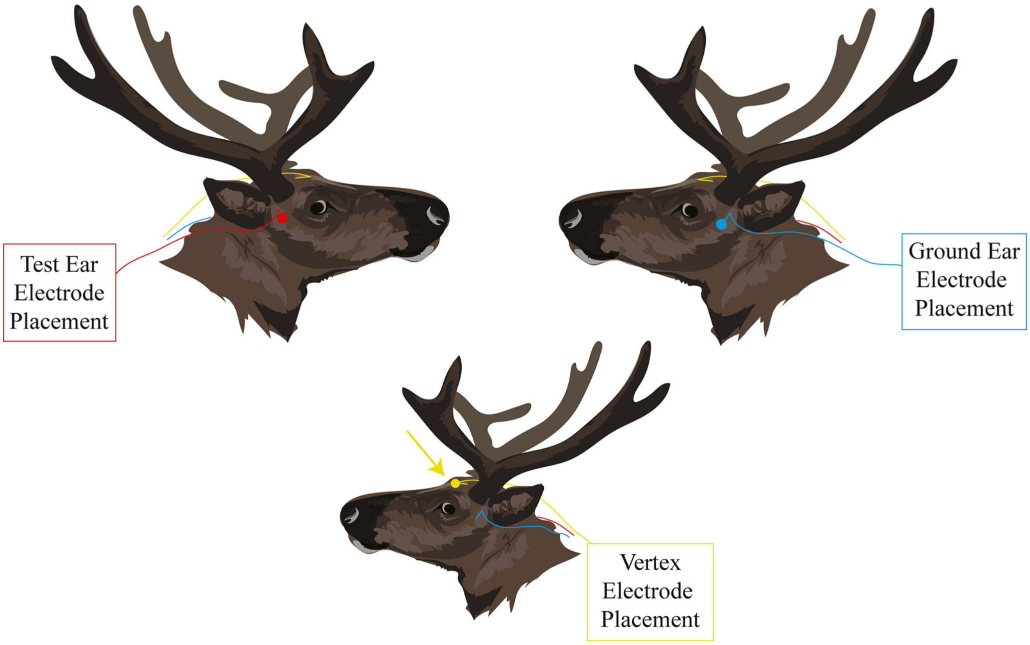

Figure 2. The approximate placement of the 3 bent-needles, Rhythmlink$^{\text{TM}}$ (Columbia, SC) subdermal electrodes used to capture the EEG (electroencephalogram) for reindeer. The test ear's electrode (negative electrode) is at the dorsal border of the zygomatic arch on the right side, the ground ear's electrode is at the dorsal border of the zygomatic arch on the left side, and the vertex electrode sites in the middle of the forehead, just above the eyes. Figure 3. Rangifer audiogram established through BAER (Brainstem Auditory Evoked Response) testing, with stimulus frequency (in Hz) on the x-axis and sensitivity threshold on the Y (in dB peSPL); thresholds are the lowest level that a sound was played and still able elicit an electrophysiological response from the subject.

communication, Intelligent Hearing Systems). A non-linear gating function like the Blackman filter provides a more precise stimulus frequency because the repetition rate prevents "spectral splatter," where the tail ends of the stimulus bleed into other frequencies (Canale et al., 2012).

Narrow spectrum signals tend to approximately resemble audiograms by conventional long-duration tones used in behavioral audiometry, although low frequency bursts are less likely to elicit an identifiable wave V (Goldstein and Aldrich, 1999). Even at the default sampling rate (1/2-second-long stimulus duration limit), the equipment is capable of getting a tone burst that was 10 cycles long, and provide low frequency stimuli (Appendix 1).

The ER-2 inserts were held at the opening of the ear canal by researchers while the auditory stimuli were being delivered. The right ear of each individual was used for testing due to the orientation of the halter's anchor in relation to the equipment and the other reindeer present within the enclosure. The ground ear was tested with a click stimulus to rule out bilateral deafness. Filter settings were 10Hz for the low pass filter and 1500 Hz for the high pass filter. The EEG was amplified 100,000 times, and the BAER results were measured from 550 averaged responses (sweeps) of the rarefaction phase. The analysis time was 12 msec, and more than 2 BAERs were run at each frequency to ensure replication based on waveform morphology, waves I, and V latency and intensity.

BAER estimated thresholds were processed for multiple frequencies from 20 to 16000Hz, in accordance with many of the frequencies tested by Flydal et al. (2001), and we tested a minimum of 3 reindeer at individual frequencies. Our frequency testing range was limited by the audio equipment used to provide the stimulus, which could only provide stimuli between 20 Hz and 20,000 Hz, or

Table 2
The mean fundamental frequency of different classes of anthropogenic noises identified from acoustic recording units placed within the North Slope of Alaska from May-September, 2019; standard deviations were not included for values cited from the literature, which sometimes stated ranges instead of means (Other values acquired from the literature include: [1]Values from Frey at al. (2007), [2]Values from Titze (1994), [3]Value from Marriot (2006), [4]Values from Bagaini et al. (2014))

Noise Class	Mean or Range Fundamental Frequency (Hz)	SD
Rangifer sesamoid clicks	6378	881.1
Rangifer vocalizations	55[1]	NA
Automobile	1382	124.6
Helicopter	612	33.4
Propeller plane	483	40.1
Jet aircraft	309	71.4
Human voice	85-255[2]	NA
Pumps	~125-500[3]	NA
Diesel generator exhaust pipe	~130[3]	NA
Seismic activity	17-102.2[4]	NA
Flaring	~60[1]	NA

around the range of human hearing. While we tested at 20 Hz and saw a response, we do not consider these responses valid because our equipment does not give a flat response at that frequency (i.e. cannot determine if the animal's brain has failed to respond to the stimulus). Due to this, and the potential for acoustic artifacts at the lower limit of our equipment, responses below 30 Hz are less reliable. The engineers of our equipment do not anticipate those artifacts to be present at ≥25 Hz (personal communication, Intelligent Hearing Systems), but out of an abundance of caution we are only presenting results at 30 Hz and above. Stimulus intensities were run initially at 30 dB nHL (a decibel scale based on the limitations of human hearing) and were converted to sound pressure levels (peSPL) as per the IHS unit calibration/conversion table, and then verified using Spectra Plus software. The intensities were increased in 10 dB nHL steps to the point of replication, i.e. when there was a repeatable response and latency repeatability of waves I and V (Figure 1). Each wave is associated with a particular part of the hearing pathway, and a disruption in the pathway will result in the downstream absence of waves (Webb 2009). The presence of the first and last waves (waves I and V) demonstrate electrical activity along the full auditory pathway, and thus are good candidates to use when identifying a repeatable response. To establish our thresholds, we used the lowest dB nHL values that an individual reindeer responded to since we were interested in identifying the best possible acuity of the species.

Estimating industrial and biological sound frequencies

We collected anthropogenic sounds using passive acoustic monitors (Wildlife Acoustics SM4) placed at 4 different locations across the North Slope of Alaska, including within oilfield infrastructure. Our acoustic monitors were within the range of the CAH and collected acoustic data daily from early May to early September, 2019. Sound files were parsed using version 2.3.3 of Audacity (Audacity team, 2020), and industrial noise signals were identified based on their sound and on their shape in the spectrogram. We identified the lowest frequency (Hz) band—or the sound's pitch (fundamental frequency) within that signal using the frequency analysis tool. We averaged the values for several noise classes we identified in our recordings (Table 2). We were unable to measure the exact distance of each sound source from the recorder. Some of the sound sources were moving objects (e.g., vehicle, aircraft). However, we only used recordings where the spectrogram of the sound source was clear and all formants were easily identifiable. Our anthrophony samples came predominately from 3 locations where the average distance from roads was 264 m, and the average distance from industrial infrastructure (e.g., drill pads, flaring pipes) was 350 m. Therefore, for all sound sources, we were well within range to measure the frequency with precision.

We used existing literature to identify the average frequency of sounds that one might encounter on the North Slope of Alaska but were not present in our acoustic recording dataset. We searched the literature using several key words and phrases: "industrial noise," "oil and gas sound frequencies," and "oil exploration seismic noise." The sounds derived from this search were: "Pumps," "diesel generator exhaust pipe," "seismic activity," and "flaring." The only biological sound frequency from our recordings that we assessed was the sesamoid click produced by *Rangifer* when walking, but we were also able to obtain vocalization frequencies from a literature search (Frey et al., 2007) (key words and phrases: "*Rangifer tarandus*" "vocalizations" "acoustic behavior"), as well as unpublished data from Ericson (1972) that described the frequency range of *Rangifer* grunts as 15-1900 Hz (excluded from our results because it has not been peer reviewed). The sesamoid click is made when tendons snap over the sesamoid bones of their ankles and make a distinctive "click." We used camera trap images that were collected at our acoustic recorders sites to confirm the presence of *Rangifer* at specific times, and then found the corresponding sound recording from our recorders. Using the same method detailed above for the industrial frequencies, we identified the fundamental frequency of the click from several recordings (Table 2). In these cases, *Rangifer* were relatively close to the recorder (<50 m), but an exact distance could not be determined from the photos.

Results

We determined that all (n = 6) of our *Rangifer* research subjects were capable of hearing frequencies at least as low as 30 Hz (Table 1). The threshold at this lower limit was 30 dB peSPL, i.e. the 30 Hz sound had to be at least 30 dB peSPL to be detected by the auditory system of our study subjects. The threshold of our 30 Hz lower limit was 30 dB peSPL lower than Flydal et al.'s (2001) (30 vs. 60 dB peSPL).

The frequency range of best sensitivity was broad, with sensitivity shown in the upper frequencies (3000 and 16,000 Hz) and the lower (30 Hz). Hearing acuity was greatest at 3000 Hz (20 dB peSPL), and the next most sensitive frequency was 16,000 Hz (25 dB peSPL). Our subjects were least sensitive around 60-500 Hz.

Threshold ranges were variable within our cohort (Table 1). We used the lowest threshold values in the audiogram to demonstrate the maximum auditory acuity (Figure 3). The greatest range of values occurred towards the lower limit of *Rangifer* thresholds, where certain individuals demonstrated much more acuity than others (Table 1).

The frequencies of common anthropogenic sounds were all within *Rangifer*'s hearing range (Table 2). This includes the frequencies of seismic activity, which occur below the previously established lower limit for the species. The frequencies (i.e., 125-500 Hz) that our research subjects were less sensitive to were expressed by some classes of aircraft (jet aircrafts and propeller planes), as well as mechanical pumps, diesel generators and the human voice (Table 2). The frequency of the sesamoid clicks (6378 Hz) was between the most sensitive frequencies we recorded in the upper range of their hearing (3000 Hz and 16,000 Hz). Industrial frequencies ranged from 20 to 1382 Hz (Table 2).

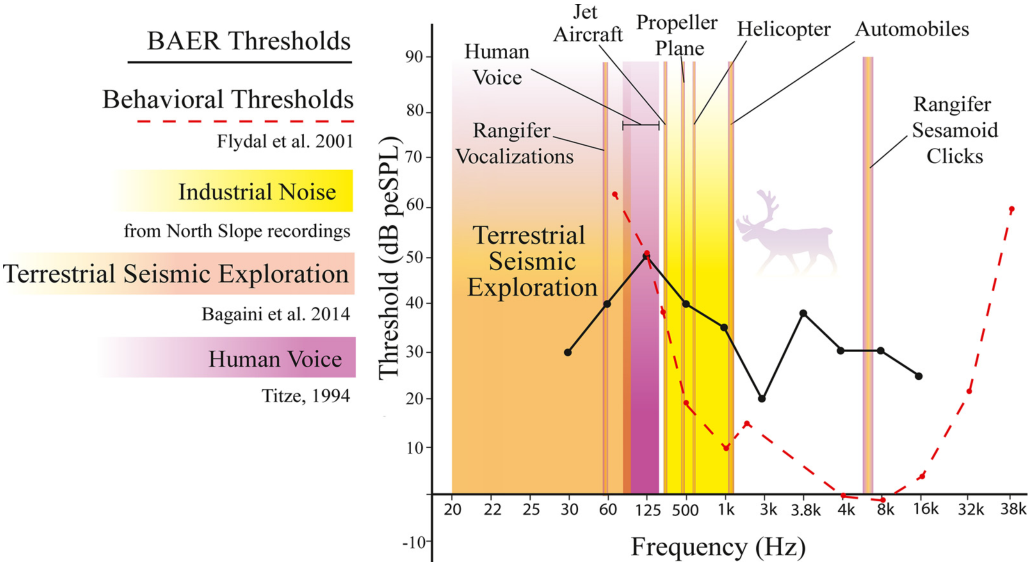

Figure 3. Rangifer audiogram established through BAER (Brainstem Auditory Evoked Response) testing, with stimulus frequency (in Hz) on the x-axis and sensitivity threshold on the Y (in dB peSPL); thresholds are the lowest level that a sound was played and still able elicit an electrophysiological response from the subject.

Discussion

Our results indicated that *Rangifer* can potentially hear frequencies at least 33 Hz lower than the lower limit previously documented by Flydal et al. (2001). Specifically, they show an expansion of the lower end of the known hearing range of *Rangifer*. From this, we can now more accurately infer the potential for a response to specific sounds. This study provides an important update to the *Rangifer* Umwelt—i.e. the world that the species perceives based on the limits of their own physiology (Van Dyck, 2011). A better understanding of *Rangifer*'s auditory Umwelt will help us improve evaluations of anthrophony's impact within their geographic range by identifying sounds that the species can detect.

In some regions of the North Slope of Alaska, rural residents have expressed concern over how sound disturbance affects their ability to harvest the species (Stinchcomb et al., 2020). Depending on the sound source, sounds can travel tens of kilometers from their origin (Bureau of Land Management, 2019). *Rangifer* are known to respond to distinctly acoustic disturbances, such as aircraft overflights (Maier et al., 1998), and more stationary acoustic disturbances created by wind turbines (Skarin et al., 2018). At their calving grounds in and around oil fields, they give infrastructure a 5 km berth (Johnson et al., 2019), an avoidance that may be in direct response to the radius of sounds caused by drill rigs (2-10 km), flares (19 km), traffic (~2 km), and aircraft overflights (17+ km), where maximum extent of the radius represents where the sound falls to ambient levels (35 dBA)(Bureau of Land Management, 2019). The acoustic frequencies of all these sounds are well within the hearing range of *Rangifer* (Figure 3). Automobiles are the only sound class that came close to our research subject's most sensitive frequency (3000 Hz), and there was no notable overlap between any industrial sound frequencies and the frequency of the sesamoid clicks. Similarly, there is no notable overlap between the industrial sounds and previously reported *Rangifer* vocalizations (Frey et al., 2007) (Figure 3). Future contributions should focus on what sounds—within the range, we have identified here—elicit a strong behavioral response in *Rangifer*.

Although the BAER and behavioral methods are both effective means of establishing a hearing range, there are significant differences between the methods in threshold sensitivity that have been demonstrated for humans, primates, and marine mammals (Gorga et al., 1988; Szymanski et al., 1999; Ramsier and Dominy, 2010). We did not anticipate that our lower frequency estimate would be markedly lower than a behavioral test because BAER methods tend to yield less sensitive thresholds at lower frequencies than behavioral methods (Gorga et al., 1988). However, the waveform morphology and wave I and V latencies were repeatable at our lower frequencies, indicating that those frequencies were reliably detected by our test subjects. In light of this, the low-frequency difference between our results and Flydal et al.'s (2001) may actually be greater. Future research using either method with proper low-frequency stimuli should be able to determine if *Rangifer* can hear sounds in the infrasonic range, i.e. below the lowest frequency humans can hear. Behavioral testing will be more accurate at determining this limit, but BAER testing allows one to test more individuals at once, and future researchers may have to consider these compromises alongside their own temporal and financial constraints.

The lower limit we established does not preclude *Rangifer*'s ability to hear their own vocalizations and suggests the species has a high acuity to those frequencies, which better aligns with evolutionary expectations (Charlton et al., 2019). The relationship between the sounds a species can make and the sounds they can hear often follow the Sensory Drive hypothesis (Endler 1992), which states that vocalizations and hearing co-evolve, and animals vocalize within the frequencies that they can best hear (Charlton et al., 2019). *Rangifer* vocalizations vary by sex and have a male and female fundamental frequency of 55 and 75 Hz, respectively (Frey et al., 2007). It is possible such results were limited by the equipment and analysis filters used by Frey et al. (2007); Frey et al.'s (2007) recorders also were not capable of registering sounds below 20 Hz, and they did not analyze acoustic information below 30 Hz when they evaluated the spectrogram of their recordings because to the bandpass filter they employed. Unpublished results from Ericson (1972) described the frequency range of *Rangifer* grunts as 15-1900 Hz.

For a wide-ranging animal like *Rangifer* with extensive migrations, the ability to hear low frequency sounds would have great utility. Low frequency sounds can be used for long distance communication (Garstang, 2004) because they attenuate less quickly than high frequency sounds (Halfwerk et al., 2011). Natural infrasound, such as that created by storm events, is generally between 1 and 10 Hz, and extends outside the hearing range for *Rangifer* that we have established thus far. *Rangifer* were not as sensitive to the frequencies of their vocalizations as we would expect, and were more sensitive to lower frequencies (30 Hz). This discrepancy could be due to individual variation within our cohort, or the equipment limitations described above. Individual differences in auditory response can result from age (our cohort ranged from 1 to 8 years old), and future studies could increase their sample size in each age class and include male subjects to quantify meaningful differences. Further research into *Rangifer* vocalizations should also utilize equipment with low-frequency capabilities to investigate whether there is a clearer relationship between auditory sensitivity and vocal frequency.

Alternatively, it is possible that *Rangifer* are tuned in to the sounds of their walking more than their vocalizations. Their characteristic sesamoid clicks have an average frequency of 6378 Hz. Because *Rangifer*'s tendon and ankle structure may vary across different individuals based on their size, it's likely that the frequency of their clicks varies more than we have established here. However, the takeaway should not be the exact frequency value, but rather that the frequency value is high, and falls in and around the regions of best sensitivity that we and Flydal et al. (2001) have identified for *Rangifer*. Generally, clicks tend to stimulate the high frequency region of the cochlea the most (Gorga et al., 2008), and the broad range of high-frequency sensitivity that both we and Flydal et al. (2001) have reported could reflect this if the purpose of such sensitivity is to locate conspecifics. Clutton-Brock (1999) has posited that these clicks are a means of keeping the herd together, but no research has been done on the topic. If such behavior helped to facilitate herd formation during migration and calving, then intense and sustained high-frequency disturbance could impact their movement and distribution.

To get an idea of the kinds of sounds *Rangifer* would encounter in the wild, we present new data on the frequencies of common industrial activities in the Arctic. By comparing the 2 datasets, we provide new insight into what sounds *Rangifer* are likely to hear due to development and how they overlap with hearing thresholds and sensitivities (Figure 3). The original audiogram established for *Rangifer* (Flydal et al., 2001) reported that reindeer could only hear as low as 63 Hz, at a threshold between 61- and 79-dB SPL. This dB level indicates that for a reindeer to hear that low frequency, it would have to be as loud as a normal human conversation if someone is about a meter away. Our acuity threshold at 60 Hz was lower (40 dB peSPL), and we found that the *Rangifer* frequency threshold of hearing may be as low as 30 Hz. The hearing threshold at that frequency was 30 dB peSPL, which is quieter than someone whispering at a 1.5 m distance. It is likely that this does not represent the absolute lower limit of *Rangifer* hearing. Our research subjects were responding to the 20 Hz stimulus produced by our equipment, but we considered this unreliable due to the probable presence of sound artifacts at this low frequency. Five out of 6 of our research subjects exhibited clear responses below 30 Hz, but these would have to be confirmed in future studies with a more reliable stimulus from equipment with lower frequency capabilities.

However, much of the concern around anthrophony-related disturbance lies with lower frequency sounds. Prior to this work, it was unclear if the *Rangifer* auditory system was capable of detecting low frequency sounds produced by seismic exploration or vocalizations of the species. Vibroseis trucks (i.e., the source of seismic sound) used in standard oil exploration methods produce much of this infrasound by using seismic waves from a vibrating plate to generate a 3D image of underground regions. Blix and Lentfer (1992) indicate the vibrating plate produces sounds around 20-30 Hz during short, 5-second bursts. Further research shows that airborne sounds generated by the trucks ranged from 17 to 102 Hz at a 20 m distance (Bagaini et al., 2014). Both frequency ranges overlap substantially with the lower half of our *Rangifer* audiogram (Figure 3). Certain individuals may be more sensitive to these low-frequency disturbances than others, based on the variation we observed within our cohort. Individual differences have been previously shown in *Rangifer*'s response to roads (Wilson et al., 2016), and sex differences have been documented intolerance of other infrastructure, with females being more sensitive than males (Helle et al., 2012). Maternal groups, in fact, demonstrate little tolerance for infrastructure around calving time (Smith et al., 1994). *Rangifer* migration models demonstrate that collective migration is often led by a small proportion of leaders (Guttal andand Couzin, 2011), an idea consistent with traditional ecological knowledge, which states that herd leaders should not be hunted as it would disrupt migration (Padilla and Kofinas, 2014). Individual differences could drive population-wide shifts in movement patterns at times when aurally sensitive individuals are in leadership positions and making decisions on behalf of the herd.

The thresholds we found at certain frequencies (such as 60, 125, and 500 Hz) that were higher than Flydal et al.'s (2001) results may be due to noise exposure prior to testing. The frequencies of commonly heard industrial equipment fall within this range, but it is unclear whether this “notch” in the curve is a true symptom of overexposure or just an artifact of the individuals tested at that frequency, since not all individuals were tested across every frequency step. Our reindeer subjects were housed near a road, and frequently exposed to the sounds of traffic and farm equipment. Temporary threshold shifts can occur due to sound exposure prior to testing (Ryan et al., 2016), which are difficult to mitigate or control for. It is possible that wild *Rangifer*—that spend a majority of their lives without industrial noise exposure—have more sensitive hearing to mechanized sounds than the thresholds presented by their captive and domestic counterparts.

It has been difficult for researchers to demonstrate that wild *Rangifer* are habituating to human disturbances, but shifts in their tolerance to human infrastructure—and the stimuli that comes with it—are evident (Johnson and Russell, 2014). Proving the presence of habituation requires that one demonstrates an individual has learned stimuli is nonthreatening, and no longer responds to it; this means repeatedly sampling the same individuals over time (Bejder et al., 2009). Individual habituation to anthrophony could be studied using an “acoustic collar” (i.e., a GPS collar with an acoustic recorder attached) (similar to Lynch et al., 2013) that would be able to jointly monitor sound exposure and behavioral movement responses over time, sampling the same individual repeatedly. This tool would also allow us to identify how tolerance to anthrophony varies between individuals, and within various habitat types.

With the completion of this study, we've been able to answer—in large part—what sounds and sound frequencies *Rangifer* could potentially hear and be disturbed by. This is the first step in a larger effort to evaluate *Rangifer*'s behavioral response to sound. This is done not only at the recommendation of Francis and Barber (2013), but also in the spirit of the Umwelt-concept, an ethological approach which recognizes that each organism may perceive the world differently than another (Van Dyck, 2011). Researchers and decision makers are better able to predict an organism's response to various stimuli by understanding the physiological constraints with which they perceive such stimuli. Our hope is that this knowledge will provide more opportunities to understand and manage the impacts of sound disturbance in Rangifer's environment, especially as anthrophony becomes more pervasive across the Circumpolar North.

Authorship statement

The idea for the paper was conceived by Megan Perra and Todd Brinkman. The experiments were designed by Sarah Barcalow, Megan Perra, Peter Scheifele, and Todd Brinkman. The experiments were performed by Peter Scheifele, Todd Brinkman, Megan Perra and Sarah Barcalow. The data were analyzed by Peter Scheifele, Megan Perra and Todd Brinkman. The paper was written by Megan Perra, Todd Brinkman, and Peter Scheifele. Appendix 2

Conflict of interest

All authors have no competing interests to declare.

Ethical statement

This research was conducted under Animal Care and Use (IACUC) protocol number 1508780-1.

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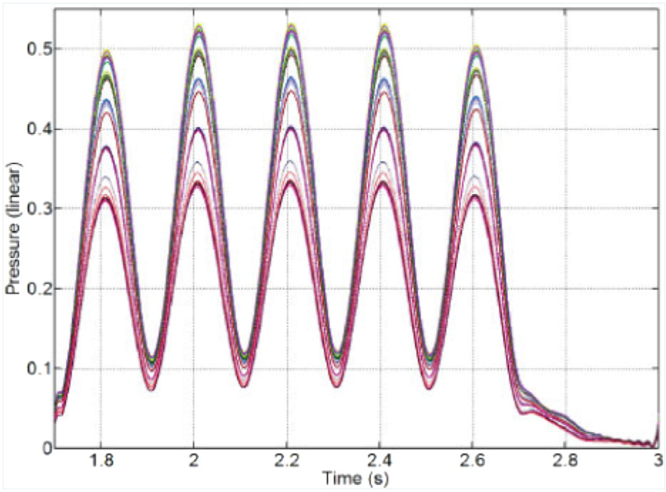
Appendix A



Appendix 1. A spectral view of a 30 Hz pulse, showing corrected measured waveforms for 30 Hz gaited tone burst testing. (Reproduced with permission from Adam J. Hill, University of Derby, Department of Electrical and Electronic Engineering).

Appendix 2

Noise floor measurements taken in 5-minute LAeq (Equivalent Continuous Sound Pressure Level) in dBA for each frequency used during the BAER testing.

Frequency (Hz)	Noise Floor (dBA)
20	38
22	38
25	38
28	40
30	42
60	46
63	38
125	37
500	35
1000	35
2000	32
3000	32
4000	32
8000	32
16,000	32
20,000	32

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