# Hearing in Two Cricetid Rodents:
# Wood Rat (*Neotoma floridana*)
# and Grasshopper Mouse (*Onychomys leucogaster*)

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The audiograms of two wood rats and three grasshopper mice were determined with a conditioned avoidance procedure. The wood rats were able to hear tones from 940 Hz to 56 kHz at a level of 60 dB (SPL), with their best sensitivity of −3 dB occurring at 8 kHz. The hearing of the grasshopper mice ranged from 1.85 kHz to 69 kHz at 60 dB (SPL), with their best sensitivity of 9 dB also occurring at 8 kHz. These results support the relation between interaural distance and high-frequency hearing and between high- and low-frequency hearing. The inability of the grasshopper mouse to hear low frequencies as well as other desert rodents such as kangaroo rats and gerbils demonstrates that not all rodents found in deserts have developed good low-frequency hearing. The degree to which general and specific selective pressures have played a role in the evolution of rodent hearing is discussed.

A comparison of the hearing abilities of rodents reveals wide variation in the ability of different species to hear high- and low-frequency sounds. Of the seven species whose hearing is known, high-frequency hearing ranges from an upper limit of 33 kHz in the chinchilla to 92 kHz in the wild house mouse. Low-frequency hearing also varies over a wide range, with the kangaroo rat hearing as low as 42 Hz while the comparable limit for the house mouse is 2.3 kHz (for a review, see H. Heffner & Masterton, 1980). Thus, rodents show much of the same diversity in hearing that has been shown to exist among mammals as a whole (cf. R. Heffner & Heffner, 1982, 1983).

For the most part, the variation in rodent hearing can be accounted for by the same general factors that have been used to explain the variation in mammalian hearing. Specifically, animals with small functional interaural distances (i.e., small heads and therefore close-set ears) have evolved better high-frequency hearing than animals with large interaural distances (i.e., large heads and wide-set ears) because the smaller animals rely more heavily on high frequencies to localize sound (e.g., H. Heffner & Masterton, 1980; Masterton & Diamond, 1973; Masterton, Heffner & Ravizza, 1969). This explanation is based on the availability of the binaural time and intensity cues used for sound localization and is supported by the high inverse correlation between functional interaural distance and high-frequency hearing (e.g., R. Heffner & Heffner, 1983).

The variation in low-frequency hearing, on the other hand, appears to be related to high-frequency hearing, at least for terrestrial mammals; that is, mammals with good high-frequency hearing generally have restricted low-frequency hearing, and vice versa. Though this relation is not as well understood as the relation between high-frequency hearing and interaural distance, the existence of a direct and reliable correlation between high- and low-frequency hearing ability has suggested that there may be some anatomical constraints on the frequency response properties of the mammalian ear (H. Heffner & Masterton, 1980).

Though the variation in mammalian hearing can largely be accounted for by general selective pressures common to all mammals, there is growing evidence that the hearing abilities of some species may be in part determined by specific selective pressure peculiar to those species. In particular, it has been noted that some mammals possess better low-frequency hearing than would be expected on the basis of their high-frequency hearing ability. Examples of this phenomenon are the kangaroo rat and the gerbil, two rodents that have developed good low-frequency hearing without any apparent sacrifice in high-frequency hearing (H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1983; Ryan, 1976; Webster & Webster, 1971).

The fact that the kangaroo rat and gerbil have unexpectedly good low-frequency hearing suggests that their hearing ability has been subject to unique selective pressures. Just what the source of these specific selective pressures may be, however, has not yet been fully determined. In the case of the kangaroo rat and gerbil, it has been suggested that rodents living in an open desert environment require good low-frequency hearing in order to avoid predators (Webster & Webster, 1971). However, as only a few species of rodents have been examined, it has not been possible to test this idea further or, for that matter, to determine whether other types of habitats or lifestyles may be associated with unusually good low-frequency hearing in rodents.

Recently, we have had the opportunity to enlarge our sample of rodent audiograms by testing the hearing abilities of two cricetid rodents, the wood rat and the grasshopper mouse. The ubiquitous wood rat was chosen because its preference for a woodland environment and its habit of building large nests above ground make it an interesting comparison with the Old and New World burrowing desert rodents. The fact that it has been found beyond the light-penetration zone of caves and is reported to rely on audition for orientation in the dark gives additional interest to the wood rat's auditory capacities (Dunning & Payne, 1979).

The grasshopper mouse was chosen because its carnivorous lifestyle makes it one of the more unusual rodents. Briefly, the grasshopper mouse is a small, nocturnal, burrowing rodent which inhabits short-grass prairies and deserts (Ruffer, 1965). Indeed, its range overlaps that of the kangaroo rat. The grasshopper mouse, however, is rarely preyed upon by owls, hawks, foxes, or coyotes, but is itself a predator, with animal material, including other rodents, comprising up to 89% of its diet (e.g., Cutter, 1958; Hansen, 1975; Horner, Taylor, & Padykula, 1964). Its predatory behavior is reflected in its relatively large home range, and it has developed a repertoire of calls for intraspecific communication over these distances (for a review, see McCarty, 1978). Finally, it has undergone specialization in both its digestive physiology and in its adrenal hormones for an aggressive predatory way of life (Clark, 1962; Horner et al., 1964). In short, the grasshopper mouse possesses carnivorous adaptions unique among rodents, which makes it an interesting subject for a study to assess the effects of a carnivorous lifestyle on hearing.

The purpose of this report is to present the results of hearing tests conducted on the wood rat and grasshopper mouse and thereby to expand the available sample of complete rodent audiograms. These results are then analyzed to determine the degree to which both general and specific selective pressures have played a role in the evolution of their hearing.

## Method

The animals were tested with a conditioned avoidance procedure in which a thirsty animal was trained to make continuous contact with its mouth on a water spout in order to receive a slow, 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 both avoided the shock and indicated that it had heard the tone.

### Subjects

*Wood rats.* One male (Rat A) and one female (Rat B) wood rat (*Neotoma floridana*), which had been trapped in Labette County, Kansas, were used in this study. The animals weighed 380 g and 260 g and were maintained on a diet of seeds and nuts.

*Grasshopper mice.* One female (Mouse B) and two male (Mice A and C) grasshopper mice (*Onychomys leucogaster*) approximately 4–12 months old and weighing 40–58 g were used. The animals were laboratory reared from mice that had been trapped in western Kansas. They were maintained on meal worms, crickets, and seeds.

Water was used as a reward for both species and was available only during the test session. Sessions were conducted daily during which the rats consumed 7–15 ml of water and the mice consumed 1.0–2.5 ml. Each animal was weighed before each session to monitor its health and deprivational state. In addition, all animals had been carefully examined and were found to be free of any signs of disease or parasites.

## Behavioral Apparatus

*Wood rats.* The wood rats were tested in a rectangular cage (30 × 15 × 20 cm) the walls and ceiling of which were constructed of ½-in. (1.27-cm) hardware cloth. The floor of the cage was constructed of 3/16-in. (4.8-mm) brass rods mounted ¼ in. (6.4 mm) apart in a Plexiglas frame. A blunted 20-ga. hypodermic needle was mounted in the middle of one end of the cage 6 cm above the cage floor and served as a water spout. The other end of the cage was hinged and served as a door. The entire cage was mounted on four legs 30 cm high.

*Grasshopper mice.* The grasshopper mice were tested in a cage constructed of ¼-in. (6.4-mm) hardware cloth mounted on a wooden frame (for details, see R. Heffner & Heffner, in press-a). The cage consisted of a larger section (50 × 25 × 25 cm) with a small compartment (10 × 8 × 9 cm) attached to the front end of the cage. A blunted 22-ga. hypodermic needle, which served as a water spout, was mounted so that it protruded just inside the front of the smaller compartment. The top of the cage could be removed to allow the animal to be placed in or retrieved from the cage.

During testing, the appropriate cage was placed on an acoustic-foam-covered table in a double-walled sound chamber (2.55 × 2.75 × 2.05 m). The water spout was connected by plastic tubing to an electrically operated water valve and a 25-ml water reservoir, both of which were located outside the chamber in an adjacent control room. A contact circuit connected between the water spout and cage floor served to detect when an animal made contact with the spout. A constant-current shock generator was connected between the spout and the cage floor. A loudspeaker was located 50–150 cm in front of the cage (with the distance chosen in order to achieve an even sound field of sufficient intensity for each frequency) and oriented toward the position occupied by the animal's head when it was licking the water spout.

## Acoustical Apparatus

Sine waves were generated by an oscillator (Hewlett-Packard 209A), switched on and off by an electronic switch (Grason Stadler 1287), attenuated with an attenuator (Hewlett-Packard 350D), filtered with a band-pass filter (Krohn-Hite 3202), and then led via either an impedance-matching transformer or an amplifier (Crown D75), to a loudspeaker (either a piezoelectric or ribbon tweeter for frequencies above 4 kHz; either a 5-in. [12.7-cm] midrange or 15-in. [38-cm] woofer for lower frequencies). This sound system proved capable of delivering undistorted tones from 250 Hz to 80 kHz at an intensity of at least 94 dB sound pressure level (SPL) as measured in the vicinity of the drinking spout. Test frequencies ranged from 250 Hz to 64 kHz in octave steps. Additional frequencies used were 45 kHz and 76 kHz for the wood rats and 80 kHz for the grasshopper mice. To reduce low-frequency background noise during low-frequency testing, the ventilating system for the building housing the test chamber was turned off when frequencies below 1 kHz were being used.

In order to avoid switching transients, the electrical signal was electronically switched with a rise–decay time of 10 ms. The tones were pulsed at a rate of 2/s, 400 ms on and 100 ms off.

The sound pressure level was measured with either a Brüel and Kjaer (B & K) 1-in. (2.54-cm) microphone (B & K 4131), sound level meter (B & K 2203), and octave filter (B & K 1613) or a ¼-in. (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. Finally, the intensity of the ambient noise in the test chamber was measured in ⅙-octave steps from 3.15 Hz to 20 kHz and in 1-octave steps from 20 kHz to 80 kHz (cf. R. Heffner & Heffner, 1982).

## 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 which was delivered as long as the animal maintained contact with the spout. This served to center the animal's head in the sound field. Once an animal had learned to drink steadily for at least 15 min, it was trained to break contact with the spout whenever a tone was presented. This was accomplished by presenting a 2/s pulsing tone for 2 s and following its offset with a mild electric shock delivered through the spout which was sufficiently intense to cause the animal to break contact with the spout. After only a few pairings of tone with shock, the animal 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. In order to provide feedback for successful avoidance, the lights in the test chamber were momentarily turned off each time a shock was delivered. Thus, the lights served 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 occasionally 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 then 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). In order 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, though the trial was presented as usual. Because this criterion was applied equally to safe and warning trials, it did not bias the results.

Auditory thresholds were determined for each frequency by reducing the intensity of the tone in 5-dB steps until the animal could no longer distinguish tone trials from silent trials. Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity by 5-dB increments extending from 10 dB below to 10 dB above the estimated threshold. The trials at each intensity were presented in blocks of three to five warning trials, and the level of shock was varied to ensure optimal performance. Threshold was defined as the lowest intensity that could be detected at the .01 chance level (Mann-Whitney $U$), which in this case was usually a suppression ratio of .25. Testing for a frequency was considered complete when the 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

### Wood Rats

The audiograms of the 2 wood rats (Figure 1) show comparatively good agreement between the 2 animals, which indicates that their audiograms are probably representative of wood rats in general. Beginning at the low frequencies, the audiograms show a steady improvement in sensitivity as frequency is increased until 8 kHz is reached. Above 8 kHz, sensitivity begins to decline, slowly at first, with the decline becoming steeper above 32 kHz. At the high-frequency end, Rat A was able to hear 76 kHz at a level of 73 dB, and Rat B, which could not hear 76 kHz, could hear 64 kHz at 79 dB. Overall, at an intensity of 60 dB, the wood rat's average range of hearing extends from 940 Hz to 56 kHz, with its "best frequency" (i.e., frequency with the lowest threshold) occurring at 8 kHz.

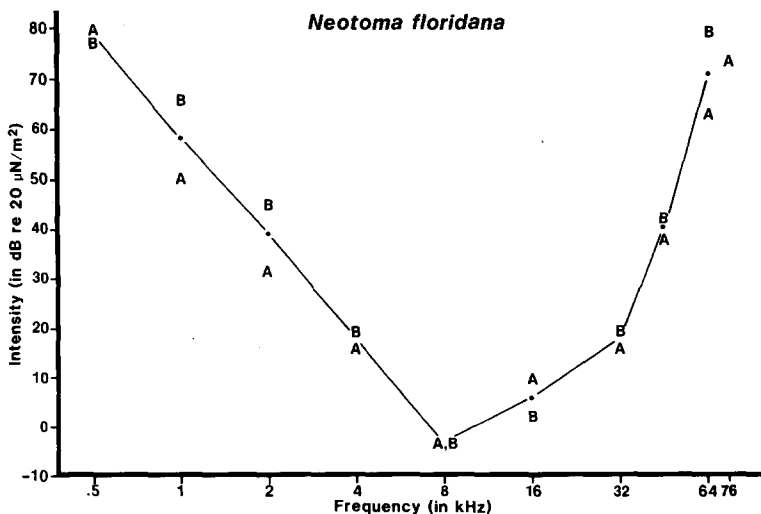In low-frequency hearing ability, the wood rat is considerably less sensitive than



*Figure 1.* Audiograms of two wood rats. (Letters represent individual animals.)

most mammals. Most other mammals tested so far can hear below 100 Hz, but the wood rat can hear no lower than 940 Hz. Such insensitivity to low-frequency sounds, however, is not unknown among small mammals, particularly insectivorous bats and some small rodents (e.g., Dalland, 1965; H. Heffner & Masterton, 1980). The other major characteristics of the wood rat audiogram, however, are not unusual. The upper limit of high-frequency hearing of 56 kHz is close to the mammalian average of 51.1 kHz, the best frequency of 8 kHz is similar to the mammalian average of 9.1 kHz, and the wood rat's best sensitivity of −3 dB (at 8 kHz) demonstrates good sensitivity, though it is not significantly better than the mammalian average of −1.3 dB (cf. R. Heffner & Heffner, 1983). In short, the most remarkable feature of the wood rat audiogram is the relative insensitivity to low frequencies.

It has been suggested that because wood rats are occasionally found in dark caves, they may use audition for orientation and obstacle detection. This idea is based on the observation that wood rats produce nonvocal (e.g., scratching) sounds which apparently enable them to detect objects in darkness (Dunning & Payne, 1979). Al-

though these sounds contain most of their energy in the low-frequency region where the rats are not particularly sensitive, it is possible that the animals use the high-frequency components of the sounds for passive echolocation.

## Grasshopper Mice

The audiograms of the 3 grasshopper mice (Figure 2) also show good agreement between animals and have the same overall shape as the wood rat audiogram. Beginning at the low frequencies, the audiograms depict a steady increase in sensitivity as frequency is increased until the best frequency is reached at 8 kHz. Above 8 kHz, sensitivity declines gradually to 64 kHz beyond which it decreases sharply. At 60 dB the average hearing range of the grasshopper mouse extends from 1.85 kHz to 69 kHz.

The low-frequency sensitivity of the grasshopper mouse is poorer than that of the wood rats. Indeed, only Mouse A could hear 1 kHz at an intensity less than 90 dB, and none of the 3 mice responded to 250 Hz and 500 Hz at an intensity of 94 dB. Only insectivorous bats and the wild house mouse are less sensitive to low frequencies
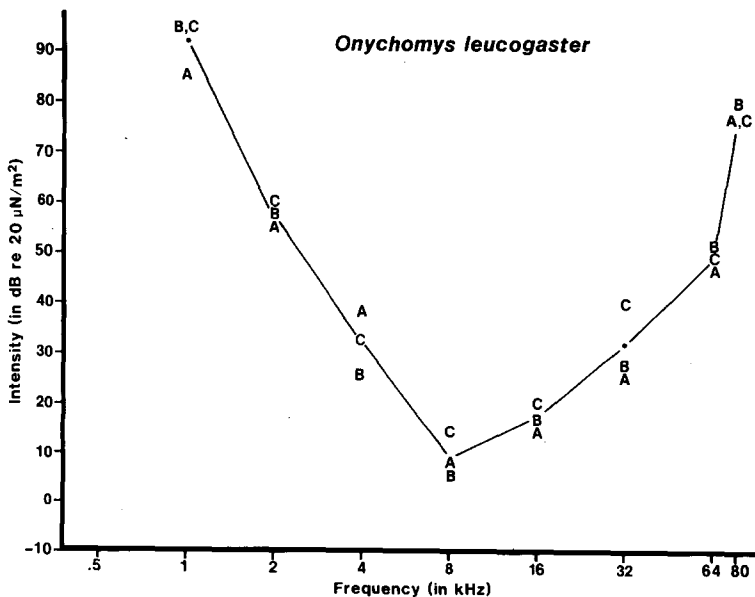


*Figure 2.* Audiograms of three grasshopper mice. (Letters represent individual animals.)

than the grasshopper mouse. On the other hand, the 69 kHz high-frequency limit of the mouse is noticeably superior to the wood rat's, and it exceeds the upper limit of most mammals other than insectivorous bats, the wild house mouse, and some cetacea. Like the wood rat, the grasshopper mouse is most sensitive around 8 kHz, though its threshold of 9 dB makes it less sensitive than the rat. Overall, then, the grasshopper mouse has noticeably poor low-frequency hearing coupled with good high-frequency hearing.

### Background Noise Level

Measurable background noise (i.e., greater than 10 dB) was present in the test chamber only at frequencies below 125 Hz, and the noise level never exceeded 15 dB. The relative quietness of the chamber at low frequencies was due to the fact that the building's ventilating system, which produced measurable low-frequency noise, was turned off when testing frequencies below 1 kHz. Because the background noise level was so far below the animals' low-frequency thresholds, their inability to detect frequencies below 1 kHz or 500 Hz could not be due to the presence of such noise but, instead, appears to be a true inability to hear low-frequency sounds. Whether the animals' thresholds at their best frequency of hearing (8 kHz) was affected by background noise cannot be as precisely determined because any noise at this frequency was below the sensitivity of the sound measuring equipment. However, as background noise levels generally fall off rapidly at higher frequencies (cf. R. Heffner & Heffner, 1983), it is very unlikely that background noise affected any part of these audiograms.

### Discussion

The inclusion of the wood rat and grasshopper mouse raises to nine the total number of rodent species whose audiograms have been behaviorally determined. In the first part of the following discussion, we compare the hearing abilities of these two species with those of other rodents. In the

second part, we compare the hearing of rodents with that of mammals in general in a discussion of the evolution of high- and low-frequency hearing.

### Auditory Characteristics of Rodents

The audiograms of nine rodents, shown in Figure 3, illustrate the diversity of hearing found in rodents. This diversity can be described in terms of low-frequency hearing, high-frequency hearing, best frequency, and best sensitivity. In comparing low- and high-frequency hearing across species, we have generally used the lowest and highest frequencies audible at 60 dB. Although a higher level, such as 70 or 80 dB, might be preferable, few animals have been tested at those limits. Because comparisons in which the 60 dB criterion is used give similar results to those in which a higher level is used (cf. Heffner & Masterton, 1980; Masterton et al., 1969), the 60 dB criterion seems preferable because it permits the inclusion of more species in the analysis.

*Low-frequency hearing.* The lowest frequency audible at a level of 60 dB, that is, the 60 dB cutoff, can be interpolated or estimated for all of the rodents except the chinchilla. As shown in Table 1, the cutoffs run from a low of 42 Hz for the kangaroo rat to 2.3 kHz for the wild house mouse. The variation in low-frequency hearing among rodents thus spans a range of nearly six octaves and is much larger than the variation found so far in any other order of mammals.

In examining Figure 3, it appears that the rodents fall into one of two groups according to their low-frequency sensitivity. The first group consists of those animals with good low-frequency hearing and includes the chinchilla, kangaroo rat, gerbil, and guinea pig. This group contains both the larger rodents in this sample (i.e., chinchilla and guinea pig) as well as those rodents with greatly enlarged bullae (i.e., the kangaroo rat, gerbil, and chinchilla; Nowak & Paradiso, 1983).

The second group consists of those rodents that are not as sensitive to low frequencies and contains the laboratory rat,
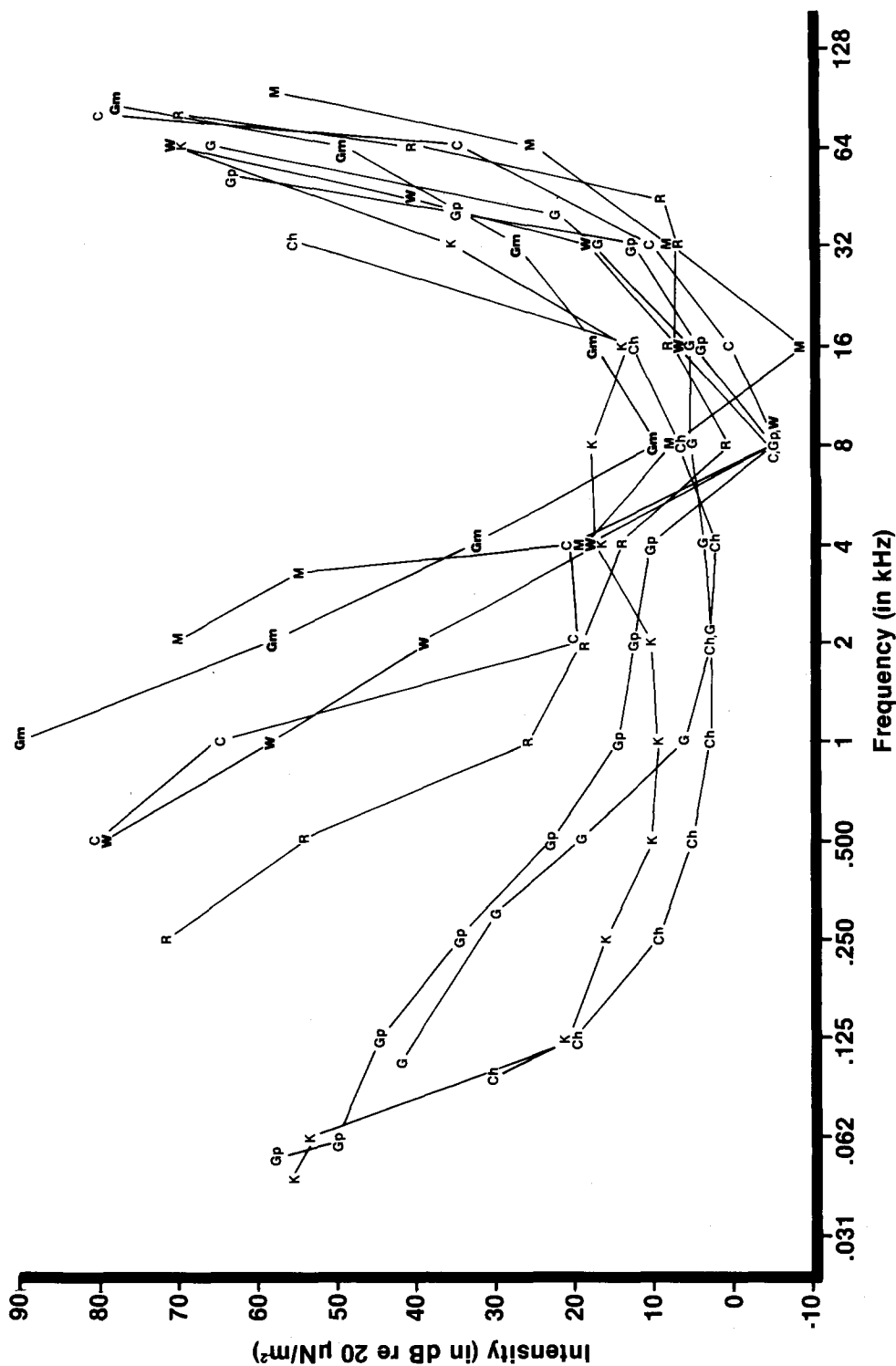
*Figure 3.* Audiograms of nine species of rodents. (Note the large variation in low-frequency sensitivity. C, cotton rat; Ch, chinchilla; G, gerbil; Gm, grasshopper mouse; Gp, guinea pig; K, kangaroo rat; M, wild mouse; R, laboratory rat; W, wood rat. For references to individual audiograms, see Figure 4.)

Table 1
*Auditory Characteristics of Rodents*

| Species | 60-dB low-frequency limit (in kHz) | 60-dB high-frequency limit (in kHz) | Best frequency (in kHz) | Lowest threshold (in dB SPL) |
|---|---|---|---|---|
| Chinchilla | — | 33 | 2.9 | 0 |
| Guinea pig | .045[a] | 49 | 8 | −6 |
| Kangaroo rat | .042[a] | 52 | 1 | 3 |
| Wood rat | .940 | 56 | 8 | −3 |
| Gerbil | .043[a] | 58 | 2.9 | 3 |
| Grasshopper mouse | 1.850 | 69 | 8 | 9 |
| Cotton rat | 1.000 | 72 | 8 | −6 |
| Laboratory rat | .400 | 72 | 8 | 0 |
| Wild house mouse | 2.300 | 92 | 16 | −10 |

*Note.* Low- and high-frequency limits defined, respectively, as the lowest and highest frequencies audible at 60 dB SPL. Animals are listed in order of high-frequency hearing ability. Data are taken from audiograms listed in the caption to Figure 4.
[a] Extrapolated value.

wood rat, cotton rat, grasshopper mouse, and wild house mouse. These are the smaller rodents that do not possess hypertrophied bullae. Thus, it appears that good low-frequency hearing in rodents is found either in the large species (i.e., the guinea pig and chinchilla) or in small rodents that have evolved hypertrophied bullae evidently as a result of special selective pressure for good low-frequency hearing.

*High-frequency hearing.* The highest frequency audible at a level of 60 dB can be interpolated or estimated for all 9 rodents. The cutoffs for these animals vary from 33 kHz for the chinchilla to 92 kHz for the wild house mouse. This variation is about 1.5 octaves and is less than the variation noted among other mammalian orders such as primates (e.g., H. Heffner & Masterton, 1980; Masterton et al., 1969). Neither the wood rat, with a cutoff of 56 kHz, nor the grasshopper mouse, with a cutoff of 69 kHz, is unusual in its high-frequency hearing.

*Best frequency of hearing.* The best frequency of hearing, as defined by the frequency with the lowest absolute threshold, is dependent to a certain extent on the particular frequencies used in testing. Though the testing of frequencies at less than octave steps is necessary for a precise calculation of best frequency, two points can be made from the present data. First, most of the rodents, including the wood rat and grasshopper mouse, have an obvious

best frequency in the range of 8–16 kHz (Figure 3 and Table 1). With the exception of the guinea pig, these are the animals with restricted low-frequency sensitivity. Second, those rodents that have a lower best frequency are the three that have hypertrophied bullae, that is, the chinchilla, kangaroo rat, and gerbil. It is of interest to note that the shift in best frequency in these three species is accompanied by a broadening of the range of good hearing such that, in contrast to the other rodents, it is difficult to select a single best frequency.

*Best sensitivity of hearing.* Best sensitivity is defined as the sound pressure level of the lowest audible intensity of the audiogram. The lowest thresholds of rodents range from 9 dB for the grasshopper mouse to −10 dB for the wild house mouse. The average lowest threshold for rodents of −1 dB is quite close to the average of −1.3 dB for all mammals (cf. R. Heffner & Heffner, 1983). The −3 dB best sensitivity of the wood rat, then, is about average, and the 9 dB best sensitivity of the grasshopper mouse makes it the least sensitive of the rodents.

*Wood rat and grasshopper mouse versus other rodents.* Neither the wood rat nor the grasshopper mouse appears to be particularly unusual in any way. Although neither hears very low frequencies, this lack of low-frequency sensitivity is a characteristic that they share with other small rodents

that lack hypertrophied bullae. Similarly, the high-frequency cutoffs of the wood rat and grasshopper mouse are within the range of other rodents. Finally, these two animals have typical best frequencies of 8 kHz, with the only noteworthy feature being that the grasshopper mouse is slightly less sensitive than the other rodents.

Although it is not surprising that the audiogram of the wood rat is similar to that of other rodents, the carnivorous grasshopper mouse might have been expected to differ in some way. Yet in spite of the fact that it has developed physiological adaptions to a carnivorous diet, there is no indication that the auditory sensitivity of the grasshopper mouse has specialized for a predatory lifestyle (cf. R. Heffner & Heffner, in press-a).

It is of interest to note that grasshopper mice do appear to rely heavily on audition to locate live prey. In the laboratory, grasshopper mice have been shown to preferentially approach the source of the sound of cricket movements as opposed to the sight of a moving cricket. Furthermore, the presence of loud white noise disrupts their ability to find and kill crickets even when visual and olfactory cues are available (Langley, 1983). Thus, the hearing ability of grasshopper mice, though not specialized in comparison with other rodents, nevertheless appears to play an important role in the location and capture of prey.

### Systematic Variation in the Limits of Mammalian High-Frequency Hearing

*Functional interaural distance.* It has been noted that among mammals high-frequency hearing is inversely related to functional interaural distance as expressed in terms of maximum $\Delta t$ (interaural distance divided by the speed of sound). This relation is illustrated in Figure 4 which shows high-frequency hearing as a function of maximum $\Delta t$. As can be seen in this figure, animals with small interaural distances, such as the grasshopper mouse and wood rat, are better able to hear high-frequency sounds than animals with larger interaural distances, such as horses, humans, and elephants. At the present time, the correlation between maximum $\Delta t$ and high-frequency hearing is $-.85$ ($p < .001$) and is based on 43 audiograms representing 41 genera. This relation is the dominant influence in mammalian high-frequency hearing, accounting for 72% of the variance. The relation, though applicable only to mammals, applies even to those highly specialized species such as the echolocators and those adapted for hearing under water (R. Heffner & Heffner, 1982; Masterton et al., 1969).

The existence of a strong inverse relation between maximum $\Delta t$ and high-frequency hearing has been attributed to selective pressure for the accurate localization of sound (e.g., R. Heffner & Heffner, 1980; Masterton et al., 1969). Briefly, there are two primary binaural cues for sound localization, the difference in the time of arrival of a waveform at the two ears ($\Delta t$ or $\Delta\theta$) and the difference in the frequency-intensity spectrum of a sound reaching the two ears ($\Delta fi$). The magnitude of both the time and intensity cues depends on the functional distance between the two ears, that is, the farther apart the ears, the larger will be the $\Delta t$ cue from any given direction of a sound source. Similarly, the $\Delta fi$ cue is greater for animals with large interaural distances, both 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.

Although the two binaural sound-localization cues are available to animals with large heads, the size of either cue is smaller in animals with functionally close-set ears. In the case of $\Delta t$, 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 $\Delta fi$ 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 animals with more widely set ears.
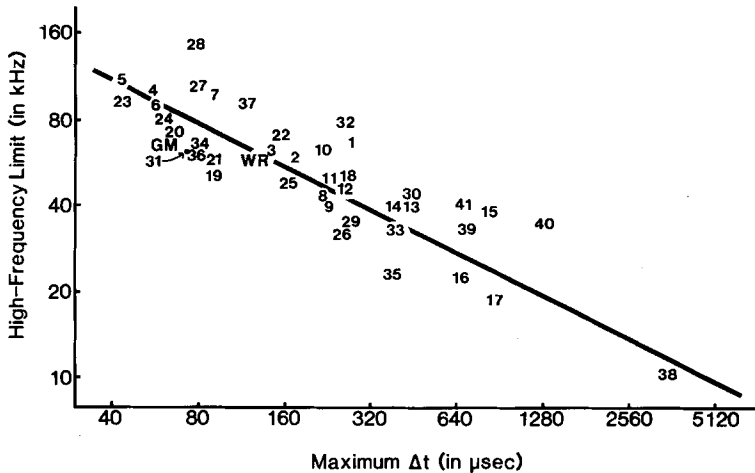
*Figure 4.* Relation between maximum Δ*t* (maximum interaural distance divided by the speed of sound) and high-frequency hearing limit (highest frequency audible at 60 dB SPL). (All high-frequency limits were determined in air except as noted. GM, grasshopper mouse [*Onychomys leucogaster*]; WR, wood rat [*Neotoma floridana*]; 1, opossum [*Didelphis virginiana*; Ravizza, Heffner, & Masterton, 1969a]; 2, hedgehog [*Hemiechinus auritus*; Ravizza, Heffner, & Masterton, 1969b]; 3, tree shrew [*Tupaia glis*; H. Heffner, Ravizza, & Masterton, 1969a]; 4, horseshoe bat [*Rhinolophus ferrumequinum*; Long & Schnitzler, 1975]; 5, little brown bat [*Myotis lucifugus*; Dalland, 1965]; 6, big brown bat [*Eptesicus fuscus*; Dalland, 1965]; 7, fishing bat [*Noctilio leporinus*; Wenstrup, 1985]; 8, slow loris [*Nycticebus coucang*; H. Heffner & Masterton, 1970]; 9, potto [*Perodicticus potto*; H. Heffner & Masterton, 1970]; 10, bushbaby [*Galago senegalensis*; H. Heffner, Ravizza, & Masterton, 1969b]; 11, owl monkey [*Aotus trivirgatus*; Beecher, 1974a]; 12, squirrel monkey [*Saimiri sciureus*; Beecher, 1974b; Green, 1975]; 13, macaque [*Macaca* sp.; Behar, Cronholm, & Loeb, 1965; Stebbins, Green, & Miller, 1966]; 14, blue monkey [*Cercopithecus mitis*; Brown & Waser, 1984]; 15, baboon [*Papio cynocephalus*; Hienz, Turkkan, & Harris, 1982]; 16, chimpanzee [*Pan troglodytes*; Farrer & Prim, 1965]; 17, human [*Homo sapiens*; Davis, 1960]; 18, rabbit [*Oryctolagus cuniculus*; H. Heffner & Masterton, 1980]; 19, kangaroo rat [*Dipodomys merriami*; H. Heffner & Masterton, 1980]; 20, cotton rat [*Sigmodon hispidus*; H. Heffner & Masterton, 1980]; 21, gerbil [*Meriones unguiculatus*; Ryan, 1976]; 22, laboratory rat [*Rattus norvegicus*; Kelly & Masterton, 1977]; 23, feral house mouse [*Mus musculus*; H. Heffner & Masterton, 1980]; 24, laboratory mouse [*Mus musculus*; Markl & Ehret, 1973]; 25, guinea pig [*Cavia porcellus*; R. Heffner, Heffner, & Masterton, 1971]; 26, chinchilla [*Chinchilla* sp.; Miller, 1970]; 27, dolphin under water [*Inia geoffrensis*; Jacobs & Hall, 1972]; 28, porpoise under water [*Tursiops truncatus*; Johnson, 1967]; 29, killer whale under water [*Orcinus orca*; Hall & Johnson, 1972]; 30, dog [*Canis familiaris*; H. Heffner, 1983]; 31, least weasel [*Mustela nivalis*; R. Heffner & Heffner, in press-a]; 32, cat [R. Heffner & Heffner, in press-b]; 33, sea lion in air [*Zalophus californianus*; Schusterman, Balliet, & Nixon, 1972]; 34, harbor seal under water [*Phoca vitulina*; Mohl, 1968]; 35, harbor seal in air [*Phoca vitulina*; Mohl, 1968]; 36, ringed seal under water [*Pusa hispida*; Terhune & Ronald, 1975]; 37, harp seal under water [*Pagophilus groenlandicus*; Terhune & Ronald, 1972]; 38, elephant [*Elephas maximus*; R. Heffner & Heffner, 1980]; 39, domestic horse [*Equus caballus*; R. Heffner & Heffner, 1983]; 40, domestic cattle [*Bos taurus*; R. Heffner & Heffner, 1983]; 41, domestic sheep [*Ovis aries*; Wollack, 1963].)

*Ultrasonic communication.* Because it has been suggested that high-frequency hearing evolved in order to use ultrasonic vocalizations for communication (e.g., Sales & Pye, 1974), it is of interest to determine whether the wood rat and grasshopper mice produce ultrasonic vocalizations. Wood rats have been observed to vocalize only when injured or fighting (Wiley, 1980), but grasshopper mice use a variety of communicatory vocalizations. Preliminary analyses have been made of the calls of mature and neonatal grasshopper mice which indicate that their vocalizations are primarily in the sonic range with fundamental frequencies below 13 kHz (Hafner & Hafner, 1979; Hildebrand, 1961). Though Hafner and Hafner originally reported that two calls of the grasshopper mouse contained a 59-kHz compo-

nent, they now consider that finding artifactual (M. S. Hafner, personal communication, March 15, 1985). However, ultrasonic communication is common among rodents (e.g., Nyby & Whitney, 1978; Sales & Pye, 1974; J. Smith, 1975; W. Smith, 1979), and it is not impossible that these animals use the upper end of their hearing range for communication.

It has been argued elsewhere that the ubiquity of ultrasonic hearing among species of mammals that do *not* produce ultrasonic vocalizations suggests that rodents did not evolve good high-frequency hearing for the purpose of ultrasonic communication (R. Heffner & Heffner, in press-a). This does not mean that the development of ultrasonic communication has had no effect on their audiogram. Indeed, it has been demonstrated that domestic house mice have a secondary peak of sensitivity in their audiogram in the frequency range of their ultrasonic vocalizations (Ehret, 1983). However, it appears that ultrasonic hearing evolved primarily in response to the need to localize sound and was later used for ultrasonic communication.



*Figure 5.* Relation between high-frequency and low-frequency hearing for 32 species of terrestrial and aerial mammals. (The relation is such that for every octave change in high-frequency hearing, there is a 4.7-octave change in low-frequency hearing. See Figure 4 for key.)

*Systematic Variation in Mammalian Low-Frequency Hearing*

It has been noted that low-frequency hearing shows greater variation between species even than high-frequency hearing (R. Heffner & Heffner, 1982). In seeking an explanation of this variation, it has been found that in mammals that hear in air, low-frequency hearing is directly correlated not with interaural distance (maximum $\Delta t$) or with body weight but with high-frequency hearing (H. Heffner & Masterton, 1980). Specifically, animals with good high-frequency hearing usually have relatively poor low-frequency hearing, whereas animals with good low-frequency hearing generally do not hear very high frequencies.

The relation between high- and low-frequency hearing is illustrated in Figure 5 for 32 species of terrestrial and aerial mammals. The correlation coefficient is high (.78) and is statistically reliable ($p < .001$). The relation is such that for every octave of high-frequency hearing gained, 4.7 oc-
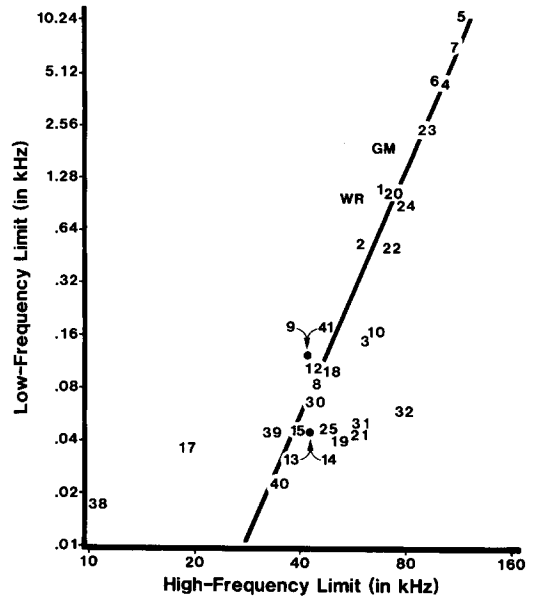
taves of low-frequency hearing are lost. As can be seen in this figure, the hearing ranges of both the wood rat and the grasshopper mouse are in agreement with the relation, that is, both species have good high-frequency hearing with consequent poor low-frequency hearing.

Inspection of Figure 5, however, reveals that there are six species that deviate significantly from the relation. These species fall into two groups: (a) the elephant and human, which do not hear as low as expected, and (b) the kangaroo rat, gerbil, least weasel, and domestic cat, which hear lower than expected. The degree to which these six species deviate from the rest of the animals is indicated by the fact that dropping them from the sample raises the correlation coefficient from .78 to .94. It is the existence of these exceptions, then, that suggests that the low-frequency portions of some species' audiograms may have been shaped by selective pressures unique to those species. The question arises as to what these selective pressures may be.

Potential explanations of the inability of humans and elephants to hear as low as predicted by their high-frequency hearing have been discussed elsewhere (R. Heffner & Heffner, 1982). Briefly, it is possible that these two species do not hear well below 16 Hz either because there is a physiological limit to low-frequency hearing in mammals or because there is no benefit from hearing that low. Further discussion on this issue, however, must await the study of additional species that possess good low-frequency hearing.

Of particular relevance to the present discussion is the second group which consists of animals that hear significantly lower than predicted by their high-frequency hearing. Originally, this group consisted of the kangaroo rat and gerbil, though recent studies have allowed us to add the least weasel and domestic cat (R. Heffner & Heffner, in press-a, in press-b). The kangaroo rat and gerbil are of particular interest because their good low-frequency hearing has been accompanied by the development of hypertrophied bullae. Indeed, it is widely believed that desert rodents need good low-frequency sensitivity in order to avoid predators and that small animals need enlarged bullae in order to transduce low-frequency sounds (e.g., Fleischer, 1978; Lay, 1972; Webster & Webster, 1984). However, recent evidence suggests that the situation may be more complex.

First, the range of the grasshopper mouse includes desert environments (indeed its range overlaps that of the kangaroo rat), yet it has not developed good low-frequency hearing. Although it might be argued that the grasshopper mouse is not preyed upon as heavily as the kangaroo rat and, therefore, has not needed to develop good low-frequency hearing, it must be noted that a small rodent living in a desert environment does not necessarily develop good low-frequency hearing. Second, it has recently been demonstrated that a very small mammal, the least weasel, is able to hear low-frequencies without having developed hypertrophied bullae (R. Heffner & Heffner, in press-a). Indeed, the least weasel, which is smaller than the kangaroo rat and the gerbil in both interaural distance and body weight, is able to hear as low as 50 Hz at 60 dB (Figure 5). Therefore, it appears that it is not necessary for a small mammal to develop hypertrophied bullae in order to hear low-frequency sounds.

Given these findings, the question remains as to why some rodents, that is, the kangaroo rat, gerbil, chinchilla, and guinea pig, have developed good low-frequency hearing, whereas others, including the two reported here, have not. In seeking an answer, it should be noted that it was at one time proposed that low frequencies were used by rodents with hypertrophied bullae for intraspecific communication (Legouix, Petter, & Wisner, 1954; Legouix & Wisner, 1955). Though it has been pointed out that these rodents do not produce low-frequency vocalizations (Webster & Webster, 1984), some of the species commonly found in large colonies, particularly the kangaroo rats and gerbils, are known to engage in foot stamping during mating and in times of general excitement or danger (e.g., Gulotta, 1971; Kenagy, 1976). Whether the use of such low-frequency signals is common among colonial rodents with good low-frequency hearing remains to be determined. On the other hand, the wood rat is reported to produce a thumping sound with its hindfeet but does not live in colonies (Wiley, 1980) and does not hear low frequencies. Just what the influence may be of communal living or foot stamping on low-frequency hearing remains to be determined.

In conclusion, it appears that the hearing ability of most rodents is determined by the same selective pressures that have shaped mammalian hearing in general. The primary source of this pressure has been the need to localize sound, which has resulted in the evolution of different high-frequency hearing abilities appropriate to the different sizes of the individual species. On the other hand, the existence of some animals with unusually good low-frequency hearing indicates that the hearing range of a mammal can also be markedly affected by selective pressures specific to that species.

### Relation of Hearing to Receptor Morphology

The variation in mammalian hearing is also of importance to the study of the me-

chanics of the ear. The previous discussion was concerned primarily with the selective pressures involved in hearing, that is, *why* the hearing ability of mammals varies. At another level there is the question as to *how* the hearing ability of mammals varies; that is, what are the physical properties of the ear that are associated with the various parameters of hearing? At present, little is known concerning the relation between receptor morphology and such parameters as high-frequency hearing, low-frequency hearing, and best sensitivity. The size of the auditory apparatus is believed to be related to frequency response and absolute sensitivity, but little quantified data are available (e.g., Fleischer, 1978; Khanna & Tonndorf, 1978; von Bekesy, 1960). Furthermore, the fact that the size of such structures as the tympanic membrane can vary within a species by a factor of two with no noticeable effect on hearing indicates that hearing ability does not vary passively with transducer size (H. Heffner, 1983). As the number of species for which audiograms are available increases, it will become possible to explore the relations between auditory structure and function.

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