

HEARING IN MAMMALS: THE LEAST WEASEL

RICKYE S. HEFFNER AND HENRY E. HEFFNER

*Laboratory of Comparative Hearing, Bureau of Child Research, and
the Museum of Natural History, University of Kansas, Box 738, Parsons, KS 67357*

ABSTRACT.—Audiograms were obtained for two least weasels (*Mustela nivalis*) using behavioral methods. The hearing range of the least weasel for intensities of 60 dB SPL extends from 51 Hz to 60.5 kHz with a region of best hearing extending from 1 kHz to 16 kHz. The least weasel appears to be similar in its hearing to other members of the order Carnivora for which data are available. The high-frequency hearing ability of the least weasel lends additional support to the relationship between functional interaural distance and high-frequency hearing, whereas its sensitivity to low frequencies in the absence of obvious morphological specialization of the middle ear makes the least weasel unusual among small mammals.

Since the nineteenth century it has been known that hearing ability varies among mammalian species (Galton, 1883). Specifically, the range of frequencies which a mammal can hear (the highest and lowest frequencies to which it responds) shows large interspecies differences. For example although the Indian elephant is unable to hear sounds higher than about 10 kHz, most mammals are capable of hearing much higher frequencies with the porpoise hearing up to 140 kHz (Fig. 1A). Similarly, low-frequency hearing varies from as low as 17 Hz in the elephant to approximately 10 kHz in the little brown bat (Fig. 1B). Thus, in mammals, high-frequency hearing varies over a range of nearly four octaves and low-frequency hearing varies by more than nine octaves. This variation is greater than that found in any other vertebrate class (cf., Dooling, 1980; Fay, 1980; R. Heffner and Heffner, 1983a; Wever, 1978).

Given this wide variation, the question arises as to the selective pressures involved in determining hearing range. Two approaches to this question are of particular interest. The first, looking for morphological correlates of hearing, has led to the discovery of the relationship between the functional head size of an animal (i.e., its interaural distance) and its ability to hear high-frequency sounds. Briefly, animals with small interaural distances (i.e., small heads and close-set ears) are better able to hear high-frequency sounds than are animals with large heads and wide-set ears (e.g., R. Heffner and Heffner, 1982). This correlation is based on the adaptive value of the ability to localize sound and the directionality of high-frequencies (Masterton et al., 1969). This relationship has been explored in 40 species of mammals and accounts for much of the variation in high-frequency hearing. Thus, the need to localize sound is believed to be a primary factor in the evolution of high-frequency hearing.

The second approach has been to determine the influence of inheritance and environment on hearing by comparing the hearing ability of animals that share a common phyletic history or common environment (H. Heffner and Masterton, 1980; Masterton et al., 1969). One example of this approach has been the discovery of relatively good low-frequency hearing in certain desert rodents (e.g., Lay, 1972; Webster, 1966). However, the use of this approach has been limited by the fact that the hearing ability of only a relatively small number of species is currently known.

In an effort to increase the size and representativeness of the sample of species whose hearing is known, we have examined the hearing abilities of the smallest carnivore, the least weasel (*Mustela nivalis*). This particular species was chosen for two reasons. First, although interaural distance is a factor in hearing, the majority of small mammals tested so far have been bats and rodents. In order to determine whether a different lifestyle would result in different hearing, it seemed desirable to examine a carnivore whose interaural distance is similar to that of a mouse or small rat. The least weasel is thus an ideal comparison for small rodents in order to determine the role of size in hearing apart from lifestyle or trophic level. Second, auditory characteristics are currently known for only three species of carnivores, two of which are domesticated. Thus,

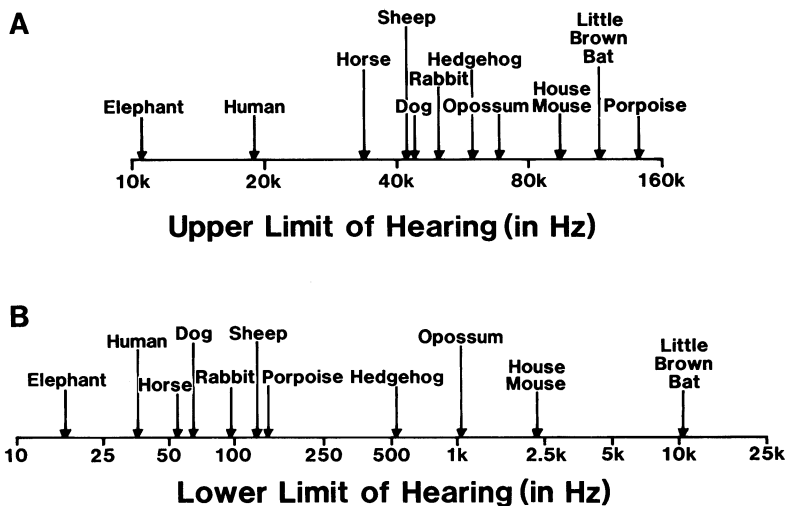


FIG. 1.—High-frequency (A) and low-frequency (B) hearing limits for 11 species of mammals. The hearing limits are defined as the highest and lowest frequencies audible at a level of 60 dB SPL.

study of the least weasel would enlarge the data base of mammalian hearing to include a wild carnivore of a previously unrepresented family (Mustelidae).

METHODS AND MATERIALS

Animals were tested using a conditioned avoidance procedure. Briefly, a thirsty animal was trained to make continuous contact with its mouth on a water spout in order to receive a slow but steady trickle of water. Tones were then presented at random intervals and followed at their offset by a mild electric shock delivered through the water spout. By breaking contact with the spout during tone presentations, the animal could successfully avoid the shock and, at the same time, indicate that it had heard the tone.

Subjects.—One male and one female least weasel (*Mustela nivalis*) approximately 2.5 years old and weighing 67 g and 54 g, respectively, were used in this experiment. They had been trapped in the vicinity of East Lansing, Michigan, and maintained in a laboratory for two years. They were housed in covered glass tanks (50 by 25 by 29 cm) in a quiet room and fed a meat paste composed of raw meat and liver, canned fish, crushed cat chow, and a vitamin supplement. This diet was supplemented by at least one live mouse each week. Water was used as a reward and was available only in the test sessions. Sessions were conducted twice daily with the animals being weighed each day to monitor their health and deprivational state. The weasels typically consumed 1.5–3.0 ml of water per session, which was sufficient to maintain them in good health.

Behavioral apparatus.—Testing was conducted in a double-walled sound-proof chamber (IAC) 2.55 by 2.75 by 2.05 m. The walls of the chamber were covered with acoustic foam and the ceiling was loosely draped with burlap to reduce sound reflection. An adjacent control room housed the behavioral control and stimulus generation equipment.

The animals were tested in a cage constructed of 0.64-cm hardware cloth mounted on a wooden frame and placed on a small foam-covered table (Fig. 2). The cage consisted of a larger section (50 by 25 by 25 cm) with a small compartment (8 by 65 by 9 cm) attached to the front end of the cage. A blunted 22 gauge hypodermic needle protruded into the front of the cage and served as the water spout. The spout was connected by plastic tubing to an electrically operated water valve and water reservoir (25 ml) which were located in the control room. A contact circuit connected between the water spout and cage floor served to detect when an animal made contact with the spout. Damp electrically conductive foam was placed on the cage floor where the animal stood in order to reduce the possibility of the animal detecting low-frequency sounds through cage vibration. A constant current shock generator was also connected between the spout and cage floor.

Sound production and measurement.—Sine waves used to produce the tones were generated by an

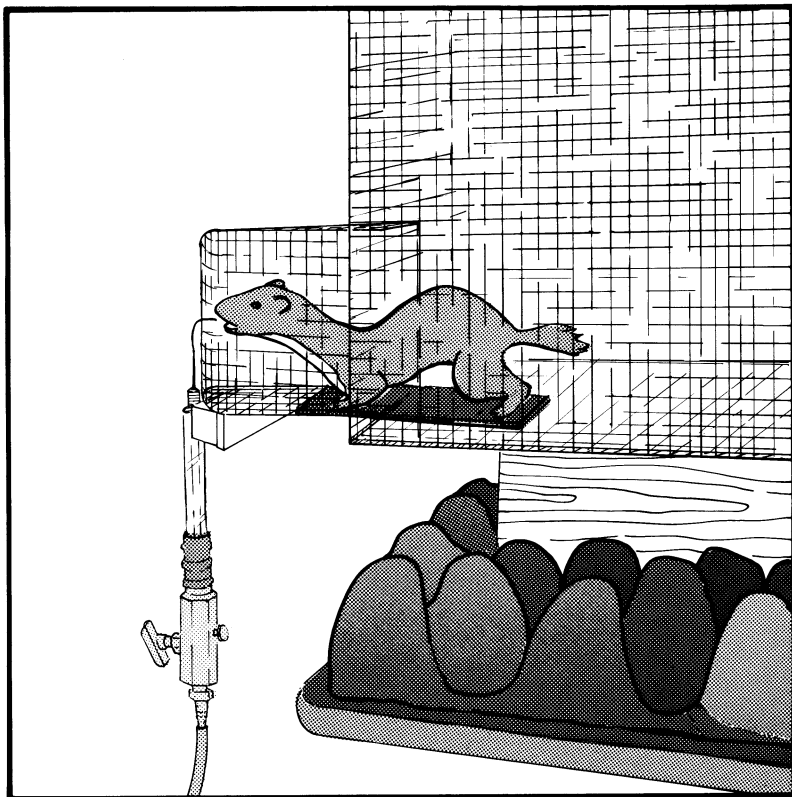


FIG. 2.—View of a least weasel in the test cage. The weasel was trained to maintain contact with the water spout except when a pulsing tone was presented from the speaker. Acoustic foam for reducing sound reflections from the table top can be seen below the cage.

oscillator (Hewlett-Packard 209A), switched on and off by an electronic switch (Grason Stadler 1287), attenuated (Hewlett-Packard 350D), filtered (Krohn-Hite 3202), and then led via either an impedance-matching transformer or an amplifier (Crown D75), to a loudspeaker, either a piezoelectric or dome tweeter for frequencies above 4 kHz, or a 12.7-cm mid-range or 38-cm woofer for lower frequencies. During testing, the loudspeakers were located at ear level 50 to 150 cm in front of the animals. This sound system proved capable of delivering undistorted tones from 16 Hz to 64 kHz at an intensity of at least 94 dB sound pressure level (SPL) in the vicinity of the drinking spout.

In order to avoid switching transients, the electrical signal was electronically switched with a rise-decay time of 10 ms for frequencies of 500 Hz and above and rise-decay times of 30, 50, 100, 150, and 150 ms for frequencies of 250, 125, 63, 32, and 16 Hz, respectively. Tones of 125 Hz and above were pulsed at a rate of two per second, 400 ms on and 100 ms off. Longer on and off times were allowed for lower frequencies to compensate for the longer rise-decay times.

The sound pressure level (SPL) re $20 \mu\text{N}/\text{m}^2$ was measured with either a Bruel and Kjaer (B & K) 2.54-cm microphone (B & K 4131), sound level meter (B & K 2203), and octave filter (B & K 1613), or a 0.64-cm microphone (B & K 4135), preamplifier (B & K 2618), microphone amplifier (B & K 2608), and filter (B & K 1613 or Krohn-Hite 3202). Sound measurements were taken by placing the microphone in the position normally occupied by an animal's ears when the animal was drinking and pointing the microphone directly toward the loudspeaker (0° incidence). Care was taken to ensure that the sound field was homogeneous in the area occupied by the animal. Low-frequency tones were checked for the presence of overtones that might be audible to the weasels. No audible overtones were found, thus ruling out the possibility that an animal might respond to an overtone produced by an inaudible primary tone. Finally, the intensity of the

ambient noise in the test chamber was also measured at each test frequency. Since the only significant ambient noise was low-frequency noise produced by the building's air conditioning system, the air conditioning system was turned off during test sessions for frequencies below 500 Hz.

Psychophysical procedure.—A thirsty animal was trained to make steady contact with its mouth on the water spout in order to receive a slow but steady trickle of water (approximately 0.2 ml/min). Once an animal learned to drink steadily, it was trained to break contact with the spout whenever a tone was presented. This was accomplished by presenting a pulsing tone for 2 s and following its offset with a mild electric shock delivered through the spout. After only a few pairings of tone with shock, the weasel learned to avoid the shock by breaking contact with the spout whenever it heard a tone. In this way, breaking contact with the spout could be used as an indication of an animal's ability to detect a tone. To provide feedback for successful avoidance, the lights in the test chamber were momentarily turned off each time a shock was delivered to indicate that the shock had been delivered and that it was safe to return to drinking.

The test procedure consisted of presenting 2-s trials with a 1-s intertrial interval (i.e., one trial every 3 s). Each trial was either a "safe" trial during which no tone was presented or a "warning" trial which consisted of a 2-s train of tone pulses. Warning trials occurred randomly from 1 to 10 trials after the previous warning trial and were followed by shock. Longer intervals between warning trials were randomly inserted to prevent an animal from using the time since the last warning trial as a cue. No trial was given in the 3 s immediately following a warning trial in order to allow an animal sufficient time to return to the water spout.

For the purpose of quantifying an animal's response, the duration of spout contact was measured in 0.1-s increments beginning 1 s after stimulus onset until 1 s later—at the end of the trial. This measured "time-in-contact" was averaged separately for the silent or safe (S) trials and the tone or warning (W) trials for each frequency at each intensity. A measure of hearing could then be expressed in the form of the ratio (S-W)/S for each stimulus intensity. In trained animals this measure varies from near zero (failure to detect a tone) to unity (perfect detection). To reduce the effects of spurious pauses, the results of a trial were automatically discarded if the animal was not in contact with the spout at any time during the 1 s immediately preceding the trial, although the trial was presented as usual. Since this criterion was applied equally to safe and warning trials, it did not bias the results.

Auditory thresholds were initially determined by reducing the intensity of the tone in 10-dB steps until the animal could no longer distinguish tone trials from silent trials. Final threshold determination was conducted by presenting tones varying in intensity from 10 dB below to 10 dB above the estimated threshold. Threshold was defined as the lowest intensity that could be detected at the 0.01 chance level (Mann-Whitney U) which in this case was usually a suppression ratio of 0.25. Testing for a frequency was considered complete when thresholds obtained in two different sessions were within 3 dB of each other. Once testing had been completed throughout the hearing range, each frequency was rechecked to ensure reliability.

RESULTS AND DISCUSSION

Audiograms of the two weasels are shown in Fig. 3 in which the thresholds are plotted as a function of frequency. The audiograms exhibit the characteristic shape of mammalian audiograms (cf. H. Heffner and Masterton, 1980). Beginning at low frequencies, the animals showed a gradual decrease in threshold to a point of greatest sensitivity at 2 kHz. Above 2 kHz, the weasels' thresholds increase slightly although they remain sensitive up to 16 kHz. Above 16 kHz, the thresholds increase gradually and then relatively steeply as the high-frequency limit of hearing is approached.

Typically, the audiograms of individuals of the same species do not differ significantly except in cases of anatomical abnormalities, noise exposure, or disease (cf. R. Heffner et al., 1971). Such cases when they do arise are easily detected because the animals display wide variation even when compared with other animals with the same disorder (e.g., Blakeslee et al., 1978; R. Heffner and Heffner, 1983b). The close agreement between the two animals suggests that these animals possessed normal hearing and that their audiograms are representative of least weasels.

Low-frequency sensitivity.—The low-frequency hearing limit (lowest frequency audible at an intensity of 60 dB SPL) for the least weasel as interpolated from Fig. 3 is 51 Hz, well below the 196 Hz average value for those mammals whose hearing is known. The least weasel is as sensitive to low frequencies as gerbils and kangaroo rats, animals which are thought to be specialized for low-frequency hearing (e.g., H. Heffner and Masterton, 1980; Lay, 1972; Webster and Webster, 1971). The only mammals known to be sensitive to lower frequencies are the

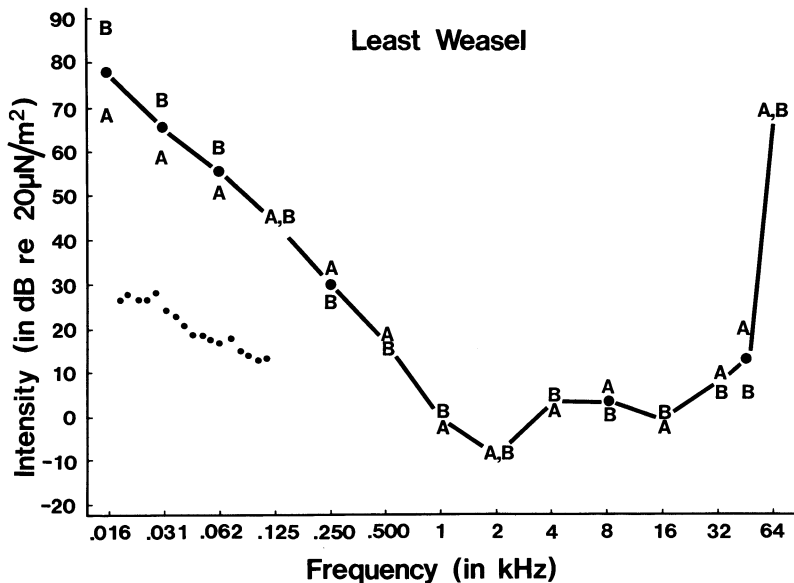


FIG. 3.—Audiogram of the least weasel. A and B represent individual animals. The dots represent background noise levels (above 100 Hz the background noise was below the sensitivity of the instruments).

Indian elephant, domestic cattle, and large primates (e.g., R. Heffner and Heffner, 1982, 1983a; Heinz et al., 1982). Thus, the low-frequency sensitivity of the least weasel is sufficiently unusual among small mammals to merit notice.

Best frequency.—The best frequency of hearing (the frequency at which an animal is most sensitive) for the least weasel is 2 kHz which again is noticeably lower than the average mammalian value of 9.1 kHz. However, the least weasel's best frequency is not as sharply defined as it is in many other mammals (cf. H. Heffner and Masterton, 1980) because least weasels have a broad range of best hearing extending from 1 kHz to 16 kHz.

Best sensitivity.—The best sensitivity (lowest absolute threshold) for the least weasel is -8 dB (at 2 kHz). This value is lower than the average mammalian value of -1.3 dB, making the least weasel one of the more sensitive mammals known, exceeded only by the wild house mouse (H. Heffner and Masterton, 1980), raccoon (Wollack, 1965), cat (Miller et al., 1963), and domestic cattle (R. Heffner and Heffner, 1983a).

High-frequency sensitivity.—The high-frequency sensitivity (highest frequency audible at an intensity of 60 dB SPL) of the least weasel is 60.5 kHz, a frequency slightly higher than the mammalian average of 51.1 kHz. While the least weasel has better high-frequency hearing than most mammals, such an ability is not unusual among mammals with small interaural distances.

Auditory Characteristics of Carnivores

With the inclusion of the least weasel, the sample of audiograms for the Carnivora contains four species representing four families—Canidae, Procyonidae, Mustelidae, and Felidae. Despite the fact that two of the audiograms are of domestic animals (cat and dog), and three families of Carnivora are not represented in this sample, a comparison of available audiograms suggests tentative conclusions concerning hearing in Carnivora.

The audiograms of the dog, raccoon, least weasel, and cat (Fig. 4) are similar with respect to the four parameters of hearing. All four are sensitive to high frequencies with the cat hearing highest followed by the least weasel, raccoon, and dog. Although the high-frequency limits in

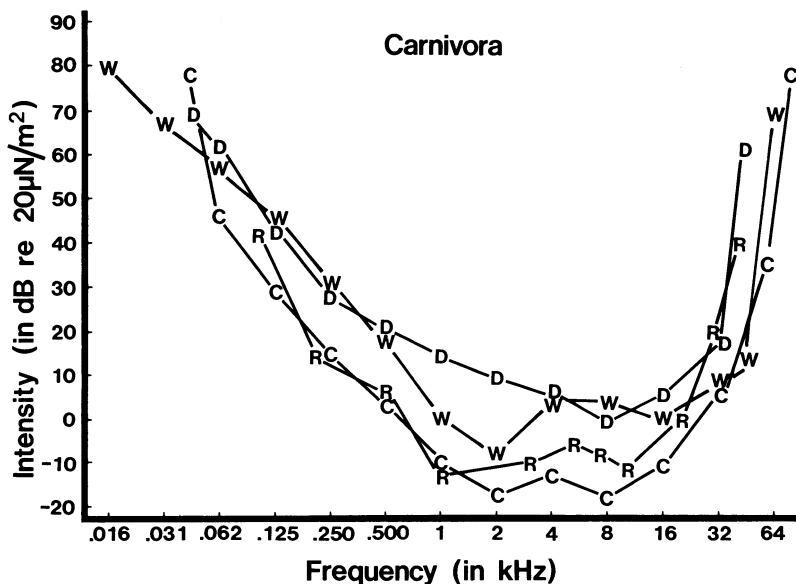


FIG. 4.—Audiograms of four species of carnivores; note overall similarity. C, cat (R. Heffner and Heffner, in press); D, dog (H. Heffner, 1983); R, raccoon (Wollack, 1965); W, least weasel.

carnivores spans a range of 35 kHz, this represents only 0.83 octave as compared with the 4 octave range in mammals as a whole. All four species are also sensitive to low frequencies. The weasel hears lowest followed closely by the cat, dog, and raccoon. The audiograms show less variation at the low frequencies than those of other orders such as primates (e.g., Masterton et al., 1969) and rodents (H. Heffner and Masterton, 1980; H. Heffner and Heffner, in press). All four carnivores have a broad range of best sensitivity which in each case lies in the range of 1 kHz to 16 kHz. In this respect carnivores differ from other orders not only in the fact that their best frequency ranges are quite similar to each other, but also in that not one shows a sharp peak of sensitivity at a single frequency as is common in other mammals (e.g., H. Heffner and Masterton, 1970, 1980). Finally, with respect to best sensitivity, the variation seen here within carnivores is no greater than that occasionally reported for a single species (e.g., H. Heffner, 1983; H. Heffner and Masterton, 1970; Miller et al., 1963).

High-frequency Hearing In Mammals

High-frequency hearing in mammals is inversely related to functional interaural distance (Δt in μs) which is defined as interaural distance divided by the speed of sound (Masterton et al., 1969). This relationship, illustrated in Fig. 5, is such that animals with small interaural distances, such as the least weasel, are better able to hear high-frequency sounds than are animals with larger interaural distances, such as horses, humans, and elephants. The correlation between maximum Δt and high frequency hearing is -0.85 ($P < 0.001$) and is based on 42 audiograms representing 40 genera (Fig. 5).

The strong inverse correlation between maximum Δt and high-frequency hearing has been attributed to selective pressure for accurate sound localization (e.g., Masterton et al., 1969; R. Heffner and Heffner, 1980). There are two primary binaural cues for sound localization: 1) the difference in the time of arrival of a sound at the two ears (Δt), and 2) the difference in the frequency-intensity spectrum of a sound reaching the two ears (Δfi). Both cues depend on the functional distance between the ears. The farther apart the ears, the larger will be the Δt cue for any given direction of a sound source. Similarly, the Δfi cue is greater for animals with large

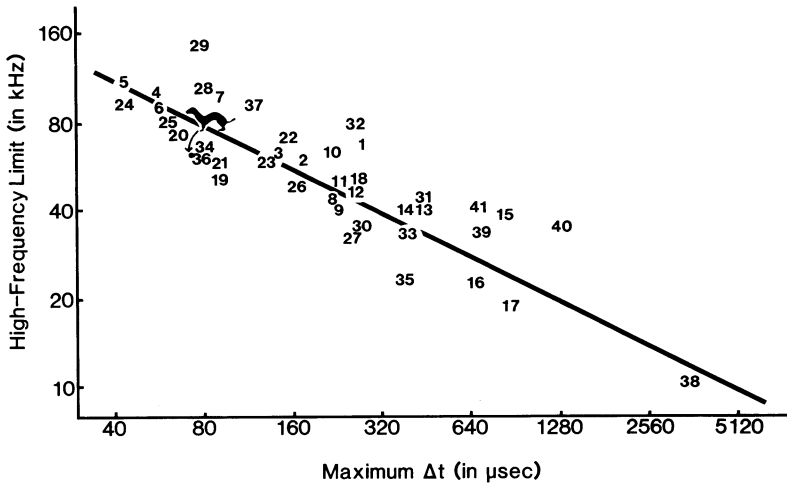


FIG. 5.—Relationship between interaural distance (maximum Δt) and the 60 dB high-frequency hearing limit. All high-frequency limits were determined in air except as noted. Silhouette, *Mustela nivalis*; 1, *Didelphis virginiana*; 2, *Hemiechinus auritus*; 3, *Tupaia glis*; 4, *Rhinolophus ferrumequinum*; 5, *Myotis lucifugus*; 6, *Eptesicus fuscus*; 7, *Noctilio leporinus*; 8, *Nycticebus coucang*; 9, *Perodicticus potto*; 10, *Galago senegalensis*; 11, *Aotus trivirgatus*; 12, *Saimiri sciureus*; 13, *Macaca* sp.; 14, *Cercopithecus mitis*; 15, *Papio cynocephalus*; 16, *Pan troglodytes*; 17, *Homo sapiens*; 18, *Oryctolagus cuniculus*; 19, *Dipodomys merriami*; 20, *Sigmodon hispidus*; 21, *Meriones unguiculatus*; 22, *Rattus norvegicus*; 23, *Neotoma floridana*; 24, *Mus musculus* (wild); 25, *Mus musculus* (domestic); 26, *Cavia porcellus*; 27, *Chinchilla* sp.; 28, *Inia geoffrensis* (under water); 29, *Tursiops truncatus* (under water); 30, *Orcinus orca* (under water); 31, *Canis familiaris*; 32, *Felis catus*; 33, *Zalophus californianus*; 34, *Phoca vitulina* (under water); 35, *Phoco vitulina*; 36, *Pusa hispida* (under water); 37, *Pagophilus groenlandicus* (under water); 38, *Elephas maximus*; 39, *Equus caballus*; 40, *Bos taurus*; 41, *Ovis aries*. For sources of individual audiograms, see H. Heffner and Heffner (in press) or R. Heffner and Heffner (1983a).

interaural distances, because the attenuation of sound is slightly greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which more effectively shadow the high-frequency content of sound. The size of both cues is smaller in animals with functionally close-set ears. In the case of Δt , the available time differences may be so small that the nervous system can detect only large changes in sound direction. However, an animal with a small head can use the Δf_i cue if it is able to perceive frequencies that are high enough to be effectively shadowed by its head and pinnae. Therefore, assuming that it is important to an animal to localize sound, animals with functionally close-set ears appear to be subjected to more selective pressure to hear high frequencies than are animals with more widely set ears.

Although the least weasel hears higher frequencies than most mammals, its 60.5-kHz high-frequency hearing limit is only 0.4 octave less than the 79.8 kHz predicted by its small (76 μ s) interaural distance and it is therefore not exceptional in this respect. Even though the relationship between high-frequency hearing and interaural distance is the dominant influence on high frequency hearing, accounting for 72% of the variance, some variation remains which may be due either to measurement error or to the existence of additional selective pressures to hear high-frequencies.

There are six points which should be noted about the relationship between maximum Δt and high-frequency hearing. First, it applies only to mammals since other vertebrate classes show little variation in high-frequency hearing (cf. Dooling, 1980; Fay, 1980; Wever, 1978). Indeed, the ability to hear much above 10 kHz appears to be a uniquely mammalian trait.

Second, the value for maximum Δt depends on the path which sound normally travels from one ear to the other as well as the velocity of sound in the particular medium. In most marine mammals, sound is transmitted through the head so maximum Δt is calculated by dividing the distance between the cochleae by the speed of sound in tissue. That the relationship is valid for aquatic mammals is illustrated by the high-frequency hearing of six species of Cetacea and Pinnipedia (Fig. 5, points 28–30, 34, 36, and 37). Furthermore, it can be seen that this relationship predicts that the harbor seal will have better high-frequency hearing underwater, where its maximum Δt is small, than in air, where its maximum Δt is larger (Fig. 5, points 34 and 35).

Third, the relationship also predicts the high frequency limits of bats and porpoises. This suggests that these animals probably did not evolve high-frequency hearing in order to use echolocation but, instead, took advantage of the high-frequency hearing which evolved as a consequence of their small interaural distance. This conclusion is supported by the 92 kHz hearing limit of a small non-echolocating mammal, the wild house mouse, which is similar to the upper hearing limits of bats.

Fourth, it is no longer justified to consider humans aberrant among mammals for their lack of ability to hear above 20 kHz. Not only is the high-frequency limit of humans close to that predicted by their maximum Δt , but a much larger animal (Indian elephant) cannot hear as high as humans. Thus, the restricted high-frequency hearing of humans seems to be a consequence of a relatively large interaural distance and not the result of a special adaptation for the reception of speech sounds, as was once widely believed (R. Heffner and Heffner, 1980).

Fifth, it appears that high-frequency hearing is a species character, not an individual character. This point is based on evidence which shows that high-frequency hearing in domestic dogs does not vary despite a wide range of head sizes (H. Heffner, 1983).

Finally, it has been suggested that high-frequency hearing evolved in order to use ultrasonic vocalizations for communication since several species of rodents are known to communicate ultrasonically (e.g., Sales and Pye, 1974). However, nearly all mammals are capable of hearing "ultrasonic" sounds (i.e., sounds above the human hearing limit of 20 kHz), but few have been shown to use their upper hearing range for communication. The vocalizations of many of these species do not contain significant high frequencies (e.g., domestic cattle whose vocalizations are generally below 1.2 kHz but which hear up to 35 kHz [R. Heffner and Heffner, 1983a; Walther, 1977] and Japanese macaques whose vocalizations are concentrated below 5 kHz but which hear up to 42 kHz [Green, 1975; Stebbins et al., 1966]). Though there is no reason to believe that high-frequency hearing evolved in rodents primarily to support ultrasonic communication, the use of ultrasound by one species (domestic *Mus musculus*) has affected its audiogram, producing a secondary peak of sensitivity in the frequency range of its vocalizations (Eheret, 1983). Nevertheless, the use of ultrasonic communication does not explain the evolution of high-frequency hearing among mammals in general, and is not necessary to explain high-frequency hearing in rodents.

Low-Frequency Hearing in Mammals

Low-frequency hearing also varies among species (e.g., Masterton et al., 1969) and is most strongly correlated not with interaural distance, but with high-frequency sensitivity (H. Heffner and Masterton, 1980). This means that animals with good high-frequency hearing generally have restricted low-frequency hearing, and vice versa. Although low-frequency hearing can be accurately predicted from high-frequency hearing for more than 80% of species ($r = 0.95$; Fig. 6), six species (elephant, human, kangaroo rat, gerbil, least weasel, and cat) are significantly deviant and reduce the correlation to $r = 0.78$. Therefore, while high- and low-frequency hearing are usually closely related, there are significant exceptions. The six deviant species fall into two groups: 1) those that do not hear nearly as low as predicted; and 2) those that hear much lower than predicted. In the first group are humans and the Indian elephant, which do not hear as low as expected based on their limited high-frequency hearing. Because these two species have the best known low-frequency hearing, it has been suggested that there might be some sort of

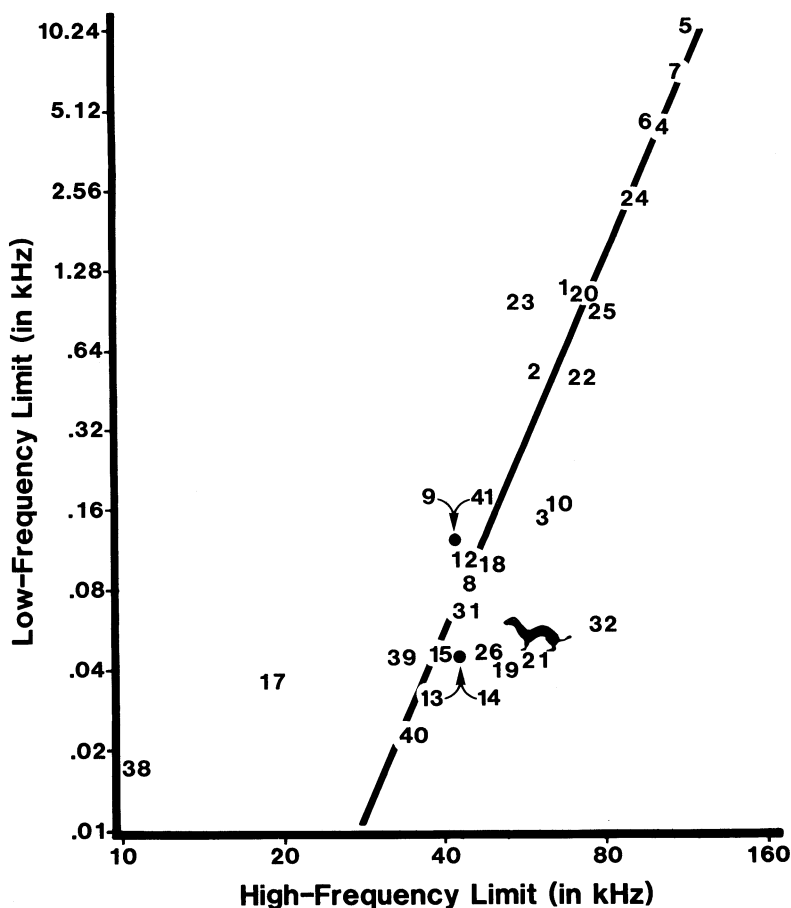


FIG. 6.—Relation between high-frequency and low-frequency hearing in 30 species of land mammals. The relation is such that for every octave change in high-frequency hearing, there is a 4.6-octave change in low-frequency hearing. The line is based on 24 species as discussed in the text. See Fig. 4 for key.

“floor effect” that prevents the hearing of frequencies below some particular low value in terrestrial mammals (H. Heffner and Masterton, 1980; R. Heffner and Heffner, 1982, 1983a). That is to say, beyond a certain point there may be either no selective advantage for further improvement or else there exists some physiological or mechanical factor preventing expansion into lower frequencies.

In the second group are species with both good high- and low-frequency hearing: the kangaroo rat, gerbil, least weasel, and domestic cat (R. Heffner and Heffner, 1985). The first mammals known to possess this capacity were the kangaroo rat, *Dipodomys merriami*, and the gerbil, *Meriones unguiculatus*. Their good low-frequency hearing has been used to argue that desert-dwelling rodents are under selective pressure to hear low frequencies and, being small mammals, they had to develop hypertrophied bullae in order to do so (Fleischer, 1978; Lay, 1972; Webster, 1966). However, the data on the least weasel suggests that these previous ideas concerning low-frequency hearing in small mammals must be modified. The least weasel's body size and low-frequency hearing ability closely resemble those of the kangaroo rat and the gerbil, but the factors used to explain the selective value of low-frequency hearing for gerbils and kangaroo rats—namely better propagation of low frequencies in desert air and predation by

snakes and owls—do not apply to the least weasel (Hatler, 1974; Lay, 1972; Rickart, 1972; Webster and Webster, 1971). Further, the least weasel contradicts the idea that small mammals require a hypertrophied bulla if they are to hear low frequencies (cf., Fleischer, 1978) since the volume of the bulla of the least weasel is only 0.15 cc, whereas that of the kangaroo rat is 0.47 cc (Webster and Webster, 1975). Based on these environmental and morphological differences between the two desert rodents and the least weasel we have concluded that there might be several different selective pressures and more than one morphological adaptation that can result in exceptional low-frequency hearing in small mammals.

ACKNOWLEDGMENTS

This research was supported by National Institutes of Health Grants NS 17850 and HD 02528 to the Bureau of Child Research, the University of Kansas. We thank B. Cushing for providing the weasels, and E. R. Hall, J. King, and B. Cushing for valuable discussions concerning weasel biology and behavior.

LITERATURE CITED

- BLAKESLEE, E. A., K. HYNSON, R. P. HAMERNIK, AND D. HENDERSON. 1978. Asymptotic threshold shift in chinchillas exposed to impulse noise. *J. Acoust. Soc. Amer.*, 63:876–882.
- DOOLING, R. J. 1980. Behavior and psychophysics of hearing in birds. Pp. 261–288, in *Comparative studies of hearing in vertebrates* (A. N. Popper and R. R. Fay, eds.). Springer-Verlag, New York, 457 pp.
- EHRET, G. 1983. Psychoacoustics. Pp. 13–56, in *The auditory psychobiology of the mouse* (J. F. Willott, ed.). Charles C Thomas, New York, 507 pp.
- FAY, R. R., AND A. N. POPPER. 1980. Structure and function in Teleost auditory systems. Pp. 3–42, in *Comparative studies of hearing in vertebrates* (A. N. Popper and R. R. Fay, eds.). Springer-Verlag, New York, 475 pp.
- FLEISCHER, G. 1978. Evolutionary principles of the mammalian middle ear. *Adv. Anat. Embryol. Cell Biol.*, 55:1–70.
- GALTON, F. 1883. *Inquiries into human faculty and its development*. The Eugenics Society, London, 270 pp.
- GREEN, S. 1975. Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study. Pp. 1–102 in *Primate behavior* (L. A. Rosenblum, ed.). Academic Press, New York, 4:1–407.
- HATLER, D. F. 1974. Foods at a golden eagle nest in central Alaska. *Condor*, 76:356–357.
- HEFFNER, H. 1983. Hearing in large and small dogs: Absolute thresholds and size of the tympanic membrane. *Behav. Neurosci.*, 97:310–318.
- HEFFNER, H., AND R. B. MASTERTON. 1970. Hearing in primitive primates: Slow loris (*Nycticebus coucang*) and potto (*Perodicticus potto*). *J. Comp. Physiol. Psychol.*, 71:175–182.
- . 1980. Hearing in glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *J. Acoust. Soc. Amer.*, 68:1584–1599.
- HEFFNER, H., AND R. HEFFNER. In press. Hearing in two cricetid rodents: Wood rat (*Neotoma floridana*) and grasshopper mouse (*Onychomys leucogaster*). *J. Comp. Psychol.*
- HEFFNER, R., AND H. HEFFNER. 1980. Hearing in the elephant (*Elephas maximus*). *Science*, 208:518–520.
- . 1982. Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Physiol. Psychol.*, 96:926–944.
- . 1983a. Hearing in large mammals: Horses (*Equus caballus*) and cattle (*Bos taurus*). *Behav. Neurosci.*, 97:299–309.
- . 1983b. Effect of cattle ear mite infestation on hearing in a cow. *J. Amer. Vet. Med. Assoc.*, 182:612–614.
- . In press. Hearing range of the domestic cat. *Hearing Res.*
- HEFFNER, R., H. HEFFNER, AND B. MASTERTON. 1971. Behavioral measurements of absolute and frequency difference thresholds in guinea pig. *J. Acoust. Soc. Amer.*, 49:1888–1895.
- HEINZ, R. D., J. S. TURKKAN, AND A. H. HARRIS. 1982. Pure tone thresholds in the yellow baboon (*Papio cynocephalus*). *Hearing Res.*, 8:71–76.
- LAY, D. M. 1972. The anatomy, physiology, functional significance, and evolution of specialized hearing organs of gerbilline rodents. *J. Morphol.*, 138:41–120.
- MASTERTON, B., H. HEFFNER, AND R. RAVIZZA. 1969. The evolution of human hearing. *J. Acoust. Soc. Amer.*, 45:966–985.
- MILLER, J. D., C. S. WATSON, AND W. P. COVELL. 1963. Deafening effects of noise on the cat. *Acta Otolaryngol.*, 176 (Suppl.):3–91.
- RICKART, E. A. 1972. An analysis of barn owl and great horned owl pellets from western Nebraska. *Prairie Nat.*, 4:35–38.
- SALES, G. D., AND J. D. PYE. 1974. *Ultrasonic communication by animals*. John Wiley and Sons, London, 281 pp.
- STEBBINS, W. C., S. GREEN, AND F. L. MILLER. 1966. Auditory sensitivity of the monkey. *Science*, 153:1646–1647.
- WALTHER, F. R. 1977. *Artiodactyla*. Pp. 655–714, in *How animals communicate* (T. A. Sebeok, ed.). Indiana Univ. Press, Bloomington, Indiana, 1,128 pp.

- WEBSTER, D. B. 1966. Ear structure and function of modern mammals. *Amer. Zool.*, 6:451–466.
- WEBSTER, D. B., AND M. WEBSTER. 1971. Adaptive value of hearing and vision in kangaroo rat predator avoidance. *Brain Behav. Evol.*, 4:310–322.
- . 1975. Auditory systems of heteromyidae:

Functional morphology and evolution of the middle ear. *J. Morphol.*, 146:343–376.

- WEVER, E. G. 1978. The reptile ear. Princeton Univ. Press, Princeton, New Jersey, 1,024 pp.
- WOLLACK, C. H. 1965. Auditory thresholds in the raccoon (*Procyon lotor*). *J. Aud. Res.*, 5:139–144.

Submitted 11 June 1984. Accepted 23 April 1985.