A Review of Northern Elephant Seal Adaptations to a Marine Environment

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In order to transition from a solely terrestrial life to an aquatic one characterized by a diverse marine environment, elephant seals have had to undergo a myriad of remarkable adaptations. The challenges imposed by this double life have resulted in some subtle yet extraordinary modifications to the standard sensory model that have allowed the northern elephant seal to survive in one of the most demanding environments on the planet. This article attempts to provide a review of what is known about two of the lesser well understood of these sensory adaptations, the senses of hearing and smell.

Audition

Investigation into northern elephant seal audition is still in its early stages; to date only Burnyce, an adult female, has been tested in a controlled setting[1]. Until further experimentation on additional subjects has been performed, it will not be known whether this data is truly representative of the species as a whole or the result of an anomalous individual. In anticipation of this however, these results will be treated as characteristic of the species.

In comparison to terrestrial carnivores and other pinnipeds, northern elephant seals show less sensitive in-air hearing, and as with many of their adaptations, it appears to be pressure related. Minimization of air spaces within the outer, middle, and inner ear prevents tissue damage resulting from extreme pressure, but reduces aerial sound conduction through the ear[2] (see Figure 1 for an illustration of basic mammalian auditory anatomy). Elephant seals have an especially narrow auditory canal that serves the dual purpose of decreasing the air space within the ear and preventing water penetration. This can be exaggerated further by the distensible cavernous tissue lining the external ear canal and middle ear that can fill with blood to further decrease the volume of air within the ear. In addition to this reduction in air space, the bony enclosure that houses the middle and inner ear is significantly inflated, and the bones of the middle ear (the ossicles) are considerably enlarged. This increase in size of the ossicles is thought to have a dampening action on high frequency hearing due to inertial constraints[1], meaning that the heavier ossicles are more difficult to move, and therefore decrease sensitivity to high frequency noise. In fact, audiograms for hearing thresholds at different frequencies for northern elephant seals share similarities with those of humans with conductive hearing loss[1].

It appears that this impairment of aerial hearing sensitivity may have been a

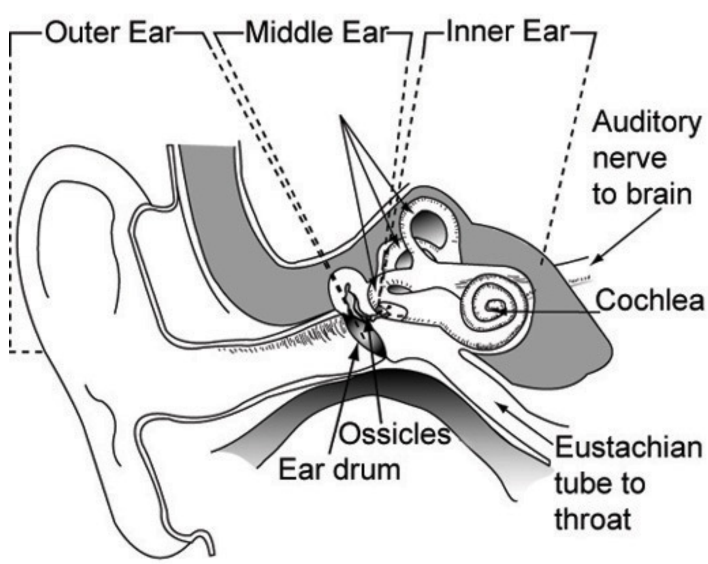


Fig. 1. Anatomy of the human ear.

trade-off in favor of improved underwater sound perception. Aquatic hearing is thought to occur through bone conduction in pinnipeds, meaning that sound is transmitted to the cochlea through surrounding soft tissue and bone rather than through the outer ear and ear ossicles (Fig. 2). This bone conduction manifests in two types, compressional and inertial. Compressional conduction results from a pressure differential across the cochlear membranes and stimulates the cochlea directly, whereas inertial conduction occurs when the temporal bone vibrates, causing the ossicles to move and stimulate the cochlea in a manner similar to aerial sound conduction. Enlargement of the ossicles could be an adaptation to enhance the signal during inertial conduction by creating a larger phase difference between different vibrating structures[3]. While bone conduction allows for greater sensitivity underwater, it does come with the challenge of impaired sound localization. In order to compensate for this, the pinniped ear complex is partially detached from the skull[1].

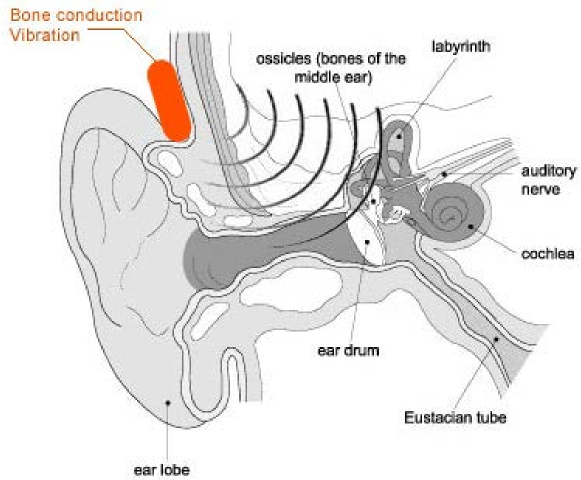


Fig. 2. Bone conduction in the human ear.

During controlled trials in 1999, Burnyce showed greatest hearing sensitivity between 3,200Hz and 15,000Hz in air, and between 3,200Hz and 45,000Hz in water[2] (see Figure 3 for an idea of what different frequencies mean in terms of human audition for a comparison). In later experiments in 2013[1], she displayed lower thresholds across the entire range of frequencies tested in air, which may have been a result of better control over ambient noise (Fig. 4 A. The black line labelled 1 corresponds to data obtained from Burnyce in the 2013 study, and the gray line labelled 2 above corresponds to her data from the 1999 study). Even with the lower thresholds reported in the more recent study, her sensitivity in air was still significantly reduced in comparison to humans and a sample of terrestrial carnivores across most of the frequencies tested (Fig. 4, Fig. 5).

Despite spending the majority of their time out at sea, elephant seals are still highly dependent upon effective vocal signaling in air during the breeding season in order to establish dominance hierarchies. It appears that elephant seals have preserved the ability to do so by developing extremely high volume, low pitched vocal signals to overcome the

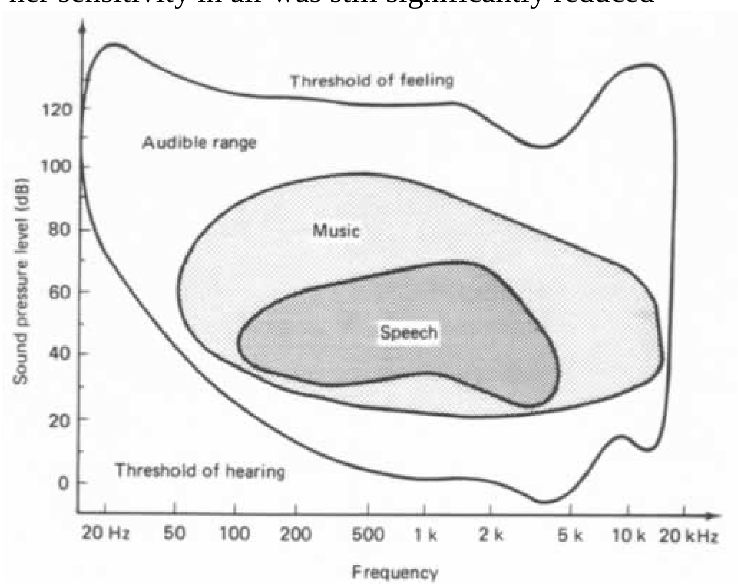
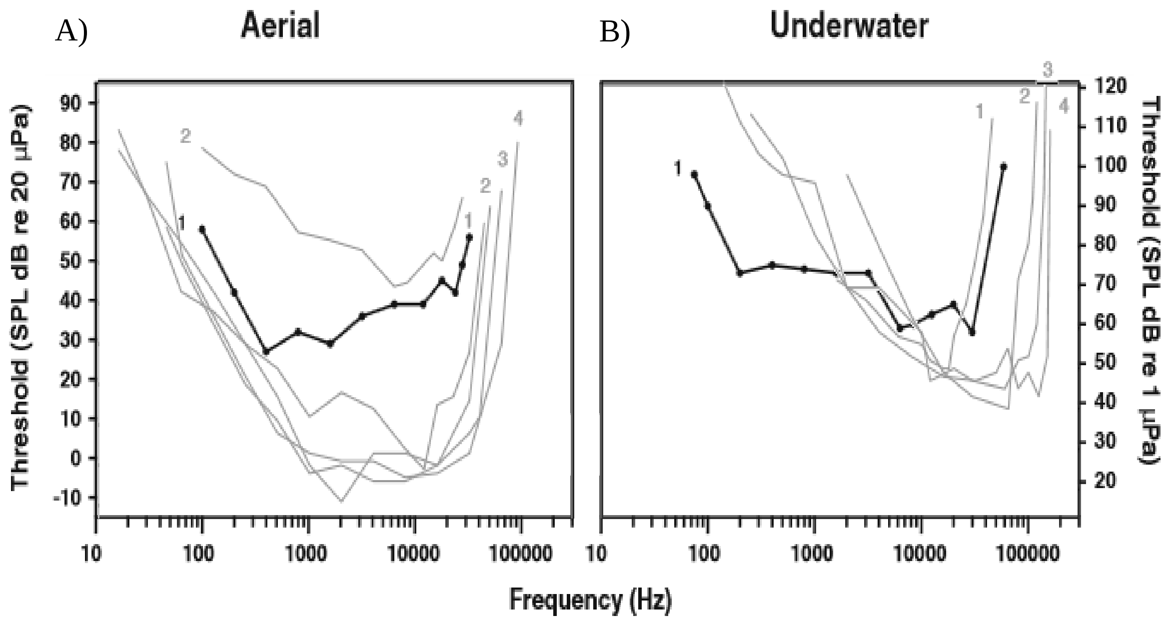


Fig. 3. Frequency ranges for notable features of human sound production and reception.



Terrestrial Carnivore Comparisons:

1. Domestic Ferret, *Mustela putorius*
2. Domestic Dog, *Canis familiaris*
3. Least Weasel, *Mustela nivalis*
4. Domestic Cat, *Felis catus*

Fully Aquatic Mammal Comparisons:

1. West Indian Manatee, *Tichechus manatus*
2. False killer whale, *Pseudorca crassidens*
3. Bottlenose dolphin, *Tursiops truncates*
4. Harbor porpoise, *Phocoena phocoena*

Fig. 4. A) Aerial threshold of hearing for a northern elephant seal at different frequencies compared to terrestrial carnivores. B) Underwater threshold of hearing for a northern elephant seal at different frequencies compared to fully aquatic mammals. Elephant seal audiograms are in black (with the exception of the audiogram above the black line labeled 2 in figure A, which shows the results of tests by Kastak and Schusterman in 1999). (Obtained from Reichmuth et. al., 2013 and modified to allow for closer comparison).

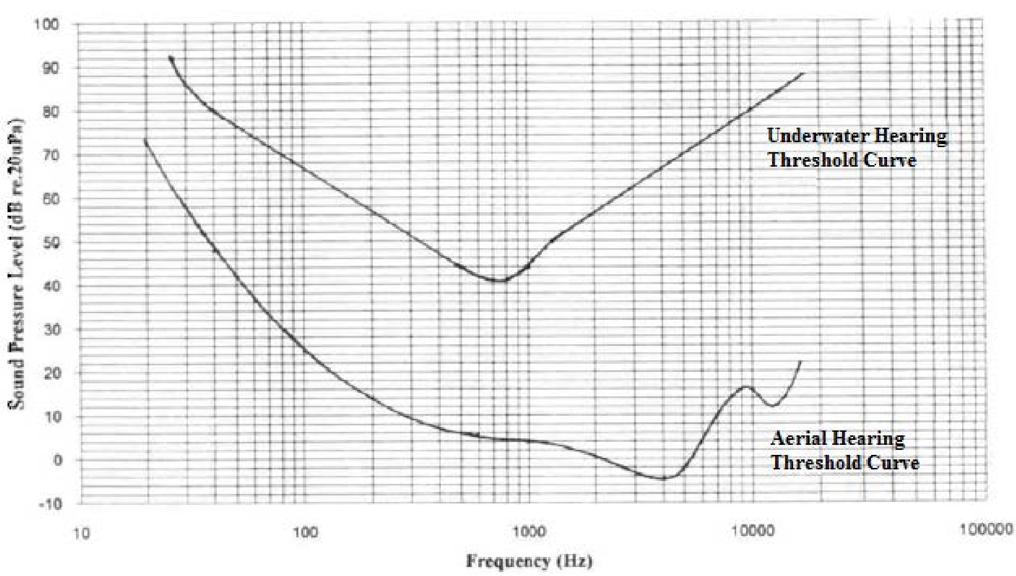


Fig. 5. Threshold of hearing for humans at different frequencies in air and water for comparison (Obtained from Parvin and Nedwell, 1995).

challenges presented by the pressure driven impediments to aerial hearing ability[2]. Such signals are easily detected and can travel great distances, thereby relaxing the selective pressure on aerial auditory sensitivity and freeing the ear up for more specialized aquatic adaptation.

In terms of underwater hearing, elephant seals display a much wider range of detected frequencies than they do with aerial sensation. It is hypothesized that aerial hearing is constrained due to the enlargement of the ossicles, resulting in a range of detectable frequencies that is narrower than the range which the cochlea is capable of encoding[1]. When the elephant seal is submerged however, hearing then occurs through bone conduction and this restriction is lifted, resulting in a broader range of detectable frequencies. It is notable that elephant seals displayed greater sensitivity to low frequency sounds in water than any of the four fully aquatic mammals tested.

1. Reichmuth, C., Holt, M., Mulsow, J., Sills, J., Southall, B. (2013). Comparative Assessment of Amphibious Hearing in Pinnipeds. *Journal of comparative physiology*, 199(2).
2. Kastak, D., and Schusterman, R.J. (1999). In-air and underwater hearing sensitivity of a northern elephant seal (*Mirounga angustirostris)*. *Canadian Journal of Zoology*, 77(11).
3. Brandt, J., and Hollien, H. (1969). Underwater Hearing Thresholds in Man as a Function of Water Depth. *Journal of the Acoustical Society of America*, 46(4P2).

Olfaction and Water Retention

Olfaction in northern elephant seals has been impacted by the specialization of the nasal cavity, driven both by a greater need to conserve heat and water, and a reduced reliance on olfaction during foraging in an aquatic environment[1]. Within the elephant seal's nasal cavity lies a dense network of bony projections called turbinates (Fig. 1). These turbinates are lined with a moist layer of tissue and can function either as respiratory turbinates, playing a role in heat and water conservation, or olfactory turbinates, which are associated with sense of smell. Respiratory turbinates are oriented to the front of the nasal cavity, while olfactory turbinates are located towards the back[1]. As the nasal cavity possesses a finite amount of surface area, this space must be portioned between respiratory and olfactory turbinates. In terrestrial species, the average ratio between olfactory and respiratory surface area is 2:1, but in elephant seals we see a dramatic reversal, with a ratio of 1:3[1]. This strikingly disproportionate preference for respiratory turbinates is thought to be a result of the strenuous water conservation and thermoregulatory challenges faced in a marine environment. Water conducts heat around twenty five times more efficiently than air, thereby necessitating adaptations for heat conservation in warm blooded animals.

Fig. 1. Elephant Seal Nasal Turbinates

In the ocean, access to fresh water is limited almost exclusively to prey items, so water preservation is essential for elephant seals. A major source of water loss can be respiration, so it was critical for elephant seals to develop a means of reducing respiratory water loss[2]. The nasal turbinates enable elephant seals to meet both of these challenges by warming air that is inhaled, and cooling air that is exhaled through a process called counter-current heat exchange (Fig. 2). Blood in the tissue of the nasal turbinates is colder than the warm air being exhaled, so the air cools as it passes through the turbinates. When this air cools, it not only reduces the amount of heat lost to the environment, but also decreases the air's ability to hold water, meaning that water vapor condenses and remains inside the seal rather than being exhaled. (For more information on elephant seal nasal turbinates, see http://www.elephantseal.org/Research-friends/Nasal%20turbinates%20Part%202%20f%20%281%29.pdf)

The reduction of the olfactory turbinates in response to this strong selection for respiratory turbinates results in a decrease in certain features of the elephant seal's ability to smell. Sense of smell can be broken into three components – the ability to detect a chemical at low concentrations (sensitivity), the ability to distinguish between odors that are similar (discrimination), and the ability to detect a wide range of different odorants (acuity)[1]. It is thought that this olfactory impairment mainly impacts the third component, leaving the other two largely unaffected[1]. This means that elephant seals are probably as sensitive to scents as their close relatives, but are unable to detect such a broad range of smells.

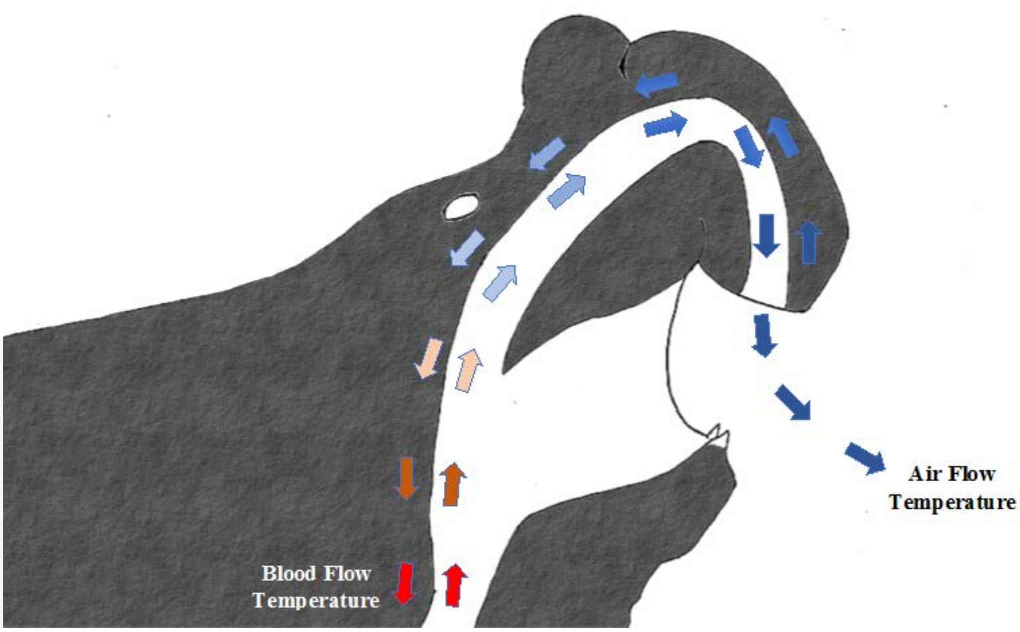


Fig. 2. Counter-current heat exchange in a northern elephant seal.

1. Van Valkenburgh, B., Curtis, A., Samuels, J. X., et al. (2011). Aquatic Adaptations in the Nose of Carnivorans: Evidence from the Turbinates. *Journal of Anatomy*, 218(3).

2. Huntley, A. C., Costa, D. P., Rubin, R. D. (1984). The Contribution of Nasal Countercurrent Heat Exchange to Water Balance in the Northern Elephant Seal, Mirounga angustirostris. *Journal of Experimental Biology*, 113(Nov).