

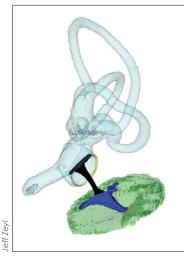
When one thinks of animals that may use infrasound, elephants and baleen whales might come to mind. These large animals communicate over long distances using acoustic signals that contain infrasonic frequencies. Besides these giants, infrasonic hearing has also been described in smaller mammals and birds that do not produce infrasonic vocalisations, such as mountain beaver, rock dove and chicken. Infrasonic hearing ability has been tested in relatively few animal species, which could mean that it is more widespread in animals than currently appreciated.

In birds, infrasonic vocalisation is quite rare. This is because relatively large volumes of air need to be displaced to produce infrasound, and most birds are too small to do this. However, there are a few exceptions. The cassowary – a large flightless bird – produces vocalisations that have some energy near 20 Hz, though the loudest components of their vocalisations are still higher frequency (not infrasonic). Male peafowls produce infrasound in their mating displays by shaking their large tail feathers, and peafowls are also able to hear infrasound. For birds such as rock dove or the chicken, which we know do not produce infrasonic vocalisations, infrasonic communication can't be the main function of infrasonic hearing. What might these birds be listening to at infrasonic frequencies?

Natural sources of infrasound include thunderstorms, surf, colliding ocean waves, and earthquakes. Some, such as thunder, are transient, while others, including surf, are more stable in space and time. Since low frequencies are much less absorbed than higher frequencies as they propagate through the air, infrasound can be detected at great distances from the source, in some cases hundreds to thousands of kilometres away. These unique features of infrasound, combined with our knowledge that some birds can detect sound in this frequency range, have led some scientists to the intriguing hypothesis that certain bird species use infrasonic cues from the geophysical environment to aid navigation. That ability might be useful for bird species that need to fly and navigate long distances as part of migration.

For my postdoctoral work at Stellenbosch University, I am working as part of an international team to investigate the possibility that seabirds use infrasound in navigation. This hypothesis confronts us with several unknowns. Can different seabird groups detect infrasound? If they can detect it, can they determine the direction of the sound? Can they distinguish between different infrasound sources? How might they change their behaviour when they hear different infrasound sources? One aspect of this project involves placing biologgers that record infrasound on albatrosses, which will help to better understand the birds' natural responses to infrasound. My contribution to the project focuses on elucidating the hearing mechanisms for detecting infrasound, and understanding the comparative auditory anatomy of seabirds.

It is not immediately obvious that birds could extract directional information from infrasound, allowing for orientation. To determine the direction of a sound, land animals typically use differences in sound level and time of arrival between the two ears. Depending on the angle of the sound source relative to the bird, the timing and amplitude information will differ slightly between each of the ears, allowing the brain to compare the two inputs and determine the direction. But for very low frequencies, the wavelengths are very long relative to the distance between the two ears, which means that the stimulus received by each ear might be so similar that it would be difficult for the brain to determine the source direction. Some alternative ideas have been proposed, such as detecting the sound direction by perceiving a shift in frequency caused by flying relative to a static sound source (this is known as the Doppler effect). Future work is needed to test these possibilities.



Little is known about the hearing abilities of seabirds, in general, so it was first necessary for us to review the evidence for their infrasonic hearing abilities and examine possible anatomical structures involved. The few birds in which infrasonic hearing abilities have been tested were not seabirds, but we know that the rock dove and some birds in the order Galliformes (chicken, guinea fowl and probably peafowl) are quite sensitive to infrasound.

3D rendering of a bird ear from a microCT scan.

while other birds such as budgerigar and mallard duck are no more sensitive than humans at these frequencies. Seabird hearing is also likely to vary a lot in different taxonomic groups. For example, diving birds show a wide range of hearing sensitivity, with relatively poorer hearing in great cormorant, but relatively good sensitivity in the Atlantic puffin.

Bird hearing relies on a well-functioning tympanic middle ear, meaning the bird has an eardrum and ear ossicle(s) that transmit sound vibrations to the sensors in the inner ear. The tympanic middle ear is quite essential for detecting airborne sounds; without it, most of the sound energy would reflect off the body surface. For most birds, the tympanic middle ear vibrates maximally at 1–5 kHz, which corresponds to the frequencies at which their hearing is most sensitive. Below these frequencies of peak vibration, vibrations typically decline at a rate of approximately 6 dB/ octave. In other words, the decline in vibration is directly proportional to the reduction of frequency.

Some bird species may have a middle ear that is particularly well-structured for low-frequency hearing sensitivity. This might be achieved by having larger cranial air cavities behind the eardrum and more flexible ligaments and cartilage in the middle ear, which would make the ear less stiff and more responsive at low frequencies. Large eardrums, which will have lower resonating frequencies, might also be an advantage for detecting infrasound. For example, we know the ostrich has very large eardrums that vibrate well at relatively low frequencies. Although we don't have any data on the ostrich's hearing abilities, we can expect that this species hears low frequencies very well.

Given that the middle ear vibrations can decline to such low levels at infrasonic frequencies, other 'extratympanic' hearing pathways could also be at play. Extratympanic pathways are sound vibrations reaching the ear through body tissues other than the tympanic middle ear. We know that for animals lacking tympanic middle ears, such as salamanders, snakes and frogs, the auditory response at low frequencies does not rely on a functional tympanic middle ear. Vestibular organs, which are sensors involved in balance and detecting the movement of the head, might also get stimulated by airborne infrasound, as their activation in response to low-frequency airborne sound has been demonstrated in some animals, as well as in humans.

Conducting infrasonic hearing tests on a large number of seabirds is not technically feasible, so we have focused on drawing inferences about hearing through a comparative study of anatomy. We collected (with permission from authorities) a diversity of naturally deceased seabirds and non-seabirds from various researchers and conservation agencies. We then scanned the ear region of the head using microCT (micro-computed tomography), which gave us a 3D rendering of the internal structures. From the scans, we measure several hearing structures, focusing largely on the middle ear. By comparing species with known superior low-frequency hearing abilities with seabirds, we can draw some conclusions about seabirds' hearing abilities. We can also see how the ear structures change in relation to bird size, and whether birds from different habitats or families have distinct ear structures.

This large anatomical dataset has also allowed us the opportunity to test other hypotheses about hearing in seabirds. Specifically, we are studying hearing structures which might be important for underwater hearing, and how these might affect hearing in air. Some seabird groups – such as cormorants, penguins and auks – spend a significant amount of time foraging in water, which is a very different acoustic environment compared to air. Most significantly, water is much denser than air, so ambient hydrostatic pressure applied to the body (and ear) can be very high as birds dive to deeper water. As a result, modifications to ear structure to enhance underwater hearing or to protect the ear from the high hydrostatic pressures might affect the ear's performance in air.

Several unknowns remain about which birds might hear infrasound, how they may detect it, and what they may gain from using that information. By compiling our anatomical data, we hope we are putting key building blocks in place for some exciting discoveries in this area.



• For more information, see the review on infrasonic hearing in birds by Zeyl et al. 2020 (https://doi. org/10.1111/ brv.12596) and the website of the seabirds and infrasound project (https:// seabirdsound. org/).

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