

Audiogram of the kea parrot, *Nestor notabilis*

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Vocal communication requires the sender to produce a sound, which transmits through the environment and is perceived by the receiver. Perception is dependent on the quality of the received signal and the receiver's frequency and amplitude sensitivity; hearing sensitivity of animals can be tested using behavioural detection tasks, showing the physical limitations of sound perception. Kea parrots (*Nestor notabilis*) were tested for their ability to hear sounds that varied in terms of both frequency and amplitude by means of a simple auditory detection task. Audiograms for three kea were similar, with the region of highest sensitivity (1–5 kHz) corresponding to the frequency of the highest amplitude in kea calls. Compared with other parrots and other bird taxa, the overall shape of the kea audiogram follows a similar pattern. However, two potentially interesting differences to the audiograms of other birds were found: an increase in sensitivity at approximately 12 kHz and a decreased sensitivity to frequencies below 1 kHz. © 2016 Acoustical Society of America.

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I. INTRODUCTION

The hearing sensitivity of species as diverse as Mongolian gerbils (*Meriones unguiculatus*) (Hamann *et al.*, 2002), scarab beetles (*Euethola humilis*) (Forrest *et al.*, 1997), loggerhead turtles (*Caretta caretta*) (Martin *et al.*, 2012), and killer whales (*Orcinus orca*) (Szymanski *et al.*, 1999) have been tested using behavioural tasks. Nonetheless, most studies of bioacoustics have focused on the avian clade (Van Dijk, 1972; Dooling *et al.*, 2000; Wright *et al.*, 2003). Audiograms of birds show considerable congruence in hearing sensitivity, with peaks falling between 2 and 4 kHz and a relatively gradual decrease in sensitivity below and above this range (Van Dijk, 1972; Dooling *et al.*, 2000; Okanoya and Dooling, 1987, 1988; Wright *et al.*, 2003). Nonetheless, most behavioural audiometry studies have not investigated the full hearing range of birds by limiting the stimuli to between 250 Hz and 10 kHz (Van Dijk, 1972; Dooling *et al.*, 2000; Farabaugh *et al.*, 1998; Wright *et al.*, 2003). Although the upper hearing limit for some species has been reached (Dooling *et al.*, 2000), more recent studies have started to look for auditory thresholds below 250 Hz (Dooling *et al.*, 2002; Heffner *et al.*, 2013; Hill *et al.*, 2014). Research on the

bioacoustics of Psittaciformes (parrots) is mostly restricted to the budgerigar (*Melopsittacus undulatus*) (Dooling, 1973; Farabaugh *et al.*, 1998; Okanoya and Dooling, 1987), with the cockatiel (*Nymphicus hollandicus*) (Okanoya and Dooling, 1987) and the orange-fronted conure (*Aratinga canicularis*) (Wright *et al.*, 2003) being the only other species for which audiograms have been produced. The findings for these three parrots mirror those of other birds in terms of the frequency ranges of highest auditory sensitivity corresponding to the region of highest power distribution in their calls (Dooling *et al.*, 2000; Lohr *et al.*, 2004; Okanoya and Dooling, 1988).

The kea (*Nestor notabilis*) is a large parrot endemic to the Southern Alps of New Zealand, an alpine habitat above the tree-line characterised by relatively consistent low frequency ambient noise from wind. Kea belong to the oldest family of parrots, having diverged from other parrots 50–65 × 10⁶ years ago (Wright *et al.*, 2008). Research into the vocal repertoire of kea (Schwing *et al.*, 2012) has shown them to produce calls with fundamentals in the 500–2000 Hz range, but with harmonics that extend far above the reported hearing range for birds (>10 kHz). Although high frequencies are susceptible to environmental attenuation (Marten and Marler, 1977), over short distances they may still be readily audible to a bird with the ability to perceive them.

The aim of this investigation was to generate an understanding of the physical limitations on behavioural aspects of kea vocal communication. We generated audiograms for kea using a behavioural detection task to test the following

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assumptions: (1) kea cannot hear the full frequency range covered by their calls, and (2) hearing range and sensitivity correspond to those found in conspecific calls. Finally, the characteristics of kea audiograms were compared to audiograms from other parrots, as well as from a range of other birds.

II. METHODS

A. Subjects

Three kea were tested, all of whom were part of the Messerli Research Institute's kea lab (Interdisciplinary Institute of the Messerli Foundation, the University of Veterinary Medicine Vienna, the Medical University Vienna, and the University of Vienna, Austria). The birds were a parent-raised juvenile male (Roku), a hand-raised sub-adult male (Anu), and a parent-raised adult male (Frowin). They were housed in a 520 m² aviary with the rest of the kea group, fed a mixed diet three times a day, and had access to water *ad libitum*.

B. Testing facility and playback

The experimental area consisted of testing room (3 m wide × 1.5 m deep × 2.2 m high), with a hatch to the outside compartment through which the test bird was required to walk (Fig. 1) to access a wire mesh tunnel (80 cm wide × 60 cm deep × 60 cm high). Two speakers [114 dB sound pressure level (SPL) max, 118 W root-mean-square, frequency response 50–20 000 Hz; LD Systems, Houston, TX] were mounted at ground level placed on either side of the tunnel (60 cm from the mesh). Each speaker had a protective cover that ensured a minimum distance of 10 cm from the speaker membrane to the animal. An inverted cup (diameter 10 cm) was placed in front of each speaker (10/20/40 cm from protective cover/speaker membrane/tunnel) to hide the presence of the reward.

Playback tones of 1000 ms duration were generated using an RZ6 Multi-I/O processor unit [Tucker-Davis Technologies (TDT), Alachua, FL] at a sampling rate of 200 kHz. A software-controlled cosine gate (RPvdsEx V. 74, TDT) created rise and fall times of 25 ms for each tone. Tones were separated from one another by 4000 ms intervals

of silence, and played continuously until the subject chose a speaker.¹ When a correct behavioural response was elicited, the playback tone was later recorded at the exact head position of the animal using a 0.5 in. microphone (type 4190, frequency response 3–20 000 Hz ± 0.2 dB, Brüel & Kjær, Nærum, Denmark) connected to a portable digital audio recorder (model 722, Sound Devices, Reedsburg, WI, sampling rate of 96 kHz with 24-bit precision). Peak intensity of tones (measured as dB pe-SPL) was calculated relative to a Brüel and Kjær sound calibrator (type 4231; producing 92 dB SPL at 1 kHz).

C. Training phase

Pre-experimental training began with the introduction of the birds into the room that would subsequently contain the experimental setup. Employing a two-cup-one-baited setup (subjects had to choose between *two cups with one baited with a peanut food reward*) to entice the birds to explore further into the room, subjects were gradually habituated to the experiment. Initially, cups were placed immediately inside the room (10 cm from hatch) and then were progressively moved further into the room until they were adjacent to the final position of the speakers (60 cm from hatch wall, 1 m from midline of the hatch). Birds were sequentially habituated to the presence of the tunnel, protective speaker box, and finally the speakers.

In synchrony with the habituation of the subjects to the experimental setup, birds were acclimated to hearing a sound from a speaker. This was achieved by playing the training sound (2 kHz pure tone at 65 dB SPL at 10 cm for 1 s), first from outside their aviary at feeding time (10×), and later also from within the aviary (2×). Within the aviary the birds were also trained to approach the speaker by presenting them with food rewards placed in front of them.

Using a two-choice setup similar to the pre-experimental training, birds were then subjected to the training sound, playing randomly from one of the two speakers, in the experimental compartment. Birds were only allowed to explore one cup before being signaled to leave the compartment by tapping on the door and subsequently closing the entrance/exit hatch slowly. All birds began to respond to the tapping alone within 1–2 sessions. Birds were trained over 15 sessions, with

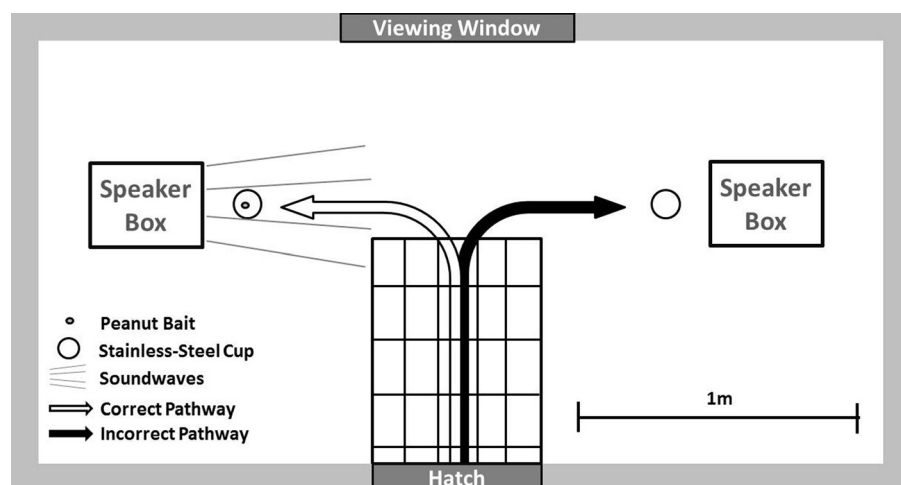


FIG. 1. Floor plan of experimental room used for testing the kea's hearing sensitivity. The kea entered through the hatch, and was required to walk through a wire-mesh tunnel before choosing the correct cup (in front of the speaker playing the sound) to retrieve a reward.

10 trials/session, and were required to achieve a correct choice criterion >85%, calculated over the final 5 sessions. All birds achieved or exceeded this threshold, and were subsequently included in the experiment.

D. Testing phase

Birds were tested over a series of sessions, with each session containing ten trials. Birds were tested at maximum once every 12 h. Within each trial, a bird would be subjected to tones at a set frequency and amplitude. Between trials, the amplitude of the tones was increased/decreased in steps of 9 dB for frequencies below 500 Hz and above 6000 Hz, and in steps of 6 dB for all other frequencies; direction of the amplitude change was dependent on success/failure at previous amplitude, with the training sound (2 kHz pure tone at 65 dB SPL at 10 cm) as the initial starting point. The success criteria for a session were set at 90% correct retrievals. In some cases the bird would achieve 80% correct choice (continuation criteria), in which case it was retested at the same frequency/amplitude. Two consecutive trials below the continuation criteria resulted in a reversal to the previous amplitude, after which two consecutive trials above the success criteria resulted in the next frequency being tested at the same amplitude. If a bird failed to reach the success criteria by the time the speaker was producing maximum amplitude output, that frequency was counted as not audible.¹ The threshold for a frequency/amplitude combination was thus defined as 90% correct reward retrievals, achieved in two consecutive sessions, and three sessions overall. Birds were presented with tones between 50 and 100 Hz in 10 Hz steps, 100 Hz and 1000 kHz in 100 Hz steps, and between 1000 and 16 000 Hz in 1000 Hz steps.

Due to the ease with which kea fall into side preference behavioural patterns (R.S., personal observation), trials within a session were semi-randomised so as to never contain more than three consecutive stimuli on the same side.

E. Comparative data

To facilitate comparison of kea auditory threshold data with that of other species obtained from the literature, change of kea absolute threshold per octave was calculated for frequencies below and above 3 kHz. The audiograms of Passeriformes (songbirds, 20 species) and of Strigiformes (owls, 13 species) were adapted from Dooling *et al.* (2000). Those of other Psittaciformes (three species) and a group of “avian auditory generalists” (ten species) were taken from Wright *et al.* (2003). Differences in absolute threshold were calculated between kea and other parrot species. Possible habitat effects from habitat background noise were also considered. The background noise amplitude at different frequencies was calculated from recordings made in low wind conditions (<0.3 m/s, or 0 on the Beaufort scale) in the kea’s habitat (Aoraki/Mount Cook and Arthur’s Pass National Parks, New Zealand). These recordings were made with a 0.5 in. microphone (type 4190, frequency response 3–20 000 Hz \pm 0.2 dB, Brüel & Kjær, Nærum, Denmark) connected to a portable audio recorder (model 722, Sound Devices, Reedsburg, WI), and were digitalized at a sampling

rate of 96 kHz with 24-bit precision. Analysis of recorded sound was done using Raven Pro with spectra constructed using a fast Fourier transform of 256-points (giving a frequency resolution of 187 Hz) and a Hanning window. Low wind conditions were chosen as they represent the constant environmental background noise in this habitat; all environmental measurements were made using a pocket weather station (Kestrel 4500 845, Kestrel Instruments, Birmingham, AL). Amplitude and frequency information for kea calls was taken from data used in Schwing *et al.* (2012).

III. RESULTS

Hearing thresholds for the three kea did not differ overall (one-way analysis of variance, $F_{2,29} = 0.069$, $p = 0.933$; Fig. 2). Kea have a relatively narrow window of increased hearing sensitivity between 1 and 5 kHz above and below which the sensitivity decreases rapidly. Peak sensitivity corresponds to the peak power in kea calls at 3 kHz (Fig. 2). The birds tested had hearing ranges between 50 and 15 000 Hz. The first octave below the peak sensitivity shows little loss in sensitivity, while the second and third octaves show a decrease in sensitivity. Above the peak sensitivity the drop is immediate and greatest over the first octave. Below 3 kHz, changes in threshold level increased at an average of 11 dB per octave, while those above 3 kHz, showed an average increase of 30 dB per octave (Table I).

The overall shape of kea audiograms follows a similar pattern to that seen in other parrots (Fig. 3), albeit with a steeper increase in threshold below 1 kHz. Threshold values for kea are most similar to the orange-fronted conure (Table II), although in the region of highest sensitivity (1–5 kHz) these are closer to those of the cockatiel. When compared with other groups of birds (Fig. 4), the general shape of the audiogram is again similar, with the greater decrease in

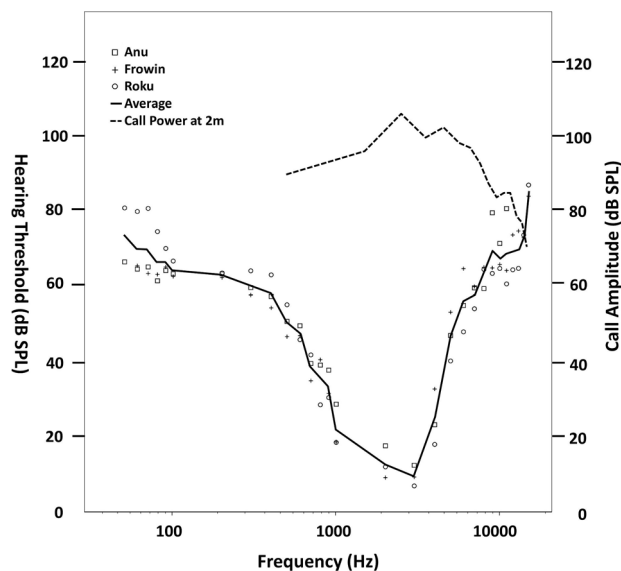


FIG. 2. Average audiogram for kea ($N = 3$, individual results as scatterplot) with power spectrum for kea call (based on Schwing *et al.*, 2012). The region of highest sensitivity was between 1 and 4 kHz for all kea (average peak, 3 kHz), corresponding to the region of highest power in kea calls (average peak 2.5 kHz).

TABLE I. Absolute threshold change in dB per octaves (threshold at frequency closer to peak sensitivity compared to threshold at frequency further from peak sensitivity) below and above peak sensitivity (3 kHz) in kea. The values show the much higher change in threshold in the octaves above the peak threshold when compared to the octaves below. Mean calculated from absolute thresholds of subjects; * estimated from 1 and 2 kHz values, ** only includes 6–11 kHz, *** only includes 60–100 Hz.

	Octave	Anu	Frowin	Roku	Average	SD
Below peak sensitivity	6th (50–100 Hz)	3.15	14.16	2.85***	9.47	6.45
	5th (100–200 Hz)	0.07	3.19	0.31	1.19	1.74
	4th (200–400 Hz)	5.94	0.50	8.00	4.81	3.88
	3rd (400–800 Hz)	18.31	34.61	13.82	22.25	10.94
	2nd (800 Hz–1.5* kHz)	15.99	13.30	26.70	18.66	7.09
Above peak sensitivity	1st (1.5*–3 kHz)	10.75	8.26	4.62	7.88	3.08
	1st (3–6 kHz)	42.66	41.04	55.53	46.41	7.94
	2nd (6–12 kHz)	25.78**	16.48	9.00	13.19	8.40

sensitivity in the frequencies below 1 kHz being the only notable difference. When the constant background noise of a kea habitat is graphed against the kea audiogram,¹ the area of loudest background noise, below 1 kHz, closely matches the region of lowest hearing sensitivity.

IV. DISCUSSION

The kea’s region of greatest hearing sensitivity corresponds to the region of greatest power in the power spectrum of the most common conspecific vocalisation (Schwing *et al.*, 2012), but does not encompass the full range of harmonics found in kea calls. From an evolutionary stand point, the functional convergence of sensitive hearing range and high amplitude call spectrum is expected, and has been found in most other bird species tested so far (Dooling *et al.*, 2000; Konishi, 1970; Lohr *et al.*, 2004; Okanoya and Dooling, 1988). There also appears to be a region of decreased loss in hearing sensitivity in the range of 11–12 kHz (above the hearing range

tested for most other bird species; Dooling *et al.*, 2000), which corresponds to an increase in power in kea calls at the same frequencies. However, further research is necessary to determine whether this is an artifact of the small sample size, and, if not, what its function might be.

The overall shape of the kea audiogram is similar to that found for other groups of birds, albeit with a steeper increase in threshold at low frequencies (<1 kHz). In comparison with other parrots, the threshold values for kea are most similar to the orange-fronted conure (Wright *et al.*, 2003), while the kea’s frequency of greatest sensitivity more closely resembles that of the cockatiel (Okanoya and Dooling, 1987). Although kea and orange-fronted conures generally inhabit more similar habitat types (forests, foothills), kea frequently venture, and nest, above the tree line in open alpine terrain (Diamond and Bond, 1999), which, in turn, is more similar in vegetation cover to the arid habitat of the cockatiel. The attenuation of sound within different types of habitat is highly specific (Marten *et al.*, 1977; Marten and Marler, 1977) and any overlap in habitat type used by two species may lead to a convergent evolutionary selection on vocalizations (Brown *et al.*, 1996; Nicholls and Goldizen, 2006), and consequently on hearing abilities. As environmental effects on frequency, amplitude, and range affect different species similarly (Bertelli and Tubaro, 2002; Boncoraglio and Saino, 2007), we expected that the budgerigar and cockatiel, which have large overlaps in habitat (Higgins, 1999), would also have the most similar audiograms among the parrots tested so far. However, the kea’s evolution toward its current state could have occurred in

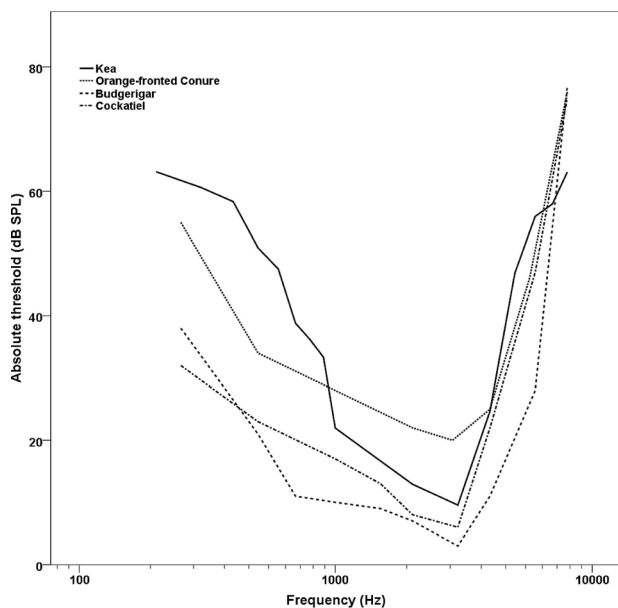


FIG. 3. Average audiogram of three parrot species compared with kea (250 Hz to 8 kHz plotted). The low frequency hearing thresholds (<1 kHz) are more similar to orange-fronted conure, while thresholds in the highly sensitive range more similar to budgerigar and cockatiel. Audiograms from non-kea parrots reproduced from Wright *et al.* (2003).

TABLE II. Absolute differences in threshold between kea and other parrot species. Thresholds from non-kea parrot species from Wright *et al.* (2003).

Frequency	Orange-fronted Conure	Budgerigar	Cockatiel
250	6.88	23.88	29.88
500	16.94	29.94	27.94
1000	6.04	11.96	4.96
2000	9.09	5.91	4.91
3000	10.44	6.56	3.56
4000	0.34	13.66	2.66
6000	9.97	27.97	8.97
8000	12.90	13.90	11.90
Mean	9.08	16.7225	11.85

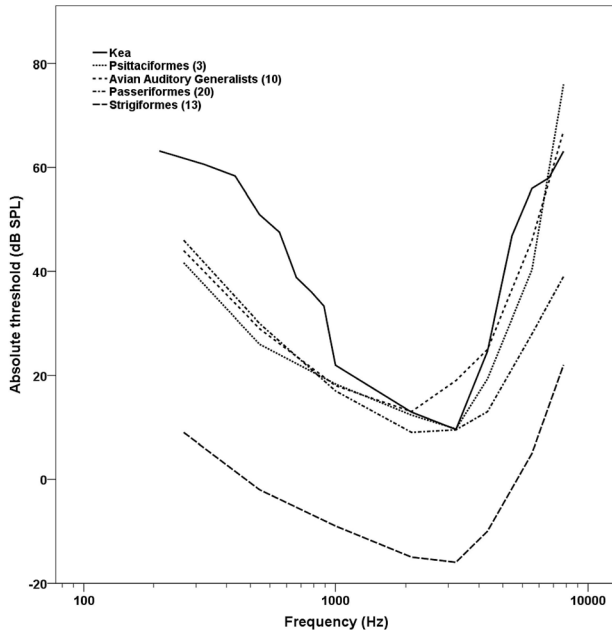


FIG. 4. Average audiograms for different avian groups (number of species tested depicted in parentheses; 250 Hz to 8 kHz plotted) compared with the kea depicting apparent loss of hearing below 1 kHz (average peak 2.5 kHz). Audiograms of Psittaciformes and avian auditory generalists reproduced from Wright *et al.* (2003). Those of Passeriformes and Strigiformes reproduced from Dooling *et al.* (2000).

different ways. One possibility is that the kea ancestor had the lowered hearing sensitivity typical of closed habitat species (like the orange-fronted conure). Over time, as individuals ventured into open montane territory, their hearing range evolved toward a heightened sensitivity in the frequency range most important to communication in open habitats. Alternatively, the kea ancestor was an open habitat species that only lost the sensitivity in the lower frequencies due to the harsh winds in the montane environment. The former of these hypotheses seems more likely because the species with which the kea shared the last common ancestor was a forest dwelling bird (Grant-Mackie *et al.*, 2003; Van Horik *et al.*, 2007). However, the effects of wind might still have further decreased the hearing sensitivity in the lower frequency range.¹ Comparisons with other parrot species from different habitats as well as audiograms from the closely related kākā (*Nestor meridionalis*), which evolved in the lower altitude forests in New Zealand, would permit a more concrete hypothesis regarding the abiotic effects on parrot hearing.

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¹See supplementary material at <http://dx.doi.org/10.1121/1.4967757> for an example of subject progression through different frequencies/amplitudes during testing and kea audiogram plotted against background noise of habitat and testing chamber.

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