Auditory performance in bald eagles and red-tailed hawks: A comparative study of hearing in diurnal raptors

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All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in

accordance with the ethical standards of the Institutional Animal Care and Use Committee of the University of Minnesota where the studies were conducted.

List of Abbreviations

ABR	auditory brainstem response
AWEA	American Wind Energy Association
ANOVA	analysis of variance
CAP	compound action potential of the auditory nerve
CN	cochlear nuclei
dB SPL	decibels sound pressure level referenced to 20 µPa
$EtCO_2$	end-tidal CO_2
Hz	Hertz (cycles/sec)
IPI	interpeak interval
IUCN	International Union for Conservation of Nature
kHz	kiloHertz
nMLD	dorsolateral mesencephalic nucleus
USDOE	Unites States Department of Energy
USFWS	United States Fish and Wildlife Service
USGAO	United States Government Accountability Office

Abstract

Collision with wind turbines is a conservation concern for eagles with population abundance implications. The development of acoustic alerting technologies to deter eagles from entering hazardous air spaces is a potentially significant mitigation strategy to diminish associated morbidity and mortality risks. As a prelude to the engineering of deterrence technologies, auditory function was assessed in bald eagles (*Haliaeetus leucocephalus*), as well as in red-tailed hawks (*Buteo jamaicensis*). Auditory brainstem responses (ABRs) to a comprehensive battery of clicks and tone bursts varying in level and frequency were acquired to evaluate response thresholds, as well as suprathreshold response characteristics of wave I of the ABR, which represents the compound potential of the VIIIth cranial nerve. Sensitivity curves exhibited an asymmetric convex shape similar to those of other avian species, response latencies decreased exponentially with increasing stimulus level and response amplitudes grew with level in an orderly manner. Both species were responsive to a frequency band at least 4 octaves wide, with a most sensitive frequency of 2 kHz, and a high frequency limit of approximately 5.7 kHz in bald eagles and 8 kHz in red-tailed hawks. Findings reported here provide a framework within which acoustic alerting signals might be developed.

Keywords: eagles, hawks, hearing, auditory brainstem response, evoked potentials

Introduction

Although the bald eagle (*Haliaeetus leucocephalus*) population is currently stable in the United States (U.S. Fish and Wildlife Service [USFWS] 2016), the long-term threat of population decline remains a conservation concern given the species' low reproductive rate combined with the potential impact of an unanticipated rise in mortality of breeding stage adults (Grier 1982; Purvis et al. 2000; Krüger and Radford 2008; Carrete et al. 2009; Tack et al. 2017). While a combination of natural risk factors have contributed to eagle mortality rates historically, anthropogenic pressures are on the rise and arguably represent the greatest current and extended threat to the long-term maintenance of stable populations (Lehman et al. 2007; Watson 2010; Haig et al. 2014; Loss et al. 2014; Tack et al. 2017).

An especially important anthropogenic enterprise of interest in this regard rests in the renewable wind energy sector. Growth in this industry represents one of many potentially significant threats to the long-term stability of eagle populations in the United States and elsewhere (Madders and Whitfield 2006; Kuvlesky et al. 2007; Smallwood and Thelander 2008; Garvin et al. 2011). Although risks to golden eagle (*Aquila chrysaetos*) populations currently outweigh those facing bald eagles (Pagel et al. 2013), mortality risks associated with human enterprise and retribution practices remain a concern for both species. When combined with protections guaranteed in the Bald and Golden Eagle Protection Act, originally enacted in 1940 (16 U.S.C. 668 *et seq.*), and its amendments that make the "taking" of eagles illegal, the development of wind turbine collision mitigation strategies is of interest to all stakeholders in the renewable wind energy industry.

One potentially viable strategy to discourage eagles from encroaching into wind farm airspaces and thereby mitigate morbidity and mortality rates associated with turbine collision is the development of alerting or deterrence technologies that employ acoustic signals. As part of an effort to guide the engineering of such technologies, exploration of the working auditory space navigated by bald eagles is the primary subject of this report. Furthermore, because access to bald eagles can be limited, we also report on findings from red-tailed hawks (*Buteo jamaicensis*) in an effort to assess the utility of this species as a potential surrogate for bald eagles in future studies.

In addition, we provide a comparative framework to assess the auditory phenotypes of bald eagles and red-tailed hawks within the larger avian taxonomy, including other birds of prey, as well as vocal learners. Birds of prey, commonly known as raptors, are generally classified into nocturnal raptors, the Strigiformes or owls, and diurnal raptors, a group that is divided taxonomically into two major orders, the Falconiformes that are part of the clade Australaves, and the Accipitriformes that belong to the Afroaves clade and includes bald eagles and red-tailed hawks (Ericson et al. 2006; Hackett et al. 2008; Kimball et al. 2013; Jarvis et al. 2014; Prum et al. 2015; Mindell et al. 2018).[1] Relative to other avian orders, auditory performance has been studied in very few raptor species, most notably the diurnal raptors, a circumstance that enhances the value of findings reported here from a taxonomic perspective. By comparing bald eagle and red-tailed hawk sensitivity curves with sensitivity curves representing two of the three avian orders of vocal learners, including the largest order, the Passeriformes (Oscines), as well as their closest relative, the Psittaciformes (both Australaves), we assess the relative taxonomy of raptor hearing within a broader avian auditory landscape.

Materials and methods:

Animals

A total of nine (9) bald eagles (*Haliaeetus leucocephalus*) ranging in age from the year of hatching to adulthood and seven (7) red-tailed hawks (*Buteo jamaicensis*) ranging in age from hatch year to the second year were included in the study (Table S1). All of the raptors participating in the study were wild birds admitted to The Raptor Center for treatment and were in the final stages of rehabilitation prior to release. Males and females of both species were included in the study (Table S1). Protocols governing the care and use of animals participating in the study were approved by the University of Minnesota Institutional Animal Care and Use Committee, and required wildlife permits were acquired from the U.S. Fish and Wildlife Service and the Minnesota Department of Natural Resources.

Assessment of auditory function

Auditory brainstem responses (ABRs) to a comprehensive battery of clicks and tone bursts varying in level and frequency were acquired and analyzed to assess auditory function. Animals were anesthetized with isoflurane to eliminate muscle activity and thereby maintain a stable, quiet recording environment. Anesthesia was initiated via mask induction using a mixture of

humidified 4-5% isoflurane with 100% oxygen (O_2) at a flow rate of 1-2 L/min. When deep sedation/general anesthesia was achieved, animals were intubated and maintained in a lightly sedated state with approximately 1.5 to 2.5% isoflurane mixed with 1-2 L/min O_2 throughout the recording session. Animals were fasted for 12-24 hours prior to anesthetization.

Respiratory rate and end-tidal CO_2 ($EtCO_2$) were monitored throughout the recording session. Typically, respiratory rates were in the range of 10-20 breaths/min and $EtCO_2$ levels were in the range of 30-50 mm Hg. If respiratory rate was low and $EtCO_2$ was high, the recording session was paused to ventilate the bird. In addition, recordings were paused periodically to assess body (cloacal) temperature, and palpebral and/or corneal reflexes. When necessary, birds were cooled using chilled plastic bottles, or were heated using an electric blanket (Harvard Apparatus, Holliston, MA) to maintain body temperature between 39 and 40°C; recording sessions were paused and animals were cooled when body temperature reached 41°C (Chaplin et al. 1984; Wasser 1986). All recordings were conducted in an electrically-shielded, sound-attenuating chamber lined with acoustic foam and equipped with a Logitech C920 HD PRO Webcam (Fremont, CA). A veterinarian continuously monitored subjects throughout recording sessions and during subsequent recovery from anesthesia. Following recording sessions, animals received supplemental fluids and electrolytes by subcutaneous administration of Ringer's lactated solution.

Using fine (30-gauge) platinum alloy subdermal needle electrodes positioned at the vertex (active, non-inverting), in the near vicinity of the outer ear aperture (reference, inverting) and over the musculature of the clavicle (ground), ABRs were recorded differentially (Grass Instruments, P511 AC preamplifier, West Warwick, RI). Voltages were amplified 100,000x, filtered (30 Hz-10 kHz) and digitized over a 15 ms epoch using a 20 kHz sampling rate. The transducer, a multi-field magnetic speaker (MF1, Tucker-Davis Technologies, Alachua, FL), was positioned 10 cm above one ear (typically the right ear). Symmetrically shaped tone bursts with 1 ms raised cosine on/off ramps and a 1 ms plateau were generated digitally (Tucker-Davis Technologies), alternated in polarity, and presented free-field at a rate of approximately 12.5 Hz; duration was increased to 9 ms with 3 ms on/off ramps when acquiring data for the 354 Hz stimulus. Click stimuli were 64 µs in duration. Stimulus levels were calibrated and reported in decibels sound pressure level (dB SPL: referenced to 20 µPa). Trials with voltages exceeding 70

μV were automatically rejected and the trial was repeated. A maximum of 500 trials was averaged for each waveform and two waveforms were obtained for each stimulus condition. The number of trials averaged per waveform was truncated manually online when waveform reproducibility was achieved (i.e., waveform peaks and valleys replicated with subjective clarity) to facilitate data acquisition efficiency and to reduce anesthesia time.

Stimulus frequency was varied from 0.35 kHz to 8.0 kHz in one-half octave steps when studying bald eagles. The upper frequency was extended to 11.3 kHz when studying red-tailed hawks. Stimulus levels were decreased in 10 dB decrements from approximately 90 dB SPL to below threshold, and levels were adjusted in 5 dB steps near threshold. Responses to click stimuli were acquired in all eagles studied and in six red-tailed hawks.

Threshold was defined as the lowest stimulus level eliciting a replicable response. Low- and high-frequency flanks of threshold-frequency curves were fitted with least-squares linear regressions to compute the slope or rate of threshold change per octave. Peak latencies were measured from the onset of the stimulus, and therefore included air conduction time, estimated to be approximately 0.29 ms. Wave I amplitudes were computed using a triangulation procedure as described in Walsh et al. (1986); however, given the double-peaked nature of wave I, the base of the triangle was extended to the negativity following wave IB. Least squares linear regressions were used to fit log-transformed latency vs. level curves and log-transformed amplitude vs. level curves using the model, $\ln(y) = \alpha + \beta x$, where the y-intercept is represented by α and slope is represented by β; the model may be expressed alternatively as $y = e^{(\beta x + \alpha)}$. In addition, a linear regression was fitted to the regression coefficient, $-1/\beta$, of latency-level curves and an exponential was fitted to $\exp(\alpha)$ as a function of log-transformed frequency. Finally, polynomial functions were used to fit the regression coefficients, $1/\beta$ and $\exp(\alpha)$, of amplitude-level curves as a function of log-transformed frequency.

Statistics

Statistical analyses were performed using R (R Core Team, 2018 version 3.5.0). A repeated-measures, linear mixed effects model was used to test for statistical significance of threshold differences to tonal stimuli between groups (species). The independent variables were frequency and group and subject was assigned the random effect factor. Degrees of freedom and significance were computed using Satterthwaite's method via the lmerTest package (version 3.0-

1). This method was also used to determine if threshold differences to tonal stimuli between sexes for each species and among juveniles (hatch year and second year) and adult individuals within a species, when available, were statistically significant. Statistical significance of differences in wave I latency vs. stimulus level, wave I amplitude vs. stimulus level for each stimulus between groups (species), wave I latency vs. stimulus frequency and amplitude vs. stimulus frequency for each level were also tested using this method, as were differences in regression coefficients (for latency-level and amplitude-level curves) as a function of frequency between species.

A single factor analysis of variance (ANOVA) was used to test for statistical significance of threshold differences to click stimuli between groups (species), to test for differences between groups for slopes of the low- and high-frequency flanks of frequency-threshold curves, and to test for differences between species in regression coefficients (of latency-level and amplitude-level curves) for click stimuli. Finally, the significance of the slope of each linear regression was tested using an ANOVA. Results of all statistical tests were considered significant when $P<.05$.

Methodology used for comparison of threshold-frequency data with other avian species

A threshold-frequency correction curve was generated to equate evoked potential thresholds acquired in this study to absolute thresholds acquired behaviorally by other investigators. Because the temporal integration of information contained in longer tonal stimuli permits a more accurate estimate of absolute sensitivity (Dooling et al. 1978; Dooling 1979; Barton et al. 1984; Dooling and Searcy 1985; Klump and Maier 1990; Okanoya and Dooling 1990; Saunders and Salvi 1993; Pohl et al. 2013), relatively long stimulus durations (e.g., typically in the range of 400 ms to several seconds) were employed in most of the behavioral studies referenced in this investigation. In contrast, evoked potentials are “onset” responses triggered by stimuli with relatively fast rise times (typically in the range of 1 ms or less) permitting the synchronous discharge of the all-or-none action potentials of auditory neurons (Goldstein and Kiang 1958; Picton et al. 1977; Burkard 1991); stimulus duration therefore is not a significant variable when acquiring ABR or VIIIth nerve compound action potential (CAP) responses (Hecox et al. 1976).

The threshold-correction curve was constructed by first fitting 3rd order polynomials to digitized threshold-frequency curves taken from avian species for which both behavioral and evoked potential thresholds were available in the literature. When considering evoked potential

studies, ABR and/or CAP thresholds were included in the analysis. Data from a total of 9 species were utilized to generate the correction curve, although data from 2 species were combined consistent with the reporting method used by one of the investigators (Gall et al. 2011). Second, fitted curves (n=41 threshold-frequency curves) were then sampled in half-octave steps throughout the responsive frequency range, and averages were calculated separately for behavioral data and evoked potential data for each species included in the analysis when multiple studies for a given species were identified. Third, threshold-frequency curves derived from behavioral studies were subtracted from threshold-frequency curves derived from evoked potential studies for each species, and differences were averaged across species, resulting in the threshold-frequency correction curve used in the investigation. These values were then subtracted from observed bald eagle and red-tailed hawk ABR threshold values to approximate absolute thresholds. The threshold corrections indicate, at least in part, the extent to which longer duration stimuli permit greater signal integration time and concomitant improvement of estimated thresholds, more accurately estimating absolute threshold values across stimulus frequency. The frequency dependence of threshold correction factors is consistent with that reported for individual avian species by others (Brittan-Powell et al. 2002, 2010; Köppl and Gleich 2007; Henry and Lucas 2008; Crowell et al. 2016; Maxwell et al. 2016).

Average bald eagle and red-tailed hawk threshold-frequency curves resulting from this analysis were subsequently compared to average threshold-frequency curves of species belonging to five taxonomic orders: Accipitriformes (n=2 species), Falconiformes (n=1), Strigiformes (n=13), Passeriformes (Oscines, n=20) and Psittaciformes (n=5). Generally, threshold-frequency curves were extracted from data acquired from behavioral studies or physiological (heart-rate) conditioning studies reported in the literature. However, when behavioral data were unavailable, threshold-frequency curves were derived from single unit or multiunit recordings of neurons within auditory nuclei (i.e., cochlear nuclei, CN or the dorsolateral mesencephalic nucleus, nMLD). In those cases, the most sensitive estimates of thresholds at characteristic frequency were extracted using a 0.25 octave-wide averaging window. Threshold-frequency data from 41 species (n=59 data sets) were digitized and each curve was fitted by a 3rd-order polynomial. Fitted curves were then sampled in half-octave steps throughout the responsive frequency range and averaged (if more than a single data set was

available) to generate average threshold-frequency curves representing each species included in the analysis. Subsequently, these curves were averaged across species to obtain the mean±1 s.d. for each taxonomic order specified above. However, given the low sample size and similarity of results for species representing Accipitriformes and Falconiformes, threshold-frequency data from these orders were combined into a single threshold-frequency data set (average±1 s.d.) for diurnal raptors.

Results

Response Waveform Morphology

As with other vertebrates, ABR waveforms representing both species were highly replicable and response amplitudes and peak latencies were level dependent, as shown qualitatively in Fig. 1. Average response waveforms generally consisted of five positive-going voltage peaks that occurred between 1.5 ms and 10.5 ms following stimulus onset. The first four peaks were sharp and well defined and occurred sequentially within 8.7 ms following stimulus onset; peak V was broad relative to earlier occurring peaks.

The number of well-defined peaks generally remained constant throughout most of the dynamic input-output range for tone bursts in the most sensitive frequency band, but decreased at stimulus levels near threshold. A single peak, wave I, was often the solitary response element remaining at the lowest levels of stimulation and later-occurring response elements dropped out of

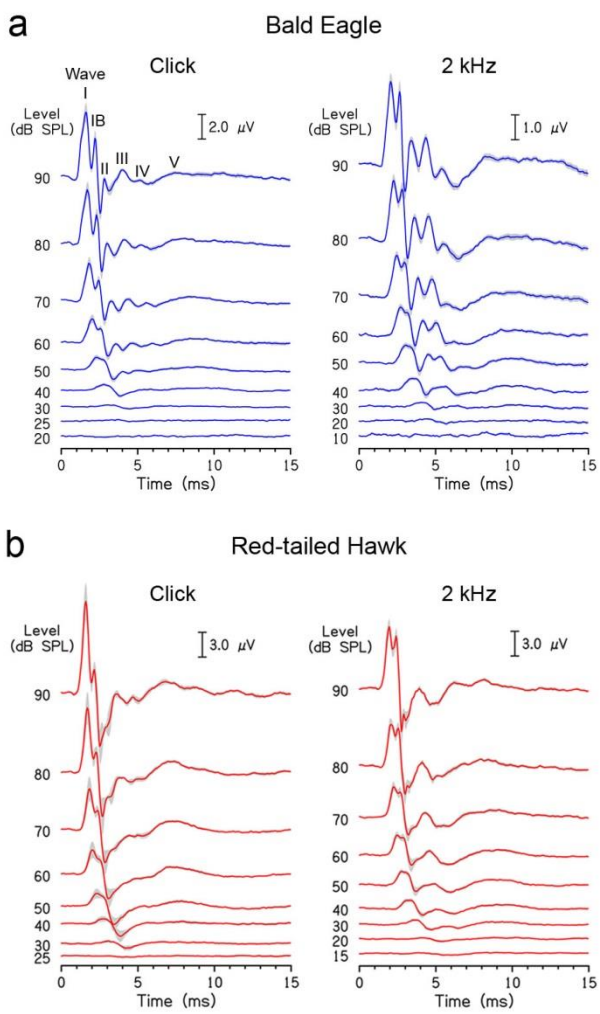

Figure 1. Auditory brainstem response waveforms averaged across individuals for bald eagles (a) and red-tailed hawks (b) are shown for click stimuli (left panels) and 2 kHz (right panels) at stimulus levels ranging from below threshold to 90 dB SPL. Gray shading indicates mean ±1 s.e.m. Note the change in amplitude scales across panels

records in an irregular fashion as stimulus levels were lowered. Peak I typically consisted of two maxima (was double peaked), and like other later-occurring, double-peaked response elements, adjacent peaks generally merged to form a single composite peak as stimulus level was reduced. Although peak IB has been identified as peak II in other studies (Brittan-Powell et al. 2005; Palanca-Castan et al. 2016), we settled on the nomenclature employed here on the basis of the intensity-dependent peak merging behavior addressed above. Additional study is required to address and resolve this question in our view.

Response waveforms elicited by tone bursts at and near 1.0 kHz were occasionally complex, exhibiting a hybrid-like character when considered at high stimulation levels. Specifically, waveforms exhibited a profile consisting of an onset response element and a trailing frequency-following component. Consistent with expectations related to sinusoidal stimulation in which signal polarity is alternated on every other trial/presentation, the frequency following component of responses reflected half the period of the stimulus frequency. For example, the frequency following component of the response exhibited an interpeak interval (IPI) of 0.5 ms in the case of 1.0 kHz. Based on findings from Snyder and Schreiner (1984) and Henry (1995), the frequency following character of the response is most likely a reflection of the high fidelity, neural frequency following response, a neurophonic, although a cochlear microphonic contribution cannot be ruled out.

Threshold vs. Stimulus Frequency Relationships

Although red-tailed hawk thresholds to tone pips ranged from approximately 5 to 15 dB lower than those observed in bald eagles, average threshold-frequency curves, alternatively referred to as sensitivity curves or audiograms, representing both species were notably similar (Fig. 2). Both were convex but asymmetric in shape with the high frequency flank of the curve rolling-off at a higher rate than the low frequency flank, i.e., 51.9±7.3 and -13.5±2.7 dB/octave, respectively, for all subjects; note that differences in the slopes on either flank of sensitivity curves representing bald eagles and red-tailed hawks were not statistically significant and, consequently, data were pooled. Both species were most sensitive to a band of frequencies ranging between approximately 0.5 and 3 kHz as measured 20 dB above the lowest threshold. The most sensitive, or best frequency, was 2 kHz in both species. Red-tailed hawks were, however, more responsive to higher frequency stimulation than bald eagles, having an upper cut-

off frequency of 8 kHz compared to 5.7 kHz. Note that only one eagle showed a replicable response at 8 kHz, whereas all red-tailed hawks were responsive at that frequency.

Differences in thresholds to tone pips were significant at the 0.002 level [F(1,14)=14.84, P=.002], such that the average bald eagle threshold was 9.4±2.6 dB higher than that of red-tailed hawks. There was also a significant main effect of frequency on auditory thresholds [F(8,112)=161.63, P<.001] and a significant interaction between frequency and group [F(8,112)=5.65, P<.001] was also observed. The click threshold difference between species was not significant.

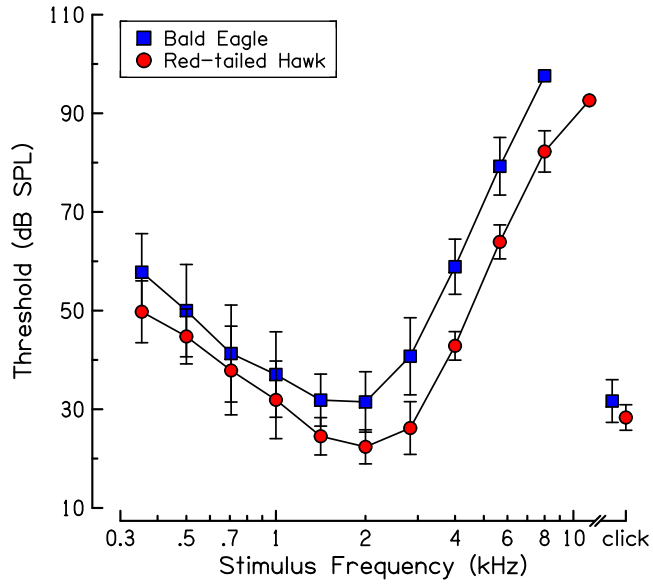

Figure 2. Average ABR thresholds (±1 s.d.) are plotted as a function of stimulus frequency and for click stimuli for each species. Note that a single eagle responded at 8 kHz and 2 hawks responded at 11.3 kHz

Average sensitivity curves representing first year (hatch year), second year and adult eagles were indistinguishable [F(2,6)=0.16, P=.86], as were those of first year and second year hawks [F(1,5)=0.69, P=.45], similar to the results that Langemann et al. (1999) obtained in the European starling (*Sturnus vulgaris*) and similar to the results observed by Krumm et al. (2017) in the barn owl *(Tyto alba)*. Likewise, differences were not observed between male and female eagles [F(1,7)=3.3, P=.11] or between male and female hawks [F(1,5)=0.15, P=.71]. In addition, and consistent with the well-known reversed size dimorphism observed in most raptor species (Snyder and Wiley 1976), the average body mass of male subjects studied was significantly lower (P<.05) than that of female subjects for each species (~17% and 20% lower for male eagles and hawks, respectively), whereas the average body mass of hawks was 74% lower (P<.001) than that of eagles (Table S1).

Suprathreshold Response Characteristics

Response Timing

As with other vertebrates, wave I response latencies decreased with increasing stimulus level in both red-tailed hawks and eagles (Fig. 3). Curves constructed for both clicks and tones were well fit by least-squares linear regressions ($\ln(y) = \alpha + \beta x$, or written alternatively as $y=e^{(\beta x + \alpha)}$) to log-transformed latencies as a function of stimulus level (Fig. 3). Level accounted for at least 94% of the variance (P<.05) for all stimuli (Table S2) except in the case of the 5.7 kHz condition for the bald eagle where response thresholds were high and responses were consequently limited to high levels of stimulation. Red-tailed hawks exhibited slightly faster response times than bald eagles for 2.0, 4.0 and 5.7 kHz (P<.001) (Fig. 3, Table S3). A significant main effect of level was also observed across all stimuli (P<.001) and a significant group (species) by level interaction was observed at 1.4 kHz and 4 kHz at the P<.001 level of significance and at 2 kHz at the P<.01 level of significance (Table S3). Furthermore, the level at which latencies decreased by a factor of *e* (i.e., x = -1/β dB SPL) versus log-transformed stimulus frequency increased along a linear track with increasing frequency (Fig. 4a), indicating that more rapid latency changes occur per unit level at lower frequencies than at higher frequencies. The regressions are statistically significant for both eagles [F(1,7)=39.1, P<.001] and hawks [F(1,7)=64.2, P<.001] and accounted for at least 87% of the variance. A statistically significant difference between species was not observed (P>.05), although a significant main effect of frequency was observed [F(8,105.3)= 13.2, P<.001], as was

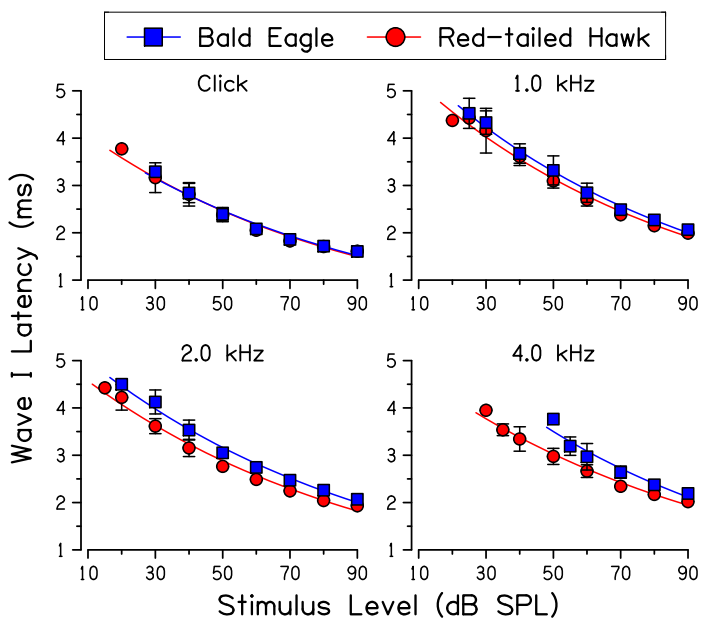

Figure 3. Average wave I latencies (±1 s.d.) are shown as a function of stimulus level for bald eagles (blue squares) and red-tailed hawks (red circles) in response to click stimuli and tone bursts of 1.0, 2.0 and 4.0 kHz. In some cases, error bars are smaller than the symbol. Solid lines represent least squares linear regressions to log-transformed latency values vs. level curves ($y=e^{(\beta x + \alpha)}$) for bald eagles (blue) and red-tailed hawks (red). Regression coefficients and results of statistical tests are provided in Tables S2 and S3, respectively, for these and other test frequencies

a group-frequency interaction [F(8,105.3)=5.6, P<.001]. The rate of latency change with level for click stimuli did not differ between groups (species) (P>.05).

Analyses of the y-intercepts [i.e., exp(α)] as a function of stimulus frequency are shown in Fig. 4b. The data, fitted by linear regressions to α (exponential curves), accounted for 88% of the variance for eagles and 66% for hawks, and the regressions were statistically significant [F(1,7)=45.9, P<.001] and [F(1,8)=13.4, P<.01] for eagles and hawks, respectively. The y-intercepts for latency-level curves were higher for lower frequency stimuli than higher frequencies. A statistically significant main effect of frequency [F(8,106.2)=7.7, P<.001] and a group-frequency interaction [F(8,106.2)=2.6, P<.05] were observed; however, differences between species were not significant (P>.05). Similarly, values for click stimuli did not differ between groups (P>.05).

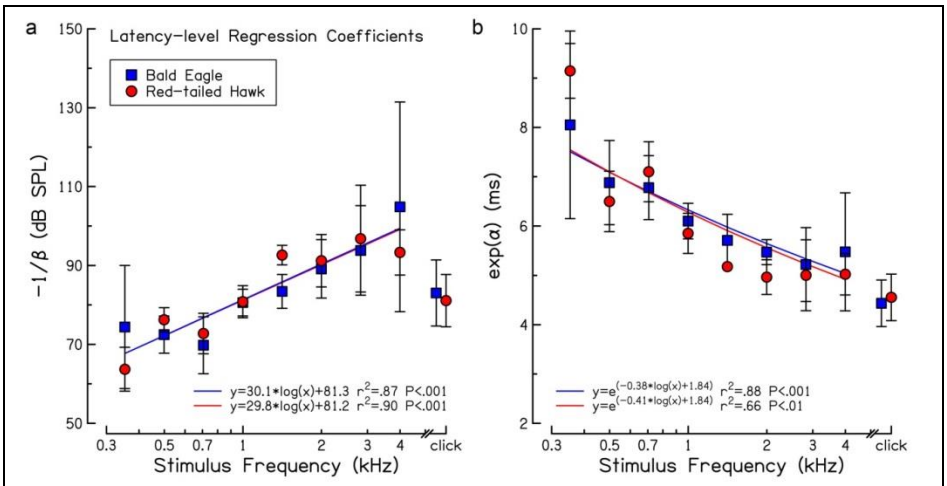

Figure 4. Regression coefficients (±1 s.d.) of log-transformed latency vs. level curves ($y=e^{(\beta x + \alpha)}$) are plotted as a function of stimulus frequency and for click stimuli for both bald eagles (blue squares) and red-tailed hawks (red circles). In (a), solid lines indicate least squares linear regressions to -1/β as a function of frequency for bald eagles (blue) and red-tailed hawks (red), and in (b) they represent exponential fits to exp(α) vs. frequency for bald eagles (blue) and red-tailed hawks (red). Coefficients are included in each frame

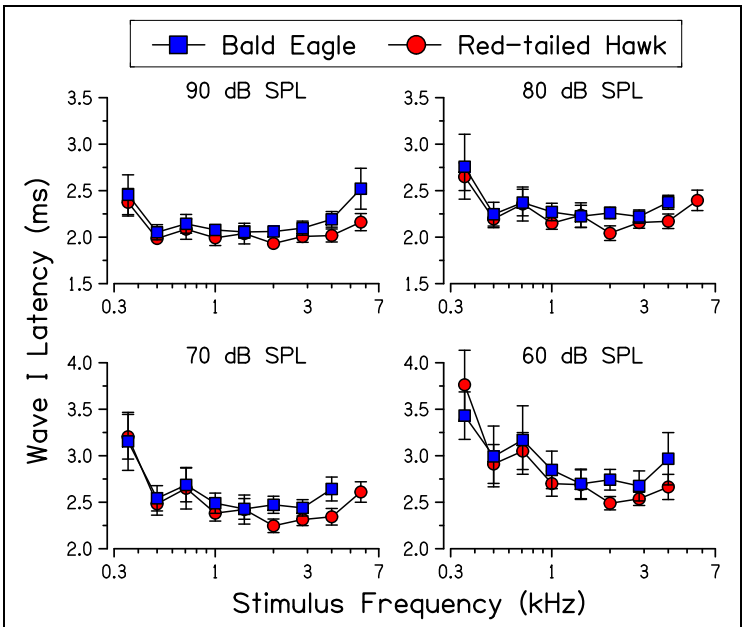

Figure 5. Average wave I latencies (±1 s.d.) plotted as a function of stimulus frequency for levels ranging from 90 dB SPL to 60 dB SPL are shown for bald eagles (blue squares) and red-tailed hawks (red circles). Note the ordinate scale spans 2 ms in all panels, but the minimum and maximum values differ across panels. Results of statistical tests are shown in Table S4 for these and other test frequencies

The relationship between wave I latency and stimulus frequency at

levels spanning much of the dynamic input-output range is considered in Fig. 5. One prominent finding is that curve shapes are dependent on stimulus level. Specifically, at 60 dB SPL and below, average latency values decreased along a somewhat exponential-appearing track as stimulus frequency increased, much like the latency-frequency profile commonly reported in most vertebrate species thus far studied. A similar but less evident inverse relationship was observed when stimulus level was 70 dB SPL. When levels were raised to 80, then 90 dB SPL, the exponential form of the curve gave way to a pattern in which latency values remained essentially constant throughout nearly the entire responsive frequency range, although latencies did increase slightly on the extreme margins in both species. A significant difference between groups (species) was observed at the highest level ($P<.01$) and at 30 to 50 dB SPL ($P<.05$), but not at intermediate (60-80 dB SPL) levels (Table S4). A main effect of frequency was observed at 30 dB SPL and higher ($P<.05$) and a significant group by frequency interaction was observed at levels above 40 dB SPL (Table S4).

Response Growth

Both species exhibited response growth patterns in which peak amplitudes increased with stimulus level, and amplitudes for red-tailed hawks were consistently higher than those recorded from bald eagles, particularly at moderate and high stimulus levels (Fig. 6). Growth curves for click stimuli and for tone pips from 0.35 kHz to 4.0 kHz were fit well by least-squares linear regressions fitted to log-transformed amplitude vs. level functions (Fig. 6), and level accounted for at least 93% of the variance for bald eagles and 88% for hawks (Table S2). Regressions

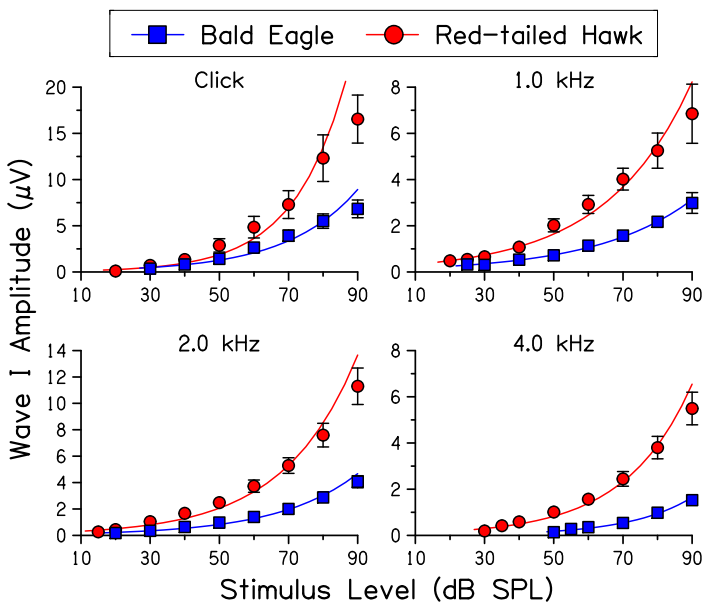

Figure 6. Average wave I amplitudes (±1 s.e.m.) are shown as a function of stimulus level for bald eagles (blue squares) and red-tailed hawks (red circles) in response to click stimuli and tone bursts of 1.0, 2.0 and 4.0 kHz. Solid lines represent least squares linear regressions to log-transformed amplitude values vs. level curves ($y=e^{(\beta x + \alpha)}$) for bald eagles (blue) and red-tailed hawks (red). Regression coefficients and results of statistical tests are provided in Tables S2 and S3, respectively, for these and other test frequencies

were statistically significant for all stimuli (P<.05). Growth of response as a function of level was significantly different between groups (species) for click stimuli (P<.01) and for all tonal stimuli (P<.05 to P<.001, Table S3), except for 0.35 kHz (P>.05). A significant main effect of level was observed for all stimuli (P<.001) and a group by level interaction was observed for click stimuli (P<.001) and for all tones from 0.35 kHz to 4.0 kHz (P<.001).

The exponential rate of amplitude growth with level, expressed as the level at which amplitudes increased by a factor of *e* (i.e., x = 1/β dB SPL) versus log-transformed stimulus frequency, is a concave function in which growth rates are slowest in the mid-frequency range and roll-off (i.e., increase in rate of growth) on the low- and high-frequency flanks of the relationship (Fig. 7a). A statistically significant main effect of frequency [F(8,106.3)=12.2, P<.001] and a frequency by group interaction were observed [F(8,106.3)=3.1, P=.003], but group (species) differences were not significant. The coefficient (1/β) for click stimuli was significantly lower for hawks than eagles [F(1,13)=12.4, P=.0037], indicating that growth rates are faster in hawks than eagles.

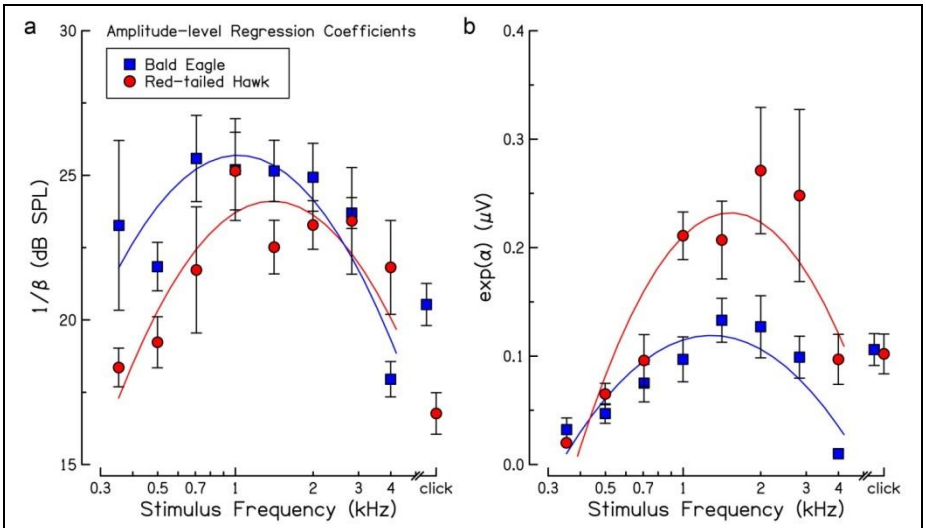

Figure 7. Regression coefficients (±1 s.e.m.) of log-transformed amplitude vs. level curves ($y=e^{(\beta x + \alpha)}$) are plotted as a function of stimulus frequency and for click stimuli for both bald eagles (blue squares) and red-tailed hawks (red circles). Solid curves represent polynomial fits to the data for bald eagles (blue) and red-tailed hawks (red). Coefficients of polynomial functions shown in (a) are $y=-18.215x^2+0.377x+25.692$ and $y=-19.223x^2+5.5005x+23.715$, for the bald eagle and red-tailed hawk, respectively; those in (b) are $y=-0.346x^2+0.0756x+0.1149$ and $y=-0.6379x^2+0.2349x+0.2105$ for the eagle and hawk, respectively, and x denotes log(kHz)

The relationship between exp(α) (i.e., the y-intercept) as a function of stimulus frequency is shown in Fig. 7b. The y-intercepts for wave I amplitude-level functions were higher for mid-frequency stimuli than lower or higher frequencies for both species. Main effects of group [F(1,14.0)=13.3, P=.0027] and frequency [F(8,106.2)=58.8, P<.001], as well as a frequency-group interaction

[F(8,106.3)=9.3, P<.001] on exp(α) were observed. A difference between species in response to click stimuli was not observed (P>.05).

As expected based upon regressions of amplitude-level curves, the largest wave I amplitudes were consistently observed at or near the best frequency, 2 kHz, regardless of level for both the red-tailed hawk and bald eagle (Fig. 8). Amplitude values rolled off at a somewhat faster rate above best frequency than below creating an asymmetric, concave-shaped relationship. Differences between groups (species) were statistically significant for all levels (Table S4), and there was a significant effect of frequency at all levels, as well as a group-frequency interaction at all levels.

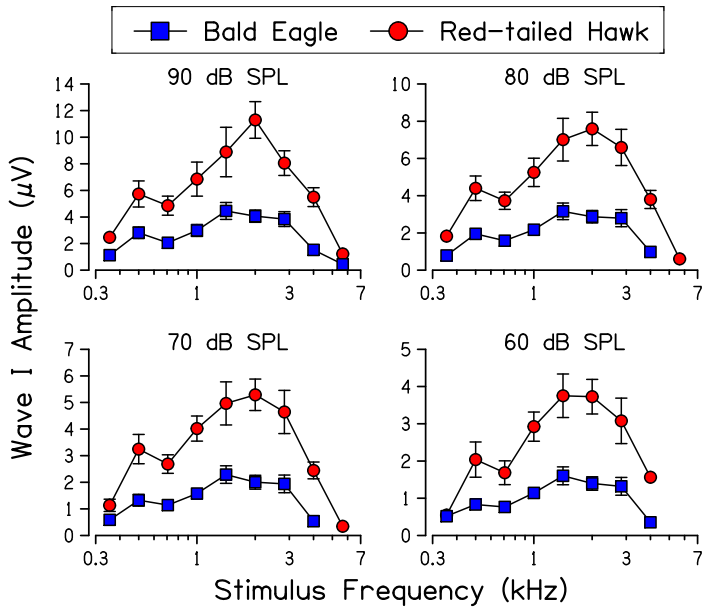

Figure 8. Average wave I amplitudes (±1 s.e.m.) plotted as a function of stimulus frequency for levels ranging from 90 dB SPL to 60 dB SPL are shown for bald eagles (blue squares) and red-tailed hawks (red circles). Note the change in the ordinate scale across panels. Results of statistical tests are shown in Table S4 for these and other test frequencies

Discussion

General Findings

Given the scarcity of diurnal raptor studies in which auditory function is addressed, mapping the working auditory space of two never before studied members of the Accipitridae family, and the first ever study of hearing in a species from the Buteoninae subfamily (i.e., red-tailed hawks) and from the Haliaeetinae subfamily of sea eagles (i.e., bald eagles), substantially advances our understanding of this largely unexplored taxonomy. In a general sense, the overall findings reported here were anticipated given expectations based on the large volume of work in which the ABR has been used as the primary measure of auditory function, a literature that dates back nearly fifty years (Jewett et al. 1970). Sensitivity curves derived from ABRs exhibit the same basic asymmetric convex shape as in other birds and mammals, response latencies decrease with increasing stimulus level and response amplitudes grow with stimulus level, both in an orderly manner.

However, one striking physiological difference distinguishing red-tailed hawks from bald eagles was evident in the response amplitude domain (cf. Figs. 6 and 8). Not only are response amplitudes larger in red-tailed hawks than in bald eagles generally, but response amplitudes grow at a faster pace with increases in level. Precisely which features of the red-tailed hawk anatomy and/or physiology underlie amplitude differences reported here is unknown, although the smaller conducting distance between response generators (brainstem nuclei/neuronal fiber tracts) and electrodes given head size differences (Stockard et al. 1978; Garcelon et al. 1985; Mlíkovský 1989; Trail 2017), combined with thinner skull dimensions (Don et al. 1993), may be contributing factors, as may be the orientation of dipole sources (Grandori 1986) and the number of auditory neurons (Hardy et al. 1982; Kujawa and Liberman 2009) synchronously discharging to the stimulus. Unfortunately, we know nothing about the inner ear morphologies in either bald eagles or red-tailed hawks, including the numbers of sensory cells and auditory neurons populating the auditory nerve and brainstem nuclei.

Given that the number of nerve terminals, and therefore, the number of activated nerve fibers, contribute prominently to ABR amplitudes (Kujawa and Liberman 2009; Sergeyenko et al. 2013; Yuan et al. 2014; Fernandez et al. 2015), it is reasonable to consider the possibility that the number of auditory nerve fibers is greater in red-tailed hawks than in bald eagles. If true, we can make a cogent argument that the difference has significant central processing implications. We would suggest, for example, that red-tailed hawks may be capable of processing temporal information more efficiently than bald eagles under these circumstances. The rationale underlying this suggestion follows naturally from an understanding that the magnitude of coherent input to timing circuits devoted to temporal processing in the central nervous system may also be enhanced, as would be performance on tasks requiring precise timing (Lopez-Poveda and Barrios 2013; Shaheen et al. 2015; Parthasarathy et al. 2019). This hypothesis is readily testable by measuring physiological responses to sinusoidally-amplitude modulated stimuli of varying modulation frequencies and the subsequent construction of temporal transfer functions (i.e., studying the phase-locking ability of auditory neurons). Temporal processing efficiencies of red-tailed hawks and bald eagles can then be assessed by comparing temporal transfer functions to arrive at a more informed understanding of the question, and we tentatively

predict that red-tailed hawks will be found to possess greater response timing attributes than bald eagles.

Response Waveforms

In contrast to the waveform morphology of diurnal raptor ABRs reported here (cf. Fig. 1), previous investigators have described the avian ABR waveform as consisting of two or three positive going voltage peaks and valleys occurring within the first few milliseconds following moderate to high level stimulation (Counter 1985; Brittan-Powell et al. 2002, 2005, 2010; Pytte et al. 2004; Caras et al. 2010; Gall et al. 2011; Lohr et al. 2013; Crowell et al. 2015; Kraemer et al. 2017; Beatini et al. 2018). Although more complex response waveforms consisting of as many as five positive going voltage peaks have been reported (Jones et al. 1987; Dmitrieva and Gottlieb 1992; Henry and Lucas 2008, 2010; Palanca-Castan et al. 2016), the most consistent pattern emerging from the literature is one in which early-occurring elements of the response dominate later-occurring elements, when such elements are observed. While it is difficult to compare ABR waveforms acquired from different investigators in different labs using, in some cases, slightly different methodologies and different experimental set-ups, in our view the ABR is sufficiently robust, particularly at higher stimulus levels, to permit qualitative comparisons of waveforms from species representing other avian orders. Consequently, we find the putative difference reported here not only of general scientific interest, but an indicator that the brainstem architecture of birds of prey may be distinctive among birds generally, a speculation that begs for the study, anatomical and physiological, of a larger species sample size.

In this regard it is nonetheless important to comment on two confounding factors that may influence the morphology of waveforms reported in the literature. The first is electrode recording position (Jewett and Williston 1971; Plantz et al. 1974; Stockard et al. 1978) and the second is the influence of anesthesia on response amplitudes and thresholds (Jewett and Romano 1972; Church and Shucard, 1987; van Looij et al. 2004). While the influence of variation in electrode position on auditory responses has not been studied in birds to our knowledge, the influence of isoflurane on ABR thresholds in barn owls has been reported (Thiele and Köppl 2018). Under isoflurane anesthesia, response thresholds are elevated and threshold variances are increased relative to values obtained using a ketamine/xylazine mixture, particularly in the mid- and high-frequency range. However, in contrast to this finding, Crowell et al. (2015) reported that

isoflurane anesthesia had no effect on ABR thresholds in lesser scaup (*Aythya affinis*) when compared to thresholds acquired using a ketamine/midazolam combination. The need to address this question in a more comprehensive manner is evident.

It is also notable that the amplitudes of later-occurring waves are often reduced to a greater extent than earlier occurring waves under deep levels of anesthesia (Jewett and Williston 1971). This finding is important because later occurring waves were prominent in the recordings that we obtained relative to findings from other investigators, suggesting that birds studied in this investigation were maintained at a lighter level of anesthesia than those in other investigations. This also suggests the possibility that more complex waveforms might be observed in birds more generally under lower levels of anesthesia, and indicating the need for comparative studies using standardized electrode montages and consideration of anesthetic level when addressing response waveform morphologies.

Size of the Basilar Papilla

As stated above, anatomical studies aimed at the characterization of peripheral and central elements of the auditory pathway are currently unavailable for either species studied here. However, based on the relationship between basilar papilla length and best frequency in species with known values for these variables, as shown by Gleich et al. (2005) and Gleich and Langemann (2011), it is theoretically possible to predict papillar length in species for which anatomical data are lacking if estimates of best frequency are available. As shown in Fig. 2, the best frequencies of red-tailed hawks and bald eagles are essentially the same, approximately 2.0 kHz. This equivalency would suggest that papillary lengths should also be essentially the same in each bird. Using the basilar papilla length versus best frequency relationship shown in Gleich et al. (2005), we would predict that papillary lengths should be approximately 4 mm in both species.

This value is consistent with expectations based on the correlation between the size of the basilar papilla and the body mass of a diverse group of avian species (Gleich et al. 2005). The body mass of adult bald eagles can be as much as six times that of the adult red-tailed hawk (1.0 versus 6.0 kg). Using the regression formula relating body mass to basilar papilla length from Gleich et al. (2005), the predicted length of the red-tailed hawk's basilar papilla is 3.5 mm and the bald eagle's predicted papillar length is 4.0 mm. Although body mass differences separating

red-tailed hawks from bald eagles are substantial in raw terms, the slope of the basilar papilla length-body mass regression line representative of avian species generally, as reported by Gleich and colleagues, is conspicuously shallow and the 0.5 mm difference suggested on the basis of this reasoning falls within the range of measurement error. In the end, the need for anatomical studies to address the issue on objective terms is clear.

How do Bald Eagles and Red-tailed Hawks Fit into the Overall Avian Auditory Landscape?

Mounting a framework to compare the hearing sensitivity of bald eagles and red-tailed hawks to other diurnal raptors classified in the order Accipitriformes is complicated by the scarcity of relevant studies within this order. Nonetheless, Klump et al. (1986) and Calford (1988) did report the hearing sensitivity of the Eurasian sparrowhawk (*Accipiter nisus*) and the Brown goshawk (*Accipiter fasciatus*), respectively. In addition, another diurnal raptor, the American kestrel (*Falco sparverius*), a member of the Falconiformes order, was studied by Trainer (1946). Thresholds reported from these three studies are plotted as symbols in Fig. 9a and third-order polynomial fits to each data set are shown in the upper inset. When combined with sensitivity findings from this investigation, this small data set can serve as the starting point of a potentially larger comparative diurnal raptor hearing project.

To that end, early efforts to arrive at a composite description of hearing among diurnal birds of prey suggest that the audiometric similarities of the group generally outweigh differences. This view is borne out in Fig. 9a, in which average threshold-frequency curves representing bald eagles and red-tailed hawks, adjusted according to the evoked potential to behavioral threshold-frequency correction curve shown in the lower inset of Fig. 9a (see Table S5), are plotted together with the mean threshold-frequency curve representing the Eurasian sparrowhawk, Brown goshawk and American kestrel (dotted curve); mean ±1 s.d. is indicated by the gray shaded area of the figure. By comparing these relationships, we arrive at the conclusion that bald eagles and red-tailed hawks essentially navigate the same basic working auditory space as other known and thus far characterized members of the group. Raptor species within the group shown here generally appear to operate in an auditory space characterized by a frequency band at least four octaves wide and centered on 2 kHz, with an upper frequency limit at 80 dB SPL between 8 and 10 kHz and a lower frequency limit likely extending below 0.2 kHz. This conclusion is of necessity tentative, given the small size of the sample, but it is a starting point.

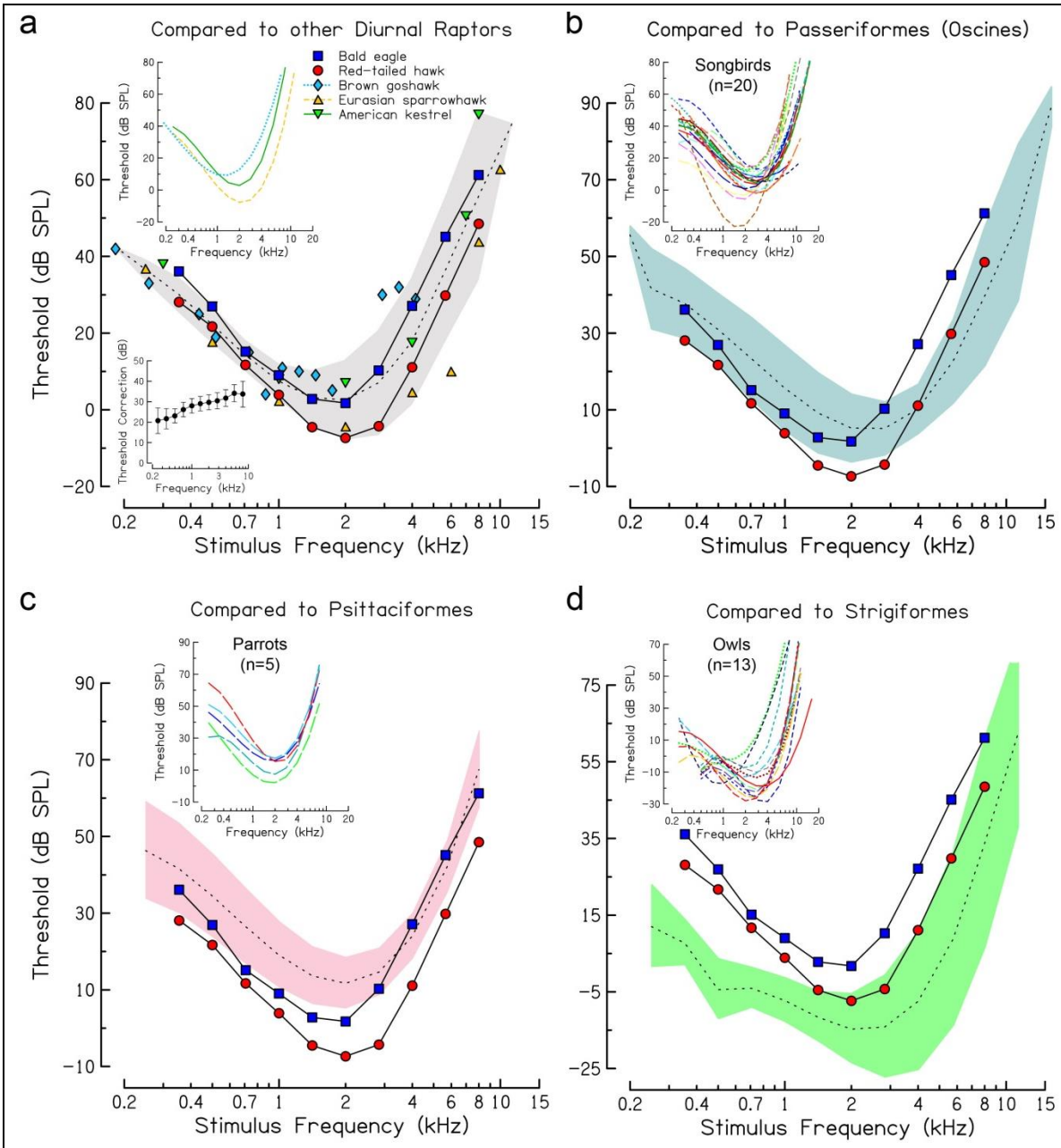

Figure 9. Comparisons of average ABR threshold-frequency curves representing bald eagles and red-tailed hawks to average threshold-frequency curves of other diurnal raptors (A), to Oscine Passeriformes (B), to members of the order Psittaciformes (C), and to members of the order Strigiformes (D). To allow direct comparison of ABR thresholds to behavioral thresholds and thresholds of single unit or multiunit clusters from auditory nuclei for other species, ABR thresholds were adjusted using the average values shown in the lower inset of panel A. Threshold correction values (±1 s.e.m.) plotted as a function of frequency were computed from avian species in which both behavioral data and evoked potential data were available. See Table S5 for a list of species contributing to the averages and references. In panel A, data from two other Accipitriformes (Brown goshawk and Eurasian sparrowhawk) and from a Falconiformes (American kestrel) are shown. Third-order polynomial fits to the data from these raptors are shown in the upper inset. Likewise, third-order polynomial fits to average audiograms from different species within each order are shown as insets in B-D. Dotted lines and shaded areas in each large panel represent the average thresholds ±1 s.d. across species. See Table S6 for species names, numbers of animals contributing to the averages, sexes, ages, and references. Note the ordinate scale spans 100 dB in all panels, but the absolute values differ across panels

As to the question of how the bald eagle and red-tailed hawk fit into the overall avian auditory landscape, a preliminary map can be drawn by comparing bald eagle and red-tailed hawk average threshold-frequency curves with the average threshold-frequency curves of species belonging to the Passeriformes and the Psittaciformes orders. The Passeriformes or perching birds make up over half of all extant avian species today, the vast majority of which are Oscines (Passeri) or songbirds (Fig. 9b), and the much smaller order of vocal learners known as Psittaciformes or parrots (Fig. 9c) contains approximately 400 species (Mayr 1946; Barker et al. 2004; Wright et al. 2008; Gill and Donsker 2019).

When compared with the average threshold-frequency curve representing Passeriformes (see Table S6), bald eagles and red-tailed hawks appear to share much, but not all, of their working auditory spaces with the average songbird (Fig. 9b). Although it is difficult to comment on its significance, bald eagles, and to a lesser extent, red-tailed hawks, appear to be slightly less sensitive to high frequency stimulation than the average songbird, while red-tailed hawks, and to a lesser extent bald eagles, appear to be slightly more sensitive to low frequency stimulation. These small differences in sensitivity curves are consistent with predictions based on body mass differences given the larger body mass of raptors generally. Likewise, the average bald eagle and red-tailed hawk sensitivity curves are similar to the average Psittaciformes' sensitivity curve (see Table S6), although the red-tailed hawk appears to be slightly more sensitive across the full responsive frequency band, and greater sensitivity of the bald eagle appears to be limited to mid- and low-frequencies (Fig. 9c).

We draw two global, tentative conclusions from this analysis. First, both bald eagles and red-tailed hawks share much of their working auditory spaces with Oscine Passeriformes, but are more sensitive to acoustic signals in the lower half of their audiometric frequency range and less sensitive than the average songbird above approximately 4 kHz. When compared with the average psittacine, bald eagles and red-tailed hawks navigate the same working auditory spaces, but are generally more sensitive than the average parrot. Second, although differences exist in the frequency ranges over which the three groups considered here are sensitive, all three overlap substantially, a finding that reflects the relatively narrow audiometric range of birds generally.

Although untested and as noted above, if thresholds were elevated under isoflurane anesthesia in bald eagles and/or red-tailed hawks as reported in barn owls (Thiele and Köppl

2018), behavioral thresholds would most likely be even lower than those estimated here, most notably in the mid- and high-frequency ranges.

Are bald eagles and red-tailed hawks auditory generalist or specialists?

One question of significant scientific interest that remains open with regard to diurnal raptors is how to classify Accipitriformes in relation to the specialist-generalist taxonomic divide. If members of the order share a common auditory sensitivity phenotype, which is an unsettled question, one straightforward approach is to compare sensitivity curves representing the four Accipitriformes' species considered here to members of Strigiformes, the owls, an avian order well known for specialized hearing. The barn owl (family Tytonidae, genus *Tyto*) is an excellent and frequently cited representative of this order, largely because the Western and American barn owls (*Tyto alba* and *T. furcata*[2], respectively) have been studied extensively and are recognized for their superior auditory sensitivity and expansive responsive frequency range (Konishi 1973; Dyson et al. 1998). Adaptations evolved in the barn owl in the form of inner ear specializations in the high frequency base of the basilar papilla that collectively enable the barn owl to detect, with remarkable sensitivity, an expanded high frequency range of acoustic events relative to other avian species (Smith et al. 1985; Fischer et al. 1988; Köppl et al. 1993; Fischer 1994; Köppl 1997). In addition to inner ear specializations, an external facial adaptation known as the facial disc, or ruff, collects sound energy and directs it inward toward the external ear aperture, thereby increasing sensitivity by as much as 20 dB (Payne 1971; Knudsen and Konishi 1979; Coles and Guppy 1988; von Campenhausen and Wagner, 2006). By comparing sensitivity and responsive frequency ranges of the barn owl and diurnal raptors (Fig. 9d), distinct differences lead us to conclude that bald eagles and red-tailed hawks, along with other diurnal raptors with known auditory phenotypes, operate as auditory generalists.

The essential rationale underlying this view is that, although similar in form, the mean threshold-frequency curve of owls is on average 20 dB lower than that of bald eagles and other representatives of the order. The generalist view taken here is reinforced by the observation that the two diurnal raptors studied here, and the other three diurnal raptor species included in this analysis, exhibit sound sensitivity profiles that are similar to species belonging to Passeriformes, a taxonomic group that is generally classified in the auditory generalists' category (i.e., they do not exhibit unusually keen hearing sensitivity in a particular frequency band).

The answer to the specialist-generalist question may be more nuanced when considering red-tailed hawks. The average sensitivity curve representing this species is similar to that of Strigiformes at and above best frequency, making red-tailed hawks look somewhat like an owl, a relatively insensitive owl, but an owl nonetheless in the hearing sensitivity realm. Findings associated with this comparative analysis strongly suggest that an unambiguous answer to the specialist-generalist question will require an extended investigation of diurnal raptor species.

Frequency-Dependence of Peak Amplitudes and Latencies

It can be argued in hypothetical terms that the asymmetric, concave shape of amplitude-frequency curves in both bald eagles and red-tailed hawks (cf. Fig. 8) is a reflection of the frequency-dependent differences in threshold reported as part of this investigation (cf. Fig. 2). Under isointensity stimulus conditions, it is reasonable to expect response amplitudes to decrease in proportion to the relative increase in threshold values observed on either side of best frequency as a consequence of the concomitant, proportional decrease in the number of activated auditory nerve fibers. This explanation can be tested by considering the shape of amplitude-frequency curves in sensation level terms, a condition in which activation energy is held constant in the frequency domain. Under these conditions, average response amplitudes remain essentially constant regardless of frequency or sensation level in bald eagles. While the same is true in red-tailed hawks at low sensation levels, average amplitude-frequency curves retain their concave shape at higher levels, albeit less prominently than in the isointensity space. It is notable that a similar profile has been reported for CAP N1-P1 responses in barn owls (Köppl and Gleich 2007). One straightforward explanation of this phenomenon is that when equal sensation level stimuli drive a roughly equal number of auditory nerve fibers at different stimulus frequencies, response amplitudes are equivalent across frequency, whereas the concave form observed in red-tailed hawks suggest that the distribution of auditory nerve fibers varies as a function of position along the basilar papilla in this species.

The pattern of response latencies in the stimulus frequency space of both species is more complicated than in the amplitude domain. At lower absolute levels, wave I latency vs. stimulus frequency curves exhibit the inverse character observed in many, if not most, vertebrates (cf. Fig. 5). A readily available explanation of this finding emerges from a general understanding of traveling wave mechanics. The basilar membranes of mammals are known to support traveling

waves, and the disturbance propagates from the higher frequency base toward the lower frequency apex consuming time as the wave advances. Likewise, the frequency-dependent influence of mammalian inner ear mechanical filter "build-up" times that are driven by outer hair cell somatic contractility contribute significantly to response timing as well. Such filter delays do not appear to influence response timing in avian species (He et al. 2003), although a more recent study suggests that short hair cells do exhibit electromechanical force generation (Beurg et al. 2013), along with active hair bundle motility (Manley and Köppl 1998). These findings suggest that the question is unsettled in birds and its resolution calls for additional investigation.

For now, however, the most commonly held view is that response latencies are determined by travel times associated with traveling waves on the basilar membrane. In that regard, von Békésy (1960) provided clear evidence that the apical portion of the chicken's (*Gallus gallus*) basilar papilla is tonotopically organized and tuned. Recently, Xia et al. (2016) reported the presence of traveling waves that propagate along the apex of the chicken basilar papilla and, like those findings, Gummer et al. (1987) demonstrated the presence of traveling waves and tonotopy in the basal half of the pigeon (*Columba livia*) basilar membrane. Based on these findings, we conclude that the inverse relationship between response latency and stimulus frequency at lower levels of stimulation observed in this study is at least partially associated with traveling wave delays along a tonotopically organized basilar membrane.

The question becomes more difficult to address when considering higher stimulus levels in which average wave I latencies remain essentially constant over a wide frequency range. One compelling explanation of this finding conflates the short, compressed stature of most avian basilar papilla (Tanaka and Smith 1978; von Düring et al. 1985; Manley et al. 1996) and the relatively steep compliance/stiffness gradient of the avian basilar membrane (von Békésy 1960). These observations, in combination with the characteristics of space-frequency maps available from a variety of investigations (Manley et al. 1987; Gleich 1989; Chen et al. 1994; Smolders et al. 1995; Köppl and Manley 1997), lead to the conclusion that the inner ear space constant of non-specialist birds is small relative to most mammals thus far studied. This, in turn, creates a scenario in which the separation of excitation patterns representing different stimulus frequencies within the audible range is constrained spatially. It can then be argued, on these grounds, that basilar membrane displacement patterns that are normally distinct in response to low-level

stimulation would become indistinct at high stimulation levels and produce responses that cannot be separated in the response latency domain. This explanation is supported by findings from Gleich (1994) who reported that ~80% of the basilar membrane in the European starling is activated at high stimulus levels (90 dB SPL) for frequencies from 0.5 to 2 kHz based on measurements of primary afferent excitation patterns, and the results are consistent with auditory nerve fiber latencies to click stimuli that overlap extensively across a wide range of characteristic frequencies in the pigeon (Sachs et al. 1974).

Is the Red-tailed Hawk a Suitable Auditory Surrogate for the Bald Eagle?

One objective of this investigation was to determine if auditory function in the red-tailed hawk is sufficiently like that observed in bald eagles to permit its usage as a surrogate species if and when necessary. Aside from interesting differences in response growth dynamics and overall sensitivity findings reviewed above, we conclude, with some reservation, that the red-tailed hawk is an appropriate surrogate for bald eagles given the similarity of response waveforms, threshold-frequency curves, and input-output characteristics. However, differences in thresholds and the high-frequency limits of hearing must-be-taken into account when extrapolating from one species to the other.

Development of acoustic deterrence protocols

A significant concern facing conservation biologists today has to do with the question, how many wind turbine related eagle fatalities constitute too many in the context of eagle ecology and conservation biology. Settling on an equitable, impartial answer to the question is difficult. Fatality resulting from encounters with a range of infrastructural elements associated with wind energy installations represents one of many natural and anthropogenic mortality risks with the potential to disrupt the stability of the currently stable U.S. eagle populations (USFWS 2016; Tack et al. 2017). The actual threat facing eagles in this regard is difficult to determine given the lack of reliable take-rate estimation protocols (Erickson et al. 2005; Smallwood 2013; Beston et al. 2015), the current and projected growth of wind energy facilities (AWEA 2018; USDOE 2015), and the voluntary nature of fatality reporting obligations (USFWS 2013). Nonetheless, because eagles are large predators with slow life histories and limited reproductive potential, a complex survival scenario exists in which local and largescale populations are vulnerable to disruption if mortality rates increase at any life stage, but especially in the case of breeding

adults (Tack et al. 2017). According to the USFWS (2016), the loss of 10% of U.S. populations, or 6% if more liberal parameters are considered, has the potential to promote a rapid decline in population abundance and threaten the stability of the currently stable population. Recognizing the complexity of survival scenarios facing eagles, and other slow life history raptors, the development of offset formulations and planning strategies are fundamentally important in the long-term effort to ward-off population crises in the future.

In addition, because the population of golden eagles in the U.S. is substantially lower than that of bald eagles (USFWS 2016), the prospect of destabilizing the golden eagle population is notably higher than it is for bald eagles, raising the protection stakes to a higher level of concern in this species. Regardless, the slow life histories of both species amplify the need for vigilance and the formulation of effective mitigation strategies is central to the success of mitigation initiatives. It is in that light that the development of acoustic alerting/deterring protocols engineered to discourage encroachment into active wind energy farms takes form.

In this regard, we suggest that findings reported here can serve as a starting point in this undertaking. One major conclusion of our study is that the bald eagle's working auditory space is constrained in the frequency domain by an upper cut-off frequency of approximately 6 kHz and a lower cut-off frequency that in all likelihood lies well below 0.35 kHz (cf. Fig. 2). Consequently, we recommend that signal designers use these data as a developmental guideline in efforts to design effective and efficient acoustic deterrent systems. Signal energy broadcast outside of this frequency band at moderate levels will not contribute to the efficacy of a deterrent, but will add an unnecessary fraction to the overall acoustic pollution budget. This is, in our view, an important consideration given contemporaneous concerns related to the production and transmission of noise broadcast by wind energy farms.

Although the red-tailed hawk population has increased significantly since the late 1960s (IUCN, 2019), members of this species share the air spaces occupied by bald eagles and other diurnal raptors (cf. Fig. 9), and therefore, would also benefit from the implementation of acoustic alerting protocols if the development of such technologies is successful.

Finally, although the development of acoustic deterrent technologies may prove successful as a risk mitigation strategy, the merit associated with the development of alternate deterrent technologies is unambiguous. However, aside from shutting turbines down when a risk is

detected (de Lucas et al. 2012), the identification of successful mitigation strategies has proven to be more difficult than perhaps expected. Strategies that include the installation of perch guards on lattice turbine towers, the implementation of rodent control programs that reduce the availability of prey at wind facilities, painting turbine blades with ultraviolet reflective paint, and painting stripes on turbine blades have been disappointingly ineffective in reducing bird mortality (Young et al. 2003; USGAO 2005, May et al. 2010; Hunt et al. 2015). Nonetheless, the identification of mitigation strategies that prevent or reduce raptor mortality at wind facilities will be a significant factor going forward in the realm of raptor conservation ecology.

Footnotes

[1]The number of diurnal raptor orders is in a state of flux as both the North American Classification Committee (NACC) and the South American Classification Committee (SACC) of the American Ornithological Society have categorized New World Vultures (Cathartidae) in a separate order, the Cathartiformes, whereas the International Ornithologists' Union currently classifies Cathartidae as a family within Accipitriformes (Chesser et al. 2019; Remsen et al. 2019; Gill and Donsker 2019). Also, Cariamiformes (seriemas), a basal order within Australaves, have been classified as diurnal raptors (Jarvis et al. 2014), although they are predominantly flightless predators.

[2]The International Ornithologists' Union recognizes *Tyto alba pratincola* as *Tyto furcata pratincola* (Gill and Donsker 2019).

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

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the Institutional Animal Care and Use Committee of the University of Minnesota where the studies were conducted."

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Supplementary Material

The following information is included in the Supplementary Material

- **Table S1**. Subject characteristics. Sex, age, and body mass of each bald eagle and red-tailed hawk included in the study.
- **Table S2**. Results of least-squares linear regression fits for wave I latency and amplitude vs. level data.
- **Table S3**. Results of statistical tests for wave I latency and amplitude vs. level data.
- **Table S4**. Results of statistical tests for wave I latency and amplitude vs. frequency data.
- **Table S5**. Species, general method, and source of threshold-frequency curves used to compute the threshold-frequency correction curve.
- **Table S6**. Species, sex, age, procedure, and source of threshold-frequency curves from other investigations.
- **Supplemental References**

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Supplemental Material

Auditory performance in bald eagles and red-tailed hawks: A comparative study of hearing in diurnal raptors

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Table S1. Subject characteristics

Bald Eagle			Red-tailed Hawk		
Sex	**Stage**	**Body Mass (kg)**	**Sex**	**Stage**	**Body Mass (kg)**
F	HY	4.30	F	HY	1.25
F	HY	4.42	F	SY	1.23
F	SY	4.25	M	HY	0.78
F	Ad	4.56	M	HY	1.00
F	Ad	4.77	M	HY	1.03
M	HY	3.41	M	HY	1.12
M	HY	3.73	M	SY	1.00
M	HY	3.77			
M	SY	3.83			
F		$\bar{X}$=4.46 kg	F		$\bar{X}$=1.24 kg
M		$\bar{X}$=3.69 kg	M		$\bar{X}$=0.99 kg

Abbreviations: F, female; M, male; HY, hatch year; SY, second year; Ad, adult;

Table S2. Results of least-squares linear regression fits for wave I latency and amplitude vs. level data

Natural Log-transformed Latency vs. Level

	Bald Eagle						Red-tailed Hawk					
Stimulus	**Slope**	**Y-int.**	**r^2**	**F-ratio**	**Signif.**		**Slope**	**Y-int.**	**r^2**	**F-ratio**	**Signif.**	
click	-0.0122	1.5126	0.9707	200.0	P<.001	***	-0.0125	1.5260	0.9736	259.2	P<.001	***
0.35 kHz	-0.0111	1.9067	0.9946	1106.9	P<.001	***	-0.0148	2.1901	0.9860	422.6	P<.001	***
0.5 kHz	-0.0134	1.9022	0.9921	627.0	P<.001	***	-0.0121	1.7751	0.9740	225.4	P<.001	***
0.7 kHz	-0.0135	1.9549	0.9913	681.8	P<.001	***	-0.0131	1.9031	0.9991	6916.5	P<.001	***
1.0 kHz	-0.0125	1.8154	0.9935	1071.3	P<.001	***	-0.0124	1.7631	0.9889	711.6	P<.001	***
1.4 kHz	-0.0123	1.7751	0.9850	526.8	P<.001	***	-0.0107	1.6543	0.9957	1842.3	P<.001	***
2.0 kHz	-0.0115	1.7243	0.9894	654.0	P<.001	***	-0.0115	1.6336	0.9857	553.0	P<.001	***
2.8 kHz	-0.0104	1.6422	0.9905	728.2	P<.001	***	-0.0108	1.6228	0.9816	426.6	P<.001	***
4.0 kHz	-0.0126	1.8826	0.9377	76.2	P<.001	***	-0.0111	1.6590	0.9847	452.7	P<.001	***
5.7 kHz							-0.0094	1.6232	0.9961	774.2	P<.01	**

Natural Log-transformed Amplitude vs. Level

	Bald Eagle						Red-tailed Hawk					
Stimulus	**Slope**	**Y-int.**	**r^2**	**F-ratio**	**Signif.**		**Slope**	**Y-int.**	**r^2**	**F-ratio**	**Signif.**	
click	0.0486	-2.1842	0.9576	136.6	P<.001	***	0.0657	-2.6527	0.9091	71.0	P<.001	***
0.35 kHz	0.0451	-3.7983	0.8802	45.1	P<.01	**	0.0486	-3.3701	0.9718	207.5	P<.001	***
0.5 kHz	0.0448	-2.9182	0.9901	503.2	P<.001	***	0.0547	-2.8652	0.9551	128.8	P<.001	***
0.7 kHz	0.0421	-2.8950	0.9311	82.1	P<.001	***	0.0459	-2.3657	0.9730	217.0	P<.001	***
1.0 kHz	0.0361	-2.1086	0.9912	789.1	P<.001	***	0.0403	-1.5160	0.9809	412.4	P<.001	***
1.4 kHz	0.0452	-2.3861	0.9345	115.1	P<.001	***	0.0450	-1.6036	0.9631	210.0	P<.001	***
2.0 kHz	0.0434	-2.3615	0.9776	306.6	P<.001	***	0.0473	-1.6434	0.9639	214.5	P<.001	***
2.8 kHz	0.0401	-2.1753	0.9938	1119.9	P<.001	***	0.0410	-1.4158	0.8773	58.2	P<.001	***
4.0 kHz	0.0558	-4.5243	0.9609	123.9	P<.001	***	0.0518	-2.7791	0.9603	170.3	P<.001	***
5.7 kHz							0.0610	-5.3051	0.9694	95.9	P<.05	*

Model: $\ln(y) = \alpha + \beta x$ where the y-intercept is represented by α and slope is represented by β (or $y = e^{(\beta x + \alpha)}$)
Note: r^2 represents adjusted r^2

Table S3. Results of statistical tests for wave I latency and amplitude vs. level data

Latency vs. Level

	Group (species)				Level				Group:Level Interaction			
Stimulus	**df**	**F-ratio**	**Signif.**		**df**	**F-ratio**	**Signif.**		**df**	**F-ratio**	**Signif.**	
click	1/13.0	0.60	P=.452	NS	1/70.7	349.1	P<.001	***	6/70.4	0.412	P=.869	NS
0.35 kHz	1/16.6	0.73	P=.404	NS	6/36.0	165.0	P<.001	***	6/36.0	2.045	P=.085	NS
0.5 kHz	1/13.8	1.37	P=.261	NS	6/63.2	326.0	P<.001	***	5/62.9	0.449	P=.813	NS
0.7 kHz	1/15.0	0.50	P=.490	NS	6/63.0	254.6	P<.001	***	6/63.0	0.303	P=.933	NS
1.0 kHz	1/15.6	3.44	P=.083	NS	8/77.5	488.5	P<.001	***	7/77.4	0.569	P=.779	NS
1.4 kHz	1/14.0	1.77	P=.204	NS	8/87.3	674.9	P<.001	***	8/87.3	5.359	P<.001	***
2.0 kHz	1/15.4	45.79	P<.001	***	8/90.1	538.4	P<.001	***	7/89.7	3.773	P<.01	**
2.8 kHz	1/17.7	2.56	P=.093	NS	8/81.9	184.8	P<.001	***	7/81.7	0.794	P=.594	NS
4.0 kHz	1/16.4	33.78	P<.001	***	8/57.0	167.1	P<.001	***	4/56.5	6.001	P<.001	***
5.7 kHz	1/25.3	19.99	P<.001	***	4/14.5	9.6	P<.001	***				

Amplitude vs. Level

	Group (species)				Level				Group:Level Interaction			
Stimulus	**df**	**F-ratio**	**Signif.**		**df**	**F-ratio**	**Signif.**		**df**	**F-ratio**	**Signif.**	
click	1/13.1	9.54	P=.009	**	7/70.3	91.5	P<.001	***	6/70.2	15.399	P<.001	***
0.35 kHz	1/18.3	1.84	P=.191	NS	6/36.7	34.1	P<.001	***	6/36.7	6.160	P<.001	***
0.5 kHz	1/14.1	8.76	P<.05	*	6/63.4	60.1	P<.001	***	5/63.2	8.623	P<.001	***
0.7 kHz	1/14.9	7.30	P=.017	*	6/63.2	71.9	P<.001	***	6/63.2	14.198	P<.001	***
1.0 kHz	1/15.8	10.24	P=.006	**	8/77.7	47.0	P<.001	***	7/77.6	7.528	P<.001	***
1.4 kHz	1/16.1	6.48	P=.022	*	8/87.7	42.9	P<.001	***	8/87.7	4.934	P<.001	***
2.0 kHz	1/14.4	24.85	P<.001	***	8/89.3	104.6	P<.001	***	7/89.2	25.503	P<.001	***
2.8 kHz	1/15.2	8.65	P<.01	**	8/81.3	89.1	P<.001	***	7/81.2	10.549	P<.001	***
4.0 kHz	1/16.2	49.58	P<.001	***	8/56.8	44.6	P<.001	***	4/56.4	13.568	P<.001	***
5.7 kHz	1/21.4	32.25	P<.001	***	4/16.7	18.1	P<.001	***				

Abbreviation: NS, not significant

Table S4. Results of statistical tests for wave I latency and amplitude vs. frequency data

Latency vs. Frequency

	Group				Frequency				Group:Frequency Interaction			
Level (dB SPL)	df	F-ratio	Signif.		df	F-ratio	Signif.		df	F-ratio	Signif.	
90	1/14.0	13.343	P=.003	**	8/113.2	39.058	P<.001	***	8/113.2	5.983	P<.001	***
80	1/14.2	4.551	P=.051	NS	8/103.9	35.594	P<.001	***	7/103.9	2.132	P=.046	*
70	1/14.1	4.081	P=.063	NS	8/100.1	66.502	P<.001	***	7/100.0	3.518	P=.002	**
60	1/13.9	1.391	P=.258	NS	7/89.1	49.203	P<.001	***	7/89.1	2.989	P=.007	**
50	1/89.0	10.120	P=.002	**	7/89.0	19.789	P<.001	***	7/89.0	3.237	P=.004	**
40	1/72.0	13.295	P<.001	***	6/69.7	16.470	P<.001	***	5/68.7	0.824	P=.537	NS
30	1/41.3	6.558	P=.014	*	5/39.4	2.631	P=.038	*	3/39.5	2.673	P=.060	NS

Amplitude vs. Frequency

	Group				Frequency				Group:Frequency Interaction			
Level (dB SPL)	df	F-ratio	Signif.		df	F-ratio	Signif.		df	F-ratio	Signif.	
90	1/14.0	17.200	P<.001	***	8/110.0	48.740	P<.001	***	8/110.0	8.625	P<.001	***
80	1/14.1	23.574	P<.001	***	8/104.1	68.147	P<.001	***	7/104.1	8.352	P<.001	***
70	1/14.1	21.371	P<.001	***	8/100.1	64.014	P<.001	***	7/100.1	6.931	P<.001	***
60	1/14.1	15.058	P=.002	**	7/89.1	44.476	P<.001	***	7/89.1	8.191	P<.001	***
50	1/15.0	11.726	P=.004	**	7/75.4	32.364	P<.001	***	7/75.3	6.577	P<.001	***
40	1/14.6	11.202	P=.005	**	6/61.7	20.420	P<.001	***	5/61.8	5.298	P<.001	***
30	1/14.8	4.608	P=.049	*	5/29.3	9.847	P<.001	***	3/29.2	5.387	P=.004	**

Abbreviation: NS, not significant

Table S5. Species, general method, and source of threshold-frequency curves used to compute the threshold-frequency correction curve.

Order	Common Name	Scientific Name	Method	Anesthetic	Reference
Anseriformes	Mallard Duck	*Anas platyrhynchos*	Behavior		Trainer (1946)[a]
			Behavior[b]		Hill (2017)
			ABR[c]	Awake	Dmitrieva and Gottlieb (1992)
	Lesser Scaup	*Aythya affinis*	Behavior		Crowell et al. (2016)
			ABR	Isoflurane	Crowell et al. (2016)
Columbiformes	Pigeon	*Columba livia*	Behavior[d]		Trainer (1946)[a]
			Behavior		Heise (1953)
			Behavior		Stebbins (1970)
			Behavior		Harrison and Furumoto (1971)
			Behavior		Hienz et al. (1977)
			Behavior[d]		Goerdel-Leich and Schwartzkopff (1984)
			Behavior[b]		Heffner et al. (2013)
			CAP	Pentobarbital	Gummer et al. (1987)
			CAP	Ket/xylazine	Reng et al. (2001)
Galliformes	Chicken	*Gallus gallus*	Behavior		Gray and Rubel (1985)
			Behavior		Saunders and Salvi (1993)
			Behavior[b]		Hill et al. (2014)
			CAP	Ket/chloropent	Rebillard and Rubel (1981)
			ABR	Ket/equithesin	Tucci and Rubel (1990)
			CAP	Ket/pentobarbital	Patuzzi and Bull (1991)
			CAP	Ket/xylazine initially, then pentobarbital	Salvi et al. (1992)
			CAP	Ket/pentobarbital	Chen et al. (1993)
Passeriformes	Brown-headed Cowbird[e]	*Molothrus ater*	Behavior		Hienz et al. (1977)
	Red-winged Blackbird[e]	*Agelaius phoeniceus*	Behavior		Hienz et al. (1977)
			ABR	Ket/midazolam	Gall et al. (2011)
	Common Canary[f]	*Serinus canaria*	Behavior		Okanoya and Dooling (1985)

Order	Common Name	Scientific Name	Method	Anesthetic	Reference
	Common Canary[f]	*Serinus canaria*	Behavior		Okanoya and Dooling (1987)
			ABR	Ket/diazepam	Brittan-Powell et al. (2010)
			ABR[g]	Ket/diazepam	Noirot et al. (2011)
Psittaciformes	Budgerigar	*Melopsittacus undulatus*	Behavior		Saunders and Dooling (1974)
			Behavior		Dooling and Saunders (1975)
			Behavior		Saunders et al. (1979)
			Behavior		Saunders and Pallone (1980)
			Behavior		Okanoya and Dooling (1987)
			Behavior		Hashino et al. (1988)
			Behavior		Hashino and Sokabe (1989)
			Behavior		Heffner et al. (2016)
			ABR	Ket/diazepam	Brittan-Powell et al. (2002)
Suliformes	Great Cormorant	*Phalacrocorax carbo sinensis*	Behavior		Maxwell et al. (2016)
			ABR	? "lightly anesthetized"	Maxwell et al. (2016)

Abbreviations: ABR-auditory brainstem response; CAP-compound action potential of the eighth nerve; ket-ketamine

[a]Source of Trainer (1946) data was Fay (1988)

[b]Threshold values included in curve fitting were limited to frequencies ≥125 Hz to emphasize frequency region of interest

[c]ABRs were recorded intracranially from 2-day old birds

[d]Median threshold values were reported

[e]Threshold values for brown-headed cowbirds and red-winged blackbirds reported by Gall et al. (2011) were combined and averaged but separated by sex. Therefore, we averaged values from Gall et al. (2011) across sex to permit comparison with behavioral thresholds reported by Hienz et al. (1977) for each species. We then averaged threshold values reported by Hienz et al. (1977) for the purpose of comparison.

[f]Includes German Roller and American Singer strains; Belgian Waterslagers were excluded due to a sex-linked genetic mutation leading to hearing impairment (Wright et al., 2004)

[g]Given the limited frequency range of data in Noirot et al. (2011), we combined it with the data from Brittan-Powell et al. (2010) prior to fitting the frequency-threshold curve

Table S6. Species, sex, age, procedure, and source of threshold-frequency curves from other investigations.

Order / Common Name	Scientific Name	Number F/M/U[a]	Age[b]	Procedure	Reference
Accipitriformes					
Brown Goshawk	*Accipiter fasciatus*	0/0/1		nMLD single unit and multiunit thresholds[c]	Calford (1988)
Eurasian Sparrowhawk	*Accipiter nisus*	1/1/0	4-11 m	Operant conditioning for food reward	Klump et al. (1986)
Falconiformes					
American Kestrel	*Falco sparverius*	0/0/1		Instrumental shock avoidance	Trainer (1946)[d]
Passeriformes					
American Robin	*Turdus migratorius*	0/0/1[e]		CN single unit thresholds[f]	Konishi (1970)
Blue Jay	*Cyanocitta cristata*	0/0/2	1 y	Operant conditioning for food reward	Cohen et al. (1978)
Brown-headed Cowbird	*Molothrus ater*	3/3/0		Operant conditioning for food reward/environment darkened for false alarms	Hienz et al. (1977)
Bullfinch	*Pyrrhula pyrrhula*	0/0/4		Operant conditioning for food reward	Schwartzkopff (1948)
Chipping Sparrow	*Spizella passerina*	0/0/1[e]		CN single unit thresholds[f]	Konishi (1970)
Common Canary[g]	*Serinus canaria*	2/2/0	adult	Operant conditioning for food reward/environment darkened for false alarms	Okanoya and Dooling (1985)
		0/1/0		Operant conditioning for food reward	Okanoya and Dooling (1987)
Common Crow	*Corvus brachyrhynchos*	0/0/1		Instrumental shock avoidance	Trainer (1946)[d]
European Starling	*Sturnus vulgaris*	0/0/6[h,i]		Instrumental shock avoidance	Trainer (1946)[d]
		0/0/7[h]		Heart rate conditioning with shock avoidance	Kuhn et al. (1982)
		0/1/0		Operant conditioning for food reward	Dooling et al. (1986)
		0/0/4		Operant conditioning for food reward/environment darkened for false alarms	Marean et al. (1993)

Order Common Name	Scientific Name	Number F/M/U[a]	Age[b]	Procedure	Reference
European Starling	*Sturnus vulgaris*	3/3/0	6-12 m	Operant conditioning for food reward/environment darkened for false alarms	Langemann et al. (1999)
Field Sparrow	*Spizella pusilla*	0/2/0		Instrumental shock avoidance	Dooling et al. (1979)
Great Tit	*Parus major*	4/3/0[h,i]	within 1st y	Operant conditioning for food reward	Langemann et al. (1998)
Hooded Crow	*Corvus cornix*	0/0/2-4[h]		Operant conditioning for food reward/environment darkened for false alarms/ misses	Jensen and Klokker (2006)
House Finch	*Haemorhous mexicanus*[j]	2/2/0	1-5 y	Instrumental shock avoidance	Dooling et al. (1978)
House Sparrow	*Passer domesticus*	0/0/1[e]		CN single unit thresholds[f]	Konishi (1970)
Red-billed Firefinch	*Lagonosticta senegala*	2/2/0	2-5 y	Operant conditioning for food reward/environment darkened for false alarms	Lohr et al. (2004)
Red-winged Blackbird	*Agelaius phoeniceus*	3/7/0		Operant conditioning for food reward/environment darkened for false alarms	Hienz et al. (1977)
Slate-colored Junco	*Junca hyemalis*	0/0/1[e]		CN single unit thresholds[f]	Konishi (1970)
Song Sparrow	*Melospiza melodia*	0/1/0		Operant conditioning for food reward	Okanoya and Dooling (1987)
		1/2/0	1-6 y	Operant conditioning for food reward/environment darkened for false alarms	Okanoya and Dooling (1988)
Swamp Sparrow	*Melospiza georgiana*	0/1/0		Operant conditioning for food reward	Okanoya and Dooling (1987)
		0/2/0	1-6 y	Operant conditioning for food reward/environment darkened for false alarms	Okanoya and Dooling (1988)
Western Meadowlark	*Sturnella neglecta*	0/0/1[e]		CN single unit thresholds[f]	Konishi (1970)
Zebra Finch	*Taeniopygia guttata*	0/1/0		Operant conditioning for food reward	Okanoya and Dooling (1987)
		3/2/0		Operant conditioning for food reward/environment darkened for false alarms	Hashino and Okanoya (1989)

Order Common Name	Scientific Name	Number F/M/U[a]	Age[b]	Procedure	Reference
Psittaciformes					
Bourke's Parrot	*Neopsephotus bourkii*[k]				Dooling (2002)[l]
Budgerigar	*Melopsittacus undulatus*	0/0/4	16 w	Instrumental shock avoidance	Saunders and Dooling (1974)
		2/2/0	6-16 w	Instrumental shock avoidance	Dooling and Saunders (1975)
		0/0/6	24-40 w	Instrumental shock avoidance	Saunders et al. (1979)
		0/0/4	6-12 m	Instrumental shock avoidance	Saunders and Pallone (1980)
		0/2/0		Operant conditioning for food reward	Okanoya and Dooling (1987)
		0/2/0	~ 1 y	Instrumental shock avoidance	Hashino et al. (1988)
		0/7/0		Instrumental shock avoidance	Hashino and Sokabe (1989)
		2/1/0	~6 m	Instrumental shock avoidance	Heffner et al. (2016)
Cockatiel	*Nymphicus hollandicus*	0/1/0		Operant conditioning for food reward	Okanoya and Dooling (1987)
Kea Parrot	*Nestor notabilis*	0/3/0	1 juvenile, 1 subadult, 1 adult	Operant conditioning for food reward	Schwing et al. (2016)
Orange-fronted Parrot	*Eupsittula canicularis*	0/0/5	5-20 m	Operant conditioning for food reward	Wright et al. (2003)
Strigiformes					
African Wood Owl	*Strix woodfordii*	0/0/2	1 y, 2 y	Operant conditioning	Nieboer and Van der Paardt (1977)
Barn Owl	*Tyto alba*[m]	0/0/1[e]		Operant conditioning for food reward	Konishi (1973)
	Tyto alba guttata	0/0/3[i]	12-24 m	Operant conditioning for food reward	Dyson et al. (1998)
	Tyto alba	0/0/4	14-25 m	Operant conditioning for food reward	Krumm et al. (2017)
Brown Fish Owl	*Ketupa zeylonensis*	0/0/1	Adult	Operant conditioning	Van Dijk (1973)
Eagle Owl	*Bubo bubo*	0/0/1	1.5 y	Operant conditioning	Van Dijk (1973)

Order Common Name	Scientific Name	Number F/M/U[a]	Age[b]	Procedure	Reference
Forest Eagle owl	*Bubo nipalensis*	0/0/1	1.5 y	Operant conditioning	Van Dijk (1973)
Great Horned Owl	*Bubo virginianus*	0/0/1		Instrumental shock avoidance	Trainer (1946)[d]
Long-eared Owl	*Asio otus*	0/0/6	0.5-≥1 y	Operant conditioning	Van Dijk (1973)
Mottled Owl	*Strix virgata*	0/0/1	>5.5 y	Operant conditioning	Van Dijk (1973)
Scops Owl	*Otus scops*	0/0/1	3.5 y	Operant conditioning	Van Dijk (1973)
Snowy Owl[n]	*Bubo scandiacus*	0/0/2	>6.5 y	Operant conditioning	Van Dijk (1973)
Spotted Wood Owl	*Strix seloputo*	0/0/1	1 y	Operant conditioning	Van Dijk (1973)
Tawny Owl	*Strix aluco*	0/0/6	0.5-5.5 y	Operant conditioning	Van Dijk (1973)
White-faced Scops Owl[o]	*Otus leucotis*	0/0/1	1.5 y	Operant conditioning	Van Dijk (1973)

[a]Sex includes the number of female, male and unknown (F/M/U designations) individuals studied

[b]Age includes day, week, month and year (d, w, m, y designations) when known

[c]nMLD, or the dorsolateral mesencephalic nucleus, both central and lateral divisions were studied, but most cells were from central division (homologous with the mammalian inferior colliculus); subjects were anesthetized with ketamine and xylazine

[d]Source of Trainer (1946) data was Fay (1988)

[e]More than one bird was tested but data were shown for 1 bird only

[f]CN, or the cochlear nuclei (cells from both magnocellularis and angularis nuclei were studied); subjects were anesthetized with urethane

[g]Includes German Roller and American Singer strains; Belgian Waterslagers were excluded due to a sex-linked genetic mutation related to hearing impairment (Wright et al., 2004)

[h]Not all birds were tested at all frequencies

[i]Median threshold values were reported

[j]The house finch, *Haemorhous mexicanus*, is formerly known as *Carpodacus mexicanus*

[k]Bourke's Parrot, *Neopsephotus bourkii*, is formerly known as *Neophema bourkii*

[l]Unpublished data from R. Dooling laboratory; we used fitted curve provided in Dooling (2002)

[m]Although the species was identified as *Tyto alba*, the American barn owl was likely the subject of study, and the International Ornithologists' Union identifies this species as *Tyto furcata pratincola*, a species (and subspecies) considered distinct from the Western barn owl (*Tyto alba*)

[n]The International Ornithologists' Union classifies the snowy owl, *Nyctea scandiaca,* as *Bubo scandiacus*

[o]The Northern white-faced owl (*Ptilopsis leucotis*) and the Southern white-faced owl (*P. granti*) were formerly combined into a single species, known as the white-faced scops owl (*Otus leucotis*)

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