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Estimation of hearing range in raptors using unconditioned responses

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Abstract We developed a new method to estimate the auditory abilities of animals using responses elicited by the presentation of auditory stimuli, without restraining or training the subjects. Using this method, we examined the hearing ranges of four raptors (a Mountain Hawk-eagle *Spizaetus nipalensis*, Northern Goshawk *Accipiter gentilis*, Common Buzzard *Buteo buteo*, and Grey-faced Buzzard-eagle *Butastur indicus*) kept in Ueno Zoo, in Japan, by presenting pure tones and white noise at two sound-pressure levels. Unconditioned responses, such as pupillary dilation and physical movements, were observed in all subjects. We then presented paired video clips of the raptors, with and without auditory stimuli, to human assayers, who were asked which clip contained the auditory stimulus. The accuracy of the human perceptual assay (HPA) suggested that the Mountain Hawk-eagle and Northern Goshawk hear frequencies from 1 to 5.7 kHz best, which is comparable to the results of an experiment with an American Kestrel *Falco sparverius* and European Sparrowhawks *Accipiter nisus*. The assayers reported that they used movements of the neck, head, and eyes, and changes in the pupils of the raptors as critical cues. Our method reliably reflected the hearing ranges of the raptors, and should be helpful for estimating the auditory capabilities of rare animals, such as the Mountain Hawk-eagle studied here.

Key words Hearing range, HPA, Raptors, Unconditioned response

Hawks and eagles, which belong to the order Falconiformes, are diurnal birds that hunt insects, birds, and small mammals, such as rabbits, voles, and mice. They usually sit on high perches, and dive at high speed when they attack prey. Therefore, they are strongly dependent on their excellent visual capacity when hunting. Their excellent visual ability is supported by the evidence that some raptors have much bigger eyes than humans, relative to their body size, and much greater visual acuity than humans (e.g., Wedge-tailed Eagle *Aquila audax*, Reymond 1985).

Auditory stimulus is also important for raptors, because it indicates that prey is approaching or that it is alarmed against them (Klump et al. 1986), that it is dangerous advance, or that hatchlings/fledglings are hungry, and so on. Few studies, however, have examined the auditory abilities of Falconiformes, which do not appear to be exceptional among avian species (Fig. 1). Trainer (1946) measured hearing in the American Kestrel *Falco sparverius* using conditioned responses elicited by, or emitted in response to, electric shocks that were preceded by pure tones. He showed that the kestrel responded to sounds at frequencies of 1–4 kHz. Klump et al. (1986) measured the audible range of European Sparrowhawks *Accipiter nisus* using discrimination training through an operant conditioning technique, and found that the hawks were most sensitive to sounds from 1 to 4 kHz. Their best frequency was 2 kHz, while they could not

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hear sounds at frequencies higher than 8 kHz. This hearing range is average in relation to birds in general, but is much narrower than that of owls and some other raptors (Dyson et al. 1998). The differences in the hearing abilities of these birds likely evolved because hawks are diurnal and they catch their prey from great distances using visual cues, whereas owls are nocturnal and they catch their prey from short distances using auditory cues.

For conservation purposes, it is necessary to know the auditory capabilities of raptors, especially those living in forested or mountain habitats, because such birds are often affected by human habitat-alternating activities such as logging, dam construction, and residential developments. Noise from these projects may influence the birds' reproductive or foraging success. Therefore, we need to be able to identify noise levels and understand how such noise might affect raptors.

Unfortunately, we do not have sufficient data on the auditory ability of raptors, mainly because many of their populations are endangered, which makes it impossible to undertake experiments that require surgery or long periods of time for the collection of data, such as electrophysiological studies and operant discrimination training. Therefore, in order to determine the auditory capabilities of raptors, we must develop non-invasive methods that can be completed over short periods.

One solution is to use unconditioned responses to sound. For example, Megela-Simmons et al. (1985) used a "reflex modification" technique to obtain audiograms of the Bullfrog *Rana catesbeiana* and Green Tree Frog *Hyla cinerea*. In their technique, the unconditioned reflex elicited by the electric shock was inhibited when the pre-stimulus, say, pure tone, preceded the presentations of the shock if the animal had detected the pre-stimulus. The audiograms measured by reflex modification technique agreed well with neural sensitivity data (Ehret & Capranica 1980; Shofner & Feng 1981). Recently, Bala and Takahashi (2000) measured the hearing curve in American Barn Owls *Tyto alba* using the pupillary dilation response elicited by the presentation of sound, and found that it was consistent with the data that Quine and Konishi (1974) obtained using operant conditioning. Although methods using unconditioned responses to sound have marked advantages over the operant conditioning method in that they do not require prior training, the subjects must be restrained during these experiments, and aversive stimulus or surgical operation is necessary to obtain small behavioral changes.

Here, we establish a method of estimating the hearing ability of unrestrained, captive raptors using responses to sound presentation, such as pupillary dilation, blinking, orienting responses, and small movements of the body. The subjects were four Japanese raptors (a Mountain Hawk-eagle *Spizaetus nipalensis*, Northern Goshawk *Accipiter gentilis*, Common Buzzard *Buteo buteo*, and Grey-faced Buzzard-eagle *Butastur indicus*) kept in a zoo. We assumed that unconditioned responses would be observed only when sound was presented, and that such responses could be used as an index of hearing. We videotaped the behavior of the raptors with and without sound presentation, and then asked human assayers who were unaware of the experimental conditions to judge whether a given video clip contained sound presentation. We called this the Human Perceptual Assay (HPA). We assumed that if the assayers could correctly categorize the clips using responses to sound presentation as discriminative cues, the HPA would then reflect the hearing capability of the raptors.

MATERIALS AND METHODS

1) Study Area

Two experimenters recorded the raptors' behavior on days when Ueno Zoo, Tokyo, was closed to the public, from 16 March 2001 to 9 July 2001. One experimenter controlled the stimulus presentation, and the other videotaped the behavior of the subjects. Two loudspeakers were placed just in front of the birds' metal cage, and the video camera was set at least 3 m behind the loudspeakers. The distance between the loudspeakers and the birds was 3 to 6 m. The sound pressure levels were adjusted for distance so that they were equal where the birds were.

After the recording, we conducted the HPA in a laboratory at Chiba University.

2) Subjects

The subjects were four raptors kept in Ueno Zoo: a male Mountain Hawk-eagle, a male Northern Goshawk, a male Common Buzzard, and a Grey-faced Buzzard-eagle of unknown sex. The Mountain Hawk-eagle had been shot in the wild and taken to the zoo; it had recovered and was flying freely in its cage at the time of the experiment. It was kept in a cage by itself. The wings of the Northern Goshawk and Common Buzzard had been injured, and neither bird could fly; these two hawks were kept in a cage with five Ural Owls *Strix uralensis*. The Grey-faced Buzzard-eagle could fly, and lived with two Common Kestrels *Falco tinninculus*.

Three male volunteers (22–30 years-old) took part in the HPA as assayers.

3) Materials

The auditory stimuli were controlled by a CD player (SL-SW404, Panasonic) and broadcast from two loudspeakers (YST-M100, Yamaha). The behavior of the raptors was recorded with a digital video camera (VL-MR1 PRO, Sharp). We used a personal computer (PCV-J15, Sony) and video presentation software (Adobe Premiere 5.1 for Windows, Adobe) for the HPA.

4) Stimuli

The sound stimuli were created using Avisoft-SAS Lab Pro software (Avisoft) with a sampling frequency of 44.1 kHz. The stimulus duration was 0.8 sec with rise-fall times of 50 ms. We prepared pure tones at eight different frequencies (0.25, 0.5, 1, 2, 4, 5.7, 8, and 11.3 kHz) and white noise. The frequencies of the pure tones were determined using the octave scale, except for 5.7 kHz, which was the geometric mean between 4 and 8 kHz. Each sound had two sound pressure levels, 50±4 dB and 74±4 dB, and the difference between the two levels was 24 dB.

5) Procedure

Sound presentation and video recording of the hawks The test sounds were presented from in front of the cage when the birds were not moving and there was relatively little external noise. The sounds were presented using the constant stimuli method (Klump et al. 1995); i.e., the stimuli were presented in random sequences within and among sessions. The inter-stimulus interval was at least 30 sec, and it was usually much longer, either because the birds were moving or there was external noise. The sound and no-sound conditions were alternately presented after the inter-stimulus interval. In the sound condition, we presented an auditory stimulus 3 seconds after pushing the button on the CD player. The procedure in the no-sound condition was the same as in the sound condition, except that no sound was broadcast. We videotaped mainly the upper part of each bird, including the head, shoulders, and abdomen, in these sessions. A session consisted of 18 sound conditions, which consisted of one sound at each of the nine frequencies and two sound-pressure levels, and 18 no-sound conditions. Experiments were conducted on three separate days for each subject, with one session per day. Therefore, 54 video clips with sound and 54 clips without sound were obtained for each subject.

HPA To determine whether the birds responded to the sound stimuli and not to the no-sound condition, we conducted the HPA. In the sound condition, the original video records were edited so that in a 4.8-sec video clip, the sound presentation period was in the middle 0.8 sec of the clip. A 4.8-sec clip of the no-sound condition was edited similarly. Two video clips, one from the sound condition and the other from the no-sound condition, were randomly paired and presented to the assayers of the HPA in windows on each side of a PC monitor, without any auditory information. Before the assay, we told the assayers five things:

1. Look carefully at the video clips presented on the left and right sides of the screen, one at a time;
2. Each clip contains a raptor, and is about 5 seconds long;
3. In one clip, a sound was played to the hawk for about half the length of the clip; no sound was played in the other clip;
4. Determine which clip contains the sound;
5. After the presentation, check the blank space with the corresponding trial number on your response sheet using a pencil.

Note that because the assayers were not told about critical cues that might suggest the presentation of the sound, they were free to use any cues in the clips to make their decision.

Before presenting the test clips to each assayer, eight training trials were run using video clips that were not used in the subsequent test session: four each from the sound and no-sound conditions. In the training session, the clips in the sound condition contained obvious behavioral changes to ensure that the assayers understood their task. During training, the assayers were shown one clip per trial, and were asked to answer yes or no to whether the clip contained a sound presentation. The researcher gave feedback (correct or incorrect) after each answer. The sequence of the trials was such that the same condition (sound or no-sound) was not repeated more than three times in a row. The assayers had more than 50% correct responses to each bird condition. The training session was only given once regardless of how the assayers performed.

In the test session, clips were presented on the left and right sides of the monitor in each trial. In one clip, sound was presented to the bird, and in the other it was not. The conditions (sound or no-sound), positions of the clips (left or right), and the starting clip of a given trial (left or right) were determined using quasi-random sequences, in which the same conditions were not repeated more than three times in a row. One block consisted of 18 trials, which included nine different sound conditions at two sound-pressure levels, and 18 clips from the no-sound condition. These clips were selected from the three separate experiments for each raptor. A session consisted of six blocks, and the 54 different clips were presented twice; therefore, 108 trials per session were run. The assayers were given all three test sessions, one for each raptor with a different sequence of trial blocks, and the orders for the four raptor species were counterbalanced among the assayers.

After the HPA trials, the assayers were asked the following questions:

1. What were the critical cues or rules they used in making their decisions?
2. Were there distinctive characteristics or consistent changes in the behavior of the different raptors?
3. How difficult was it to make a decision, and what was your general impression of the tasks?

Calibration Calibration was performed by placing a sound-level meter with a 1/3 octave band filter at 3, 5, and 6 m from the loudspeaker. These were the distances at which the birds perched during the experiment. Ambient noise level was also measured at the same distances for each 1/3 octave. For the 250-Hz test frequency, some of the harmonic distortion products were as intense as 10 dB below the fundamental. Therefore, the data for the 250-Hz tone was excluded from further analyses. For the other test frequencies, harmonic distortion within the audible range (assuming 15 kHz at most) was at most 30 dB below the fundamental at each test frequency for each harmonic. The 1/3 octave noise level was converted into a spectrum level by subtracting the logarithm of the bandwidth. The signal level was at least 50 dB above the ambient noise. This suggests that no masking occurred at the test frequencies, and that the thresholds obtained here reflect true, unmasked thresholds.

6) Statistics

We calculated the response accuracy of three assayers in each bird condition for each sound condition (Fig. 2). The average accuracy of the HPA was calculated for the three assayers in the six trials for each sound condition, in which each raptor condition was presented once per block. The accuracy at frequencies of 1 to 4 kHz was calculated separately (upper panel of Fig. 3), because it is assumed that the raptors can hear sounds at these frequencies (Fig. 1; Trainer 1946; Klump et al. 1986). Consistency of the decisions made by the assayers was also calculated at these frequencies to determine whether they used the same cues for their decisions in each trial. If all the assayers made the same decision (sound presence or absence), then it was counted as 1. If there was a difference among the decisions, then it was counted as 0. We performed a binomial test to examine the difference between the accuracy or consistency and expected value. The chance level was set at 0.5 for accuracy, and 0.25 for consistency. To examine the difference of the accuracy and the consistency among birds, one-way analysis of variance (one-way ANOVA) was conducted, and then Tukey's HSD test was used for multiple comparisons. In addition, we calculated the kappa κ to measure the agreement of the judgment by the assayers (Siegel & Castellan 1988).

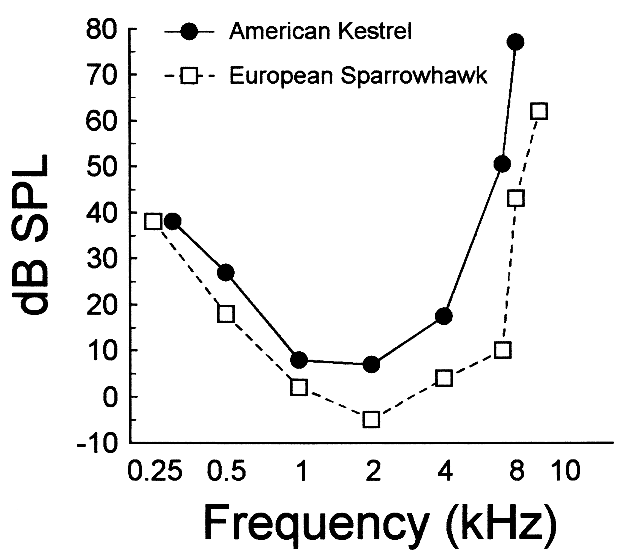

Fig. 1. Audiograms of the American Kestrel (Trainer 1946) and European Sparrowhawk (replotted from Klump et al. 1986).

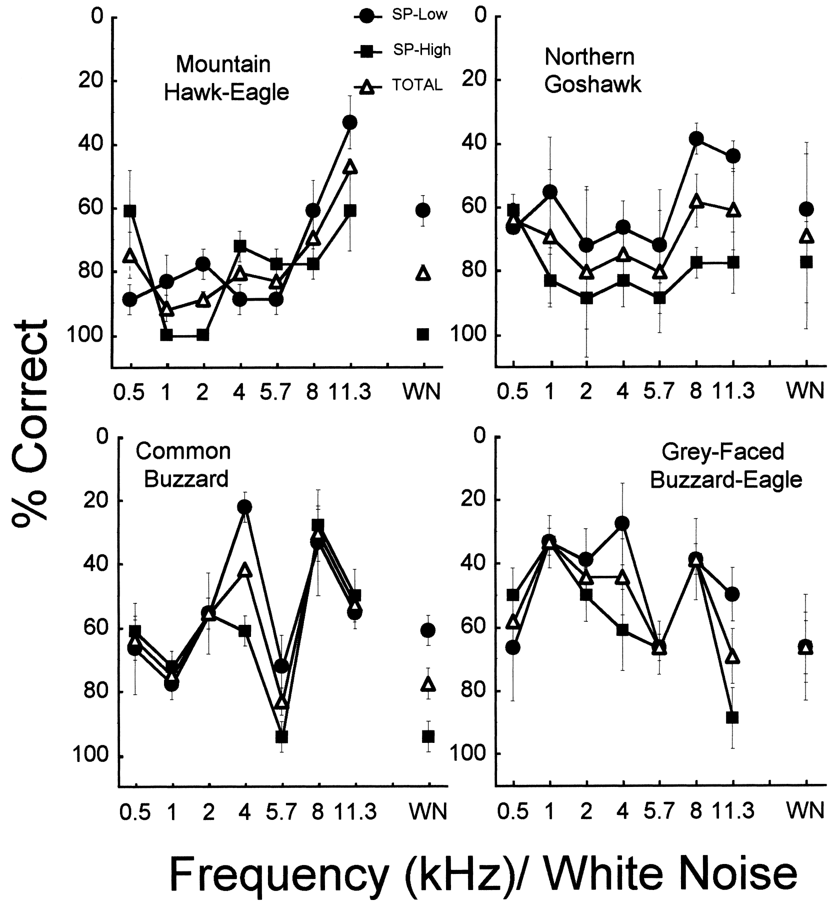

Fig. 2. Response accuracy of the human perceptual assay (HPA) of raptors, with SD. The numbers and letters on the horizontal axis represent the sound frequency and white noise (WN) presented to the raptors. There are separate plots for the low- (SP-Low) and high- (SP-High) pressure levels, and total (TOTAL), which was calculated regardless of the sound-pressure level. Note that the vertical axis is reversed (the origin is at the top of the y-axis) to compare the shapes of the curves with audiograms obtained in other studies (Fig. 1).

RESULTS

The average accuracy was calculated for the total and the two sound-pressure levels (Fig. 2). The total accuracy for the Mountain Hawk-eagle was 77.1%, for the Northern Goshawk 69.1%, for the Common Buzzard 60.1%, and for the Grey-faced Buzzard-eagle 52.8%. Comparison between the accuracy of the HPA at frequencies of 1 to 4 kHz and the chance level probability (upper panel of Fig. 3) revealed a significant difference for the Mountain Hawk-eagle (87.0%, $N=108$, $z=7.60$, $P<0.01$) and for the Northern Goshawk (75.0%, $N=108$, $z=5.10$, $P<0.01$), but not for the Common Buzzard (57.4%, $N=108$, $z=1.44$, $P>0.05$) or Grey-faced Buzzard-eagle (40.7%, $N=108$, $z=1.83$, $P>0.05$). There was a significant difference among the birds ($N=12$, $F=9.25$, $df=3$, $P<0.01$), and following multiple comparison revealed that there was significant difference between the Grey-faced Buzzard-eagle and the Mountain Hawk-eagle ($N=3$, $P<0.01$), and the Northern Goshawk ($N=3$, $P<0.05$).

The assessment of the assayers (Fig. 2) was that they were 80% accurate for sounds at frequencies of 1 to 5.7 kHz in the Mountain Hawk-eagle, in both sound-pressure conditions. There is a steep decrease in accuracy from 5.7 to 11.3 kHz under low sound-pressure conditions, and from 8 to 11.3 kHz under high sound-pressure conditions. For the Northern Goshawk, the accuracy level of HPA was more than 80% from 1 to 5.7 kHz, but only under high sound-pressure conditions. The difference in the human performance between the sound-pressure conditions was clearer for this bird than for any of the other three

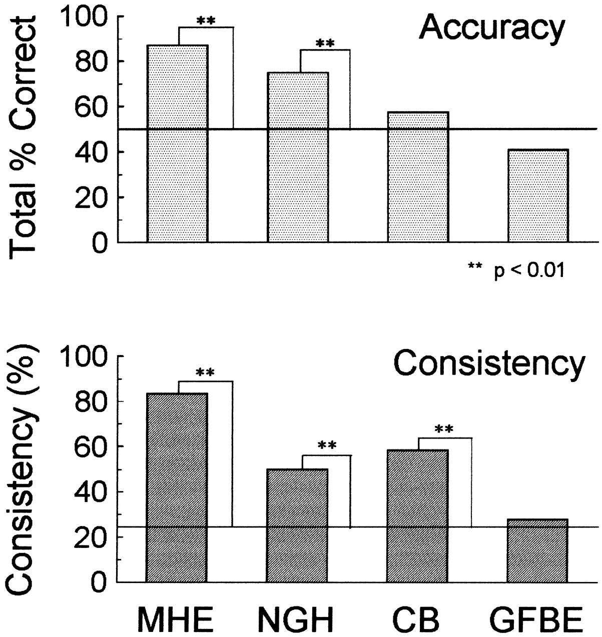

Fig. 3. Response accuracy (upper) and consistency (lower) of the three human assayers in the HPA of each raptor (MHE: Mountain Hawk-eagle; NGH: Northern Goshawk; CB: Common Buzzard; GFBE: Grey-faced Buzzard-eagle). The data were collected from the responses to the video clips with sound frequencies of 1, 2, and 4 kHz. In the upper panel, the solid line indicates the chance level of performance (50%). Consistency means the percentage of trials in which all three assayers made the same decision (sound presence/absence). The solid line indicates the chance level (25%). Asterisks indicate statistically significant differences between the data and a given chance level.

raptors. Under the low sound-pressure condition, the accuracy did not reach 80% at any frequency. The shapes of the curves obtained from the HPA of these two species were similar to those of the audiograms in Trainer (1946) and Klump et al. (1986).

By contrast, the performance in the HPA for the Common Buzzard and Grey-faced Buzzard-eagle (Fig. 2) oscillated markedly, depending on the sound frequency. In the Grey-faced Buzzard-eagle, the greatest accuracy under the high sound-pressure condition was for 11.3-kHz, the frequency at which the humans were not so accurate for the other three raptors. For the Common Buzzard, it was the highest for 5.7 kHz, and the lowest for 8 kHz. In these two birds, no consistent change in accuracy was observed with sound condition, for either frequency or sound pressure level.

Except for the Grey-faced Buzzard-eagle, the accuracy in response to the white noise condition was comparatively high, and for the higher sound-pressure level it increased to around 80%.

The interviews of the assayers after the HPA experiment revealed that all of them used movements of the neck, head, and pupil, blinking, and behavioral changes seen in the video clip as cues for their decisions. Although the Mountain Hawk-eagle was not generally active, the assayers reported that its behavior changes were the most distinct of the four species, and one assayer noticed whether it blinked with one or both eyes. In the Northern Goshawk, two of the assayers reported that they divided the video clips into two categories based on the distinctiveness of the behavior changes. In the Common Buzzard, all of the assayers had difficulty detecting pupillary changes, because the border between the pupil and the iris is not clear in this species.

The consistency of the decision among the assayers (lower panel of Fig. 3) was above chance level (25%) in the Mountain Hawk-eagle (83.3%, $N=36$, $z=7.89$, $P<0.01$), the Northern Goshawk (50.0%, $N=36$, $z=3.27$, $P<0.01$), and the Common Buzzard (58.3%, $N=36$, $z=4.43$, $P<0.01$), but not in the Grey-faced Buzzard-eagle (40.7%, $N=36$, $z=0.19$, $P>0.05$). The difference among them was significant (one-way ANOVA, $N=24$, $df=3$, $F=9.96$, $P<0.01$). Further comparison between each species revealed that the consistency of the Mountain Hawk-eagle was higher than that of the Northern Goshawk (Tukey's HSD test, $HSD=1.73$, $N=6$, $P<0.05$), and the Grey-faced Buzzard-eagle ($N=6$, $P<0.01$), and that of the Common Buzzard was higher than that of the Grey-faced Buzzard-eagle ($N=6$, $P<0.05$). Thus, it was clear that both the response accuracy and consistency were high for the Mountain Hawk-eagle, whereas they differed for the Northern Goshawk and the Common Buzzard (higher response accuracy and lower consistency in the former, and they were reversed in the latter). By contrast, both of them were lower in the Grey-faced Buzzard-eagle. Kappa statistic also showed the same trend, that the agreement of the judgment was significantly above chance for the Mountain Hawk-eagle ($\kappa=0.51$, $z=2.18$, $P<0.05$) and Common Buzzard ($\kappa=0.43$, $z=4.30$, $P<0.01$), but not for the Northern Goshawk ($\kappa=0.11$, $z=0.76$, $P>0.05$) or the Grey-faced Buzzard-eagle ($\kappa=0.01$, $z=0.09$, $P>0.05$).

DISCUSSION

This study showed that the responses of the raptors to sound presentation and the accuracy of our HPA could be used to measure their hearing ranges. The validity of our method was suggested by the similarity between the response accuracy to the Mountain Hawk-eagle and Northern Goshawk and the audiograms obtained in the prior experiments. The American Kestrel and European Sparrowhawk heard frequencies from 1 to 4 kHz best (Fig. 1), and the response accuracy of the HPA in the Mountain Hawk-eagle and Northern Goshawk was greater to sounds from 1 to 5.7 kHz (Fig. 2). In addition, the Mountain Hawk-eagle and Northern Goshawk showed clear and consistent responses to sounds within that range, as suggested by the performance that was significantly different from chance in those species. The high accuracy and consistency in HPA in the Mountain Hawk-eagle suggest that the assayers used the same behavioral cues that were well coincident with the sound presentation and had small variability. By contrast, in the Northern Goshawk, although all the assayers reported that it was easy to detect behavioral changes in this species, the high accuracy with lower consistency than that of the Mountain Hawk-eagle suggests that the assayers used the various behavioral cues that coincided with the sound presentation. It is possible that the Northern Goshawk was more sensitive to the sound stimuli than any of the other species. Assuming that there should not be a big difference in the auditory abilities of these species of raptor, the audibility range was from 0.5 to 8 kHz, with the best hearing range from 1 to 6 kHz.

This study might be criticized on the basis that the hearing ability of the raptors may not be identical with the response accuracy in the HPA. We also admit that our methodology cannot be used in all cases. Our observations indicated that the behavioral changes in response to sound presentation in the Common Buzzard and Grey-faced Buzzard-eagle were inconsistent. These birds often moved actively after being presented with sounds at frequencies of 8 or 11.3 kHz, which are reported to be beyond the hearing range of European Sparrowhawks (Klump et al. 1986), whereas they did not respond to sounds at 1 or 2 kHz, which are thought to be within their ranges. This inconsistency in their responses is why the performance of the HPA for these species was not statistically different from chance. By contrast, the Mountain Hawk-eagle and Northern Goshawk consistently showed behavioral changes to the sounds, and this was reflected in the higher HPA performance (upper panel of Fig. 3). The reasons for these differences may be owing to the native habitats of these species. Mountain Hawk-eagles and Northern Goshawks usually perch in trees while foraging and roosting, whereas Common Buzzards and Grey-faced Buzzard-eagles live and hunt in open fields in flatlands. The former two species would be more used to hearing sounds distorted by obstacles than the latter two species. In the present experiment, pure tones were broadcast from speakers set in front of each bird's cage. Thus, it is possible that the tones were more strange to the Mountain Hawk-eagle and the Northern Goshawk than to the Common Buzzard and the Grey-faced Buzzard-eagle, and that they would be more sensitized. In addition, such habitat conditions would affect their movements on hearing the sounds. Mountain Hawk-eagle and Northern Goshawk may move actively in order to detect environmental changes visually, whereas Common Buzzard and Grey-faced Buzzard-eagle may move inactively in order not to be seen by preys in flatlands. Since our method relies on unconditioned responses to sound, it is not useful for species with small or few behavioral changes, such as Common Buzzards and Grey-faced Buzzard eagles. It is necessary to consider the specific ecology and behavior of the subject before applying our method. To confirm the hypothesis outlined above, we must increase the number of subjects to determine the generality of the behavioral characteristics to the sound observed in this study.

One could argue that the birds kept in a zoo may have become de-sensitised or habituated to certain auditory stimuli because they are continuously exposed to the sounds made by visitors. However, the pure tones used in the present study do not exist in a natural environment, and it was presumed to be the first time for the birds to hear these sounds. Additionally, the coincidence of the behavioral change with the sound presentation frequently observed in the subjects, precluded the possibility of loss of sensitivity to such kind of sounds.

Because the raptors other than the Mountain Hawk-eagle were kept in their cages together with other birds such as owls which are known to have greater sensitivity to the sound than hawks, consideration must be given to the fact that the subject birds could have used their behavioral changes to the sounds. However, such an effect would have been small, because the Common Buzzard, which showed inconsistent behavioral changes to the sounds, was kept in the cage with the Northern Goshawk which proved to be more sensitive than the buzzard.

We cannot say that the function (Fig. 2) represents the absolute hearing threshold in these raptors. However, the accuracy curve of the HPA measured using two different sound-pressure levels could be considered an equal-loudness curve for the raptors, reflecting the audible range under given conditions. By running additional tests using sounds at the best-heard frequencies and different sound-pressure levels, we should be able to estimate other auditory properties, such as absolute thresholds and frequency cutoffs.

In conclusion, our method is useful for estimating the hearing ranges of some raptors, and does not require training or restraints. The accuracy of the HPA reflected the hearing ranges of the birds. In addition, because we presented the sounds in front of the birds' usual cages, the possible effects of interference should have been minimal. Our method can be applied to animals in captivity and possibly even to those in the wild.

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