#### **ORIGINAL PAPER**



# Hearing in Indian peafowl (Pavo cristatus): sensitivity to infrasound

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#### Abstract

Despite the excitement that followed the report of infrasound sensitivity in pigeons 40 years ago, there has been limited followup, with only eleven species of birds having auditory thresholds at frequencies below 250 Hz. With such sparse data on low-frequency hearing, there is little understanding of why some birds hear very low frequencies while others do not. To begin to expand the phylogenetic and ecological sample of low-frequency hearing in birds, we determined the behavioral audiogram of the Indian peafowl, *Pavo cristatus*. Peafowl are thought to use low frequencies generated by the males' tail feathers and wing flutters during courtship displays, and their crest feathers are reported to resonate at infrasound frequencies. The peafowl were able to respond to frequencies as low as 4 Hz, and their hearing range at 60 dB SPL extended from 29 Hz to 7.065 kHz (7.9 octaves). Removing the crest feathers reduced sensitivity at their resonant frequencies by as much as 7.5 dB, indicating a modest contribution to detectability in that range. However, perforation of the tympanic membranes severely reduced sensitivity to low frequencies, indicating that sensitivity to low frequencies is mediated primarily by the ears and cannot be attributed to some other sensory modality.

Keywords Infrasound · Bird hearing · Animal psychophysics · Operant conditioning · Vibrotactile detection

## Introduction

Forty years ago, the low-frequency hearing ability of pigeons was investigated as part of a series of studies designed to determine if homing pigeons used low-frequency sounds for navigation (Kreithen and Quine 1979). Obtaining thresholds at 200 Hz and lower, that study showed that pigeons have better low-frequency hearing than humans—in other words, they hear infrasound—a discovery that has been replicated (Heffner et al. 2013).

Since then, there have been two lines of research into the use of infrasound by birds. One is the continued study of pigeons' use of infrasound for navigation (e.g., Hagstrum 2019). The other explores whether sensitivity to infrasound is common among birds. However, only nine species of birds have been tested at frequencies below 250 Hz. Of those species that have been studied, domestic chickens were found to be even more sensitive to infrasound than pigeons (Hill et al. 2014). On the other hand, budgerigars (Heffner et al. 2016),

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mallard ducks (Hill 2017), and Japanese quail (Strawn and Hill 2020) do not hear infrasound.

With so little data on low-frequency hearing in birds, there is little confidence in ideas as to why some birds hear very low frequencies, whereas others do not (e.g., Zeyl et al. 2020). To begin to address the need for a broader phylogenetic and ecological sample of birds, one possibility is to examine a species thought to use low frequencies in communication. Peafowl use loud calls and males produce lowfrequency flutter displays of their wings and tail-feather train to attract females. However, these flutter displays are primarily visual and can be detected without relying on hearing low frequencies. Recently, Kane et al. (2018) recorded strong resonance from the crest feathers and the filoplumes (short sensory feathers at the base of the crest feathers) to a narrow range of frequencies centered around 25.5 Hz. This raised the possibility that peafowl might perceive infrasound, but that its detection might be mediated through the somatosensory system.

Accordingly, we tested the hearing of Indian peafowl (*Pavo cristatus*) at frequencies from 4 Hz to 10 kHz. To determine if some or all of their low-frequency detection bypasses the ears, the crest feathers and filoplumes were removed and their sensitivity in the range from 8 to 32 Hz

re-tested. Finally, the tympanic membranes were punctured at the end of the study and low-frequency sensitivity again tested as a final control.

## Methods

The method of conditioned suppression/avoidance was used to obtain absolute thresholds for the Indian peafowl for pure tones ranging from 4 Hz to 10 kHz. The peafowl were trained to continuously peck a key to obtain access to food at regular intervals, then to suppress pecking in the presence of a tone to avoid a mild electric shock. Suppressing pecking when a tone was presented indicated that the bird had detected the sound and it was rewarded with access to food. If the bird continued pecking during a tone, a mild electric shock was delivered.

## Subjects

Three Indian peafowl *Pavo cristatus* obtained from a local breeder, one male (labeled A) and two females (labeled B and C), were used in this study. They were group-housed in a room with free access to water. Chicken food (Purina Layena Crumbles) was used as a reward and the animals were weighed daily (when on test) to monitor their health and deprivational status. All birds were 9 months old at the beginning of testing. At the time of crest removal, they were 21 months old and both birds were just sexually mature with the male beginning to display his train and the females beginning to lay eggs. The male crest consisted of 21 feathers, average 5.76 cm length, the female crest had 18 feathers, average length 4.6 cm. These lengths are within the range reported for adults (Kane et al. 2018).

#### **Behavioral apparatus**

Testing was conducted in a double-walled sound chamber (Industrial Acoustic Co., model 1204;  $2.55 \times 2.75 \times 2.05$  m), the walls and ceiling of which were lined with eggcrate foam and the floor carpeted to reduce sound reflections.

The peafowl were tested in a cage  $(100 \times 55 \times 85 \text{ cm})$  constructed of hardware cloth  $(2.54 \times 5.08 \text{ cm})$  and mounted on four wooden supports  $(5.08 \times 10.16 \text{ cm})$ , raising the base of the cage 45 cm above the floor of the sound chamber. The bottom of the cage was lined with two layers of thick carpeting (approx. 2.5 cm) to further reduce substrate-borne vibrations.

A contact switch, consisting of a clear plastic disk (3 cm diameter, 1 mm thick) with an embedded red LED served as the response key. This key was mounted at the front of the cage, 66 cm above the cage floor. The lighted LED was momentarily switched off when the key was pecked,

providing feedback to the bird. Access to chicken food was provided by a solenoid-controlled food hopper that, when operated, would come up at the bottom of the cage to allow the peafowl to feed for 3 s. The entire feeder mechanism was placed 53 cm below the response key so that it would not interfere with the sound field.

Electric shock (Coulbourn Regulated Animal Shocker, model E13-14) was delivered via leads hanging from the top of the cage to bead chains around the base of the peafowl's wings. (For a description of the bead chain application, see Heffner et al. 2013, Hoffman 1960, and Stein et al. 1971.) The birds were trained and tested using shock levels (0.2–0.6 mA, 1.5-s duration) that were individually adjusted to the lowest level that produced a consistent suppression response to an obviously audible signal. The shock was defined as mild, because the peafowl never developed a fear of the response key and readily returned to pecking the key after the shock had been delivered. A 25-W light bulb, placed above the loudspeaker, was turned on concurrently with the shock.

## **Acoustical procedures**

Pure tones were generated and gated on and off at zero crossing using Tucker-Davis Technologies (TDT) equipment and associated RPvds software. The output of the processor (TDT Real-Time Processor, model RP2) was then routed to an attenuator (TDT, model PA4), filtered (Krohn-Hite 3550), amplified (Crown D75A), monitored on an oscilloscope (Tektronix TDS 210), and sent to the loudspeaker. Characteristics of the different frequencies and the speakers used to present these tones are as follows:

Frequencies of 250 Hz and below were presented as single 2-s pulses, with rise–decay times of 50 ms at 250 Hz, and a longer rise–decay time of 100 ms for frequencies 125 Hz and below. These lower frequency signals did not contain multiple pulses as the longer rise–decay times would have significantly reduced the number of cycles at maximum amplitude and possibly raised the threshold. At 500 and 750 Hz, the signal contains two pulses (900 ms on, 100 ms off) with 20 ms rise–decay times, while frequencies of 1 kHz and higher were pulsed 4 times (400 ms on, 100 ms off; 10 ms rise–decay). The electrical signals were band-passed filtered at 1/3 octave above and below center frequency before being sent to the amplifier.

Various loudspeakers were used to present the sounds, with the same frequency often tested with different speakers. A 15-in (38.1 cm) subwoofer (TC Sounds Axis) in an unported enclosure ( $65 \times 65 \times 120$  cm) was used for frequencies up to 32 Hz, while a 12-in (30.5 cm) woofer was used for frequencies from 60 to 125 Hz. Frequencies from 250 Hz to 2 kHz were presented using either a 5.5-in (14 cm) woofer (Infinity Primus 163) or a 5-in (12.7 cm) woofer (Optimus Pro 77). A piezoelectric speaker (Motorola KSN 1005) or ribbon tweeter (Foster E110T02) was used for frequencies 2.8 kHz and higher.

All speakers were placed at least 1 m in front of the test cage. Unlike the placement of other speakers to directly face the bird ( $0^{\circ}$  incidence), the subwoofer was turned  $180^{\circ}$  to prevent the bird from cueing to the movement of the speaker diaphragm. An added benefit to this arrangement was that intensity of the low-frequency signals (4–32 Hz) were boosted as much as 6 dB by standing waves, thus increasing the saliency of the signal at the beginning of the test.

The sound pressure level (SPL re 20  $\mu$ N/m<sup>2</sup>) of the stimulus was measured using a 1/4-inch (0.635 cm) microphone (Bruel & Kjaer 4939, calibrated down to 2 Hz), measuring amplifier (Bruel & Kjaer 2610), and a spectrum analyzer (Zonic A&D 3525 FFT Analyzer) to verify the signal and check for overtones. Sound measurements were taken by placing the microphone in the area occupied by a peafowl's head when it was pecking the response key and pointing it directly at the loudspeaker (0° incidence). Multiple readings were taken within the area of the peafowl's head to further ensure that sound intensity was uniform within that space. No correction for orientation was required when measuring low frequencies presented from the subwoofer (4-32 Hz), as the microphone was omnidirectional at these frequencies. Daily measurements of low-frequency background noise in the test chamber showed unmeasurable levels that were below the electrical noise generated within the measuring equipment itself. At midrange and higher frequencies, background noise remained at least 20 dB below the eventual thresholds, hence did not interfere with the bird's ability to detect the acoustic signals. Subsequent measurements also revealed no harmonics or distortion in the acoustic signal at threshold-level intensities.

#### **Behavioral procedure**

The peafowl were first trained to peck the response key to obtain 3-s access to food. The number of pecks required for food access was then increased from one to 3 or 4 pecks every 2 s. Because they varied in their rate of pecking, individuals having a slow peck rate were required to peck fewer times than those with a naturally faster peck rate. They were then trained to stop responding (after the initial peck) when a tone was presented. If the bird continued pecking during a tone, a mild shock (1.5 s duration) was delivered. If the bird stopped pecking, it both avoided the shock and was given 3-s access to food at the end of the trial. Thus, in this procedure, the shock was avoidable, and the bird was rewarded for both hits and correct rejections, but not for misses and false alarms.

This procedure in which the bird pecks during silent trials, and suppresses its pecking when tones were present, is the same conditioned suppression/avoidance procedure that was used to determine the hearing abilities in a wide range of mammals, and has also been used successfully to test other bird species (e.g., Heffner et al. 2013).

A session consisted of a series of 2-s trials, each with an intertrial interval of no less than 500 ms. The intertrial interval ended after 500 ms or when the bird returned to pecking after collecting a reward or receiving a shock.

Because each trial was initiated by the first key peck, it ensured that the peafowl's head was directly in front of the loudspeaker and the bird was attending to the task. The response of a bird was defined by whether or not it pecked during the last 300 ms of the trial. The short delay of 1.7 s (from the onset of the 2-s trial) provided the bird sufficient time to react to a tone. If the bird suppressed pecking during this 300-ms period, a response was recorded. The response was classified as a hit if a tone was presented and as a false alarm if there was no tone. Pecking during the last 300 ms of a tone trial was scored as a miss, followed by a 1.5-s shock. The bird gained 3-s access to food at the end of a trial if it had made a correct response, i.e., it pecked during a silent trial (correct rejection) or it stopped pecking during a tone trial (hit).

Each trial had a 22% probability of containing a tone. The number of trials varied between 40 and 70 tone trials (and 160–280 associated silent trials) per session, depending on the amount of food each peafowl had received in the previous session or during weekends on free feed. However, once trained, a threshold could be obtained for each bird in each session lasting 30–50 min.

A single frequency was tested in each session. Absolute thresholds were determined by presenting tone trials at suprathreshold intensities and successively reducing the amplitude in 5-dB steps until the peafowl no longer responded to the tone above chance (p > 0.01, binomial distribution). At suprathreshold levels, fewer tone trials (usually four) per intensity were presented, while at intensities ranging from about 20 dB above to 10 dB below threshold, the number of trials per block at the same intensity was increased to eight.

Hit and false alarm rates were determined for each block of tone and associated silent trials at each intensity. The hit rate was corrected for the false alarm rate to produce a performance measure according to the following formula: Corrected Hit Rate = Hit rate – (Hit rate × False alarm rate) (Heffner and Heffner 1995). This measure proportionally reduces the hit rate by the false alarm rate and varies from 0 (no hits) to 1 (100% hit rate with no false alarms).

Threshold was defined as the intensity corresponding to a Corrected Hit Rate of 0.50, which was usually determined by interpolation. Threshold testing for a particular frequency was considered complete when the thresholds obtained in at least three different sessions were stable (neither systematically increasing nor decreasing) and within 3 dB of each other. Threshold testing began at 4 kHz and progressed higher to 10 kHz, then down through lower frequencies to 4 Hz and finally replicating all frequencies back up to 9 kHz.

## **Crest removal**

The peafowl's crest and associated filoplumes (the fine mechanosensitive feathers at the base of the larger crest feathers) have been reported to resonate at a narrow range of frequencies between 19.2 and 32.4 Hz (Kane et al. 2018). To investigate whether this vibrotactile stimulus might contribute to their responses to frequencies in this range, additional thresholds were determined for the male (A) and one female (C) peafowl at 8, 16, 20, 25, and 32 Hz, before and after removal of all crest feathers and immobilizing any remnant filoplumes with the stiff hair gel (Schwarzkopf Got2b Ultra Glued).

## Tympanic membrane perforation

Tympanic membrane perforation significantly reduces sensitivity to low frequencies in both mammals and birds (Voss et al. 2001; Hill et al. 2014) and can indicate the degree to which low-frequency sensitivity in peafowl relies on the auditory system. After the crests and filoplumes had fully regrown (approximately 5 months), the same two peafowl were anesthetized with isoflurane and, with the aid of a dissecting microscope, multiple perforations with a 20-gauge hypodermic needle were made in the tympanic membranes of both ears. The columellae remained intact. The birds were

**Fig. 1** Audiogram of three Indian peafowl, *Pavo cristatus* with a human audiogram for comparison (gray line, Jackson et al. 1999). Thresholds were obtained at frequencies ranging from 4 Hz to 10 kHz, with best hearing at 1 kHz. Background noise at all frequencies remained well below thresholds. A, B, and C represent thresholds of the individual animals and the black line represents their mean thresholds then tested daily at 8, 20, and 32 Hz for 8 days to assess hearing loss and subsequent recovery.

## Results

The peafowl adapted relatively easily to the test cage and learned to peck the response key to receive rewards. Training the animals to listen for sounds and then to be reliable observers of low-intensity sounds required approximately 75 daily sessions, after which they produced reliable thresholds. Complete audiometric testing required another 90 days, followed by additional threshold testing after removal of the crest feathers and filoplumes, and finally, after eardrum puncture.

## Audiogram

As shown in Fig. 1, there was good agreement between individvidual peafowl with the greatest difference between individuals being 7 dB at 5.6 kHz. The peafowls' good sensitivity (20 dB or lower) ranged from about 750 Hz to 2 kHz, with best sensitivity at 1 kHz. Their hearing range at a level of 60 dB SPL extends from 29 Hz to about 7.065 kHz, a range of 7.9 octaves. High-frequency sensitivity was tested up to 10 kHz, but, like most birds, they were unable to respond to such high frequencies at comfortable listening levels. At low frequencies, the peafowl continued to respond well to frequencies as low as 8 Hz. At 4 Hz, detection thresholds ranged between 92- and 98-dB SPL.



## **Role of the crest feathers**

The peafowl's crest and associated filoplumes have been reported to resonate at a narrow range of frequencies between 19.2 and 32.4 Hz (Kane et al. 2018). As shown in Fig. 2, removing the contribution of the crest feathers and filoplumes reduced sensitivity at 16, 20, and 25 Hz by 3-7.5 dB, with the female being slightly more affected than the male. Neither individual showed significant change in threshold at frequencies below (at 8 Hz) and slightly above (at 32 Hz) the reported resonant frequencies of the crest feathers. The mild loss of sensitivity at the crest resonance frequencies suggests that the crest apparatus may have



**Fig.2** Hearing loss after the crest feathers and filoplumes were clipped at scalp level and gel applied. There was a consistent but mild loss of sensitivity at the frequencies around the greatest resonance, 20–25 Hz, of the crest feathers. A and C represent the male and female peafowl, respectively

contributed to the detectability of frequencies in the range of 16–25 Hz. With only two individuals, we cannot speculate whether females rely more on detecting these frequencies using the crest apparatus, even though they are known to be the targets of the wing shaking and tail-feather flutter displays of the peacock.

### Tympanic membrane perforation

Just as tympanic membrane perforation reduced sensitivity to low frequencies in other species (Voss et al. 2001; Hill et al. 2014), it also severely reduced sensitivity at 32 Hz and below in peafowl. Figure 3 shows that 4 h after puncturing the tympanic membrane in two peafowl, the male had a 22-dB loss at 8 Hz and the female could not respond to 8 Hz at 100 dB SPL, the highest intensity producible without distortion, indicating a loss greater than 26 dB. At 20 Hz, their losses were 15 dB and 27 dB, respectively, and at 32 Hz, both peafowl suffered a 19 dB loss. The following 2 days, thresholds were only slightly improved (by about 1-5 dB). But by the third day in the male and the fourth day in the female, thresholds began to improve noticeably, and by the eighth day, both animals achieved thresholds in their normal range. Such quick recovery to normal thresholds is common (e.g., Hill et al. 2014) and indicates that the membrane heals quickly.

The extensive loss of sensitivity following eardrum puncture, by as much as 27 dB at and below 32 Hz, indicates that infrasound detection by peafowl is indeed auditory, and their detection of low frequencies cannot be attributed simply to somatosensory detection of substrate vibration or reliance on vibration of the crest feathers, which, as shown in Fig. 2, contributed about 6 to 7 dB of sensitivity. Indeed, there is

**Fig. 3** Hearing loss following bilateral eardrum puncture in a male and female peafowl. Hearing loss was first tested 4 h post-puncture, then daily until thresholds stabilized within the normal range. The female showed the greatest loss and could not detect the lowest frequency (8 Hz) at 100 dB SPL (indicated by the arrows) until the fourth day following puncture



no indication that the intact crest and filoplumes reduced the impact of tympanic membrane perforation on the detection of 20 Hz since the hearing loss and recovery at 20 Hz was very similar to the loss at the slightly higher and lower frequencies at which the crest feathers did not resonate. This raises the possibility that the somatosensory component contributed by the crest/filoplume apparatus might act through the auditory pathway—such convergence of the auditory and somatosensory pathways is not unknown (e.g., Wild 1995). (Any potential contribution to sensitivity from particle velocity stimulation of the crest feathers is not known.)

## Discussion

## Low-frequency hearing in birds

From an anthropocentric view, it is of interest to determine which species hear frequencies lower than humans (i.e., detect frequencies below about 32 Hz at lower levels than humans), because such species may be using sound in ways we do not expect. By this definition, there are now three species of birds that hear "infrasound": Pigeons (Kreithen and Quine 1979; Heffner et al. 2013), domestic chickens (Hill et al. 2014), and now Indian peafowl. Whether such infrasonic hearing involves different anatomical or physiological mechanisms is already under investigation (for a review, see Zeyl et al. 2020). The possibility in chickens of a second mechanism has been suggested because they required additional training, especially at 32 Hz, before their final thresholds could be obtained, implying that they may perceive lower frequencies differently from higher frequencies (for details, see Hill et al. 2014). Although no such training effect was seen in the peafowl, the possibility of different mechanisms underlying the perception of low frequencies remains intriguing. Peafowl do rely on the auditory system to detect low frequencies as shown by the severe loss of sensitivity following puncture of the tympanic membrane, but there is also evidence of some contribution of the crest apparatus within the frequency range of approximately 16-25 Hz.

An estimate of resonance of the apical end of the basilar membrane in Galliformes, based on stereovilli bundle morphology, may also hint at a separate mechanism underlying low-frequency hearing (Corfield et al. 2013). The apical resonance frequencies estimated for seven Galliformes all suggested very similar lower hearing limits of about 200 Hz. We now know that three of those species—domestic chickens (Hill et al. 2014), Japanese quail (Strawn and Hill 2020), and now Indian peafowl—all hear well below the estimated 200 Hz resonance limit of the basilar papilla. Such an extension of sensitivity below the resonance of the apical end of the basilar papilla suggests that additional factors are likely to contribute to low-frequency sensitivity—perhaps electrical tuning of hair cells as noted by Corfield and colleagues (2013), and/or a firing rate/volley mechanism in the auditory nerve similar to that in mammals that hear low frequencies (Heffner et al. 2001).

The variation of low-frequency hearing in birds is important for the study of the selective pressures affecting avian hearing as well as for the mechanisms employed. Figure 4 shows the range of low-frequency hearing in birds as measured by the lowest frequency detectable at an intensity of 60 dB SPL. The 60-dB level has been useful in comparing both high- and low-frequency hearing in mammals (e.g.,



**Fig. 4** Low-frequency hearing limits at 60 dB SPL, note log scale (Bullfinch-Schwartzkopff 1949; Red-winged blackbird and Brownheaded cowbird—Heinz et al. 1977; Pigeon—Kreithen and Quine 1979, Heffner et al. 2013; Canary—Okanoya and Dooling 1987; Human—Jackson et al. 1999; Orange-fronted conure, extrapolated from 52 dB threshold at 250 Hz—Wright et al. 2003; Budgerigar—Heffner et al. 2016; Domestic chicken—Hill et al. 2014; Kea parrot—Schwing et al. 2016; Great cormorant, extrapolated from 53 dB threshold at 500 Hz—Maxwell et al. 2017; Mallard duck—Hill 2017; Japanese quail—Strawn and Hill 2020)

Heffner et al. 2001). Although other levels may eventually prove useful for making other comparisons, the use of a less stringent level such as a 30-dB or 40-dB definition of low-frequency hearing reveals much less variation among birds, hence is less desirable as a measure for exploring their variation in low-frequency capabilities. As Fig. 4 shows the low-frequency hearing limits of few birds have been determined; indeed, few species have been tested below 250 Hz. Altogether, the 13 low-frequency limits available appear to form a continuum ranging from 9 Hz (Domestic chicken, Hill et al. 2014) to approximately 400 Hz (Great cormorant, Maxwell et al. 2017). To understand how low frequencies are used, or not used, by birds of different lineages and lifestyles, we will need to know the low-frequency hearing abilities of a much larger and more representative sample of species. Such data are needed to help us interpret the underlying anatomical and physiological mechanisms, and perhaps provide insight regarding the functions served by hearing very low frequencies (cf. Zeyl et al. 2020).

#### Navigation

It was initially proposed that sensitivity to very low frequencies in pigeons might be an adaptation for navigation during migration (Kreithen and Quine 1979; Hagstrum 2019). However, that rationale for infrasound sensitivity cannot apply to chickens and peafowl, both of which are poor flyers and do not navigate long distances. On the other hand, mallard ducks migrate over long distances and do not hear infrasound (Hill 2017). Hence, although infrasound might be used for long-distance navigation, it is not essential. The hearing of so few other bird species has been tested at low frequencies that we are left with few theories as to why some birds hear infrasound and others do not. Moreover, we cannot assume that very low frequencies play only a single role in the lives of animals.

## Courtship

The vocal calls of peafowl include frequencies ranging from about 150 Hz to as high as 8 kHz (Takahashi and Hasegawa 2008; Yorzinski and Anoop 2013). These frequencies encompass much of their hearing range, including the frequencies to which they are most sensitive. But much attention has been given to their visual courtship displays, which also produce very-low-frequency sound. Males pulse/shiver their highly visible train and rotate their wings, producing frequencies below 20 Hz, to which nearby females respond (Freeman and Hare 2015). These displays seem to be necessary for successful mating and we now know that the associated low-frequency sounds are audible across the short distances at which they are used. These low frequencies also stimulate the crest feathers (Kane et al. 2018) and our results show that such vibrotactile input improves detectability of frequencies of 16–25 Hz, but only by about 6–7.5 dB.

# Conclusion

As we learn more about the low-frequency hearing of birds from different lineages, lifestyles, and sizes, we may see patterns that are not yet apparent. That has been the case with mammals for which we now know that low-frequency hearing is bimodally distributed, with some species hearing below 300 Hz but others not hearing below 500 Hz (Heffner et al. 2001, 2020). That pattern was not revealed until the low-frequency limits of nearly 50 different mammals had been determined. The hearing of birds is important, because the variation of their auditory anatomy and physiology contribute to our appreciation of the different mechanisms that are used to achieve basic auditory functions. As the lowfrequency limits of more birds are determined, it will be of interest to compare birds of different lifestyles to mammals to provide further insight into both the mechanisms that make low-frequency hearing possible and elucidate the functions of low-frequency hearing.

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#### **Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

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