Hearing

Henry E. Heffner
Rickye S. Heffner

This essay focuses on the hearing abilities of animals (*what* they hear) and the selective pressures involved in the evolution of hearing (*why* they hear as they do). The data consist of behaviorally determined measures of hearing in vertebrates and insects—the two groups of animals in which hearing is most highly developed. These are supplemented, where necessary, with electrophysiological measures of hearing.

Hearing is the ability to respond to sounds—which by definition are vibrations transmitted either through air, water, or ground (substrate)—using a receptor for which such vibrations are the most effective stimulus (Wever, 1978). The ability to hear confers three advantages. The first is the ability to *detect* sounds, which are usually produced by other animals. The second is the ability to *localize* a sound so that an animal can either approach or avoid the sound source. Finally, hearing enables an animal to *identify* sound sources so that it may respond appropriately; this last category includes the interpretation of communication signals and language, as well as the identification of predators, prey, and conspecifics.

There are a number of behavioral conditioning procedures that can be used to assess hearing in mammals, birds, and fish, while unconditioned responses to sound can be elicited from many amphibians and insects. However, there are virtually no behavioral techniques for assessing hearing in reptiles. Electrophysiological measures (such as the electrical response of the receptor, auditory nerve, or central nervous system) may be used to obtain an estimate of an animal's hearing ability. However, neural responses do not accurately predict an animal's behavioral sensitivity; the presence of a neural response does not always mean that an animal

can hear a sound, and the inability to record a response does not always mean that the animal cannot hear it.

Detection of Sound

The most basic measure of hearing is the audiogram, which consists of the absolute thresholds for pure tones throughout an animal's hearing range. Four features of audiograms that are useful for cross-species comparisons are the highest and lowest frequencies an animal can hear at a sound pressure level (SPL) of 60 dB (re 20 μPa, the standard sound pressure reference level, where Pa = Pascals), the frequency of best sensitivity, as well as the intensity at best threshold (Masterton, Heffner & Ravizza, 1969). As shown in Figure 1, the values for humans are 17.6 kHz for high-frequency hearing, 31 Hz for low-frequency hearing, and 4 kHz for the best frequency of hearing, at which point the best sensitivity is −10 dB.

Localization of Sound

Sound-localization *acuity* is typically measured by presenting a sound from one of two loudspeakers and determining the smallest angle of separation that can be discriminated 50% of the time. Sound-localization *accuracy* is the precision with which an animal orients to a sound (i.e., the average error). Because sound-localization performance can vary depending on the spectrum and duration of the stimulus used, the standard stimulus for comparative purposes is often a brief broad-band signal such as a click or noise burst.
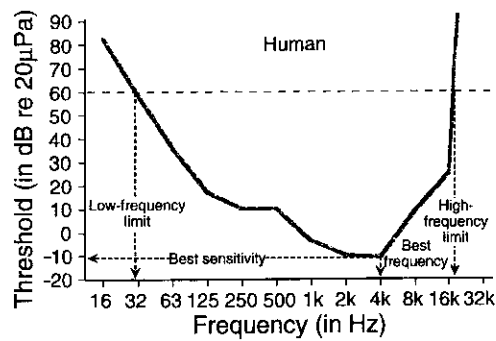
Figure 1. Human audiogram with shaded line indicating thresholds at octave frequencies. This is the average audiogram of seven individuals tested under the same conditions used to test animals, that is, in a sound-proof chamber with the tones presented via a loudspeaker. H. E. Heffner & R. S. Heffner (1992), p. 161.

Identification of Sound

The identification of sound refers to the ability to respond to a sound, not in terms of the physical characteristics of the sound but in terms of the biological characteristics of the sound's source (Masterton, 1992). Thus, the physical characteristics of a sound are used to infer the nature and disposition of the sound source (e.g., whether it is a predator, prey, or conspecific). This can be studied in the laboratory by training animals to discriminate sounds based on natural categories or in the field by observing the reactions of animals to recorded sounds.

Mammals

The evolution of mammals from the reptilian ancestor was marked by the development of three anatomical auditory features: (1) an external ear or pinna, (2) a three-bone middle ear, and (3) a coiled inner ear or cochlea, which contains the receptor cells. These three features are related to the fact that mammals generally have better sensitivity than other animals and are the only vertebrates that hear well above 10 kHz. Indeed, it has been suggested that mammals owe much of their evolutionary success to their sense of hearing (Stebbins, 1983).

Although all mammals possess the same basic middle and inner ears, the ability of mammals to detect and localize sound shows large species differences. Much of the variation appears to be part of a general "mammalian plan," stemming from the fact that a major

source of selective pressure in the evolution of mammalian hearing has been the need to localize sound in order to direct the eyes to sound sources.

Detection of Sound

Behavioral audiograms are available for over 70 species of mammals representing 12 different orders (see Fay, 1988). The audiograms shown in Figure 2 illustrate the variation found among mammals, particularly with regard to high- and low-frequency hearing. Using the 60-dB cutoff points, high-frequency hearing varies by more than 4 octaves, with the Indian elephant hearing up to only 10.5 kHz while some bats and cetacea hear over 100 kHz. However, subterranean mammals have degenerate hearing, and the upper limit of the blind mole rat, for example, is only 5.9 kHz. Low-frequency hearing shows even greater variation, ranging from 17 Hz for the elephant to 10.3 kHz for the little brown bat, a range of over 9 octaves.

High-Frequency Hearing. The explanation for the variation in high-frequency hearing is that it allows mammals to use both binaural spectral differences and pinna cues to localize sound (H. E. Heffner & R. S. Heffner, 1992; R. S. Heffner & H. E. Heffner, 1992a). Briefly, there are two binaural sound localization cues: the difference in the time of arrival and the difference in the frequency-intensity spectrum of a sound reaching the two ears. For both cues, the magnitude of the binaural difference depends on the size of an animal's head; that is, the further apart the ears, the larger will be the time and spectral differences in the sound reaching the two ears. Although both binaural locus cues are readily available to animals with large heads, their effectiveness is diminished in animals with close-set ears. However, a small animal can increase the magnitude of the spectral difference cue available to it if it is able to hear frequencies that are high enough to be effectively shadowed by its head and pinnae. Thus, the smaller an animal's head, the higher it must hear in order to obtain a usable binaural spectral-difference cue.

High-frequency hearing is even more important for using the pinnae to localize sound. Briefly, a pinna acts as a directional filter that modifies the spectrum of a sound reaching the eardrum as a function of the location of the sound source. This directional effect is not only
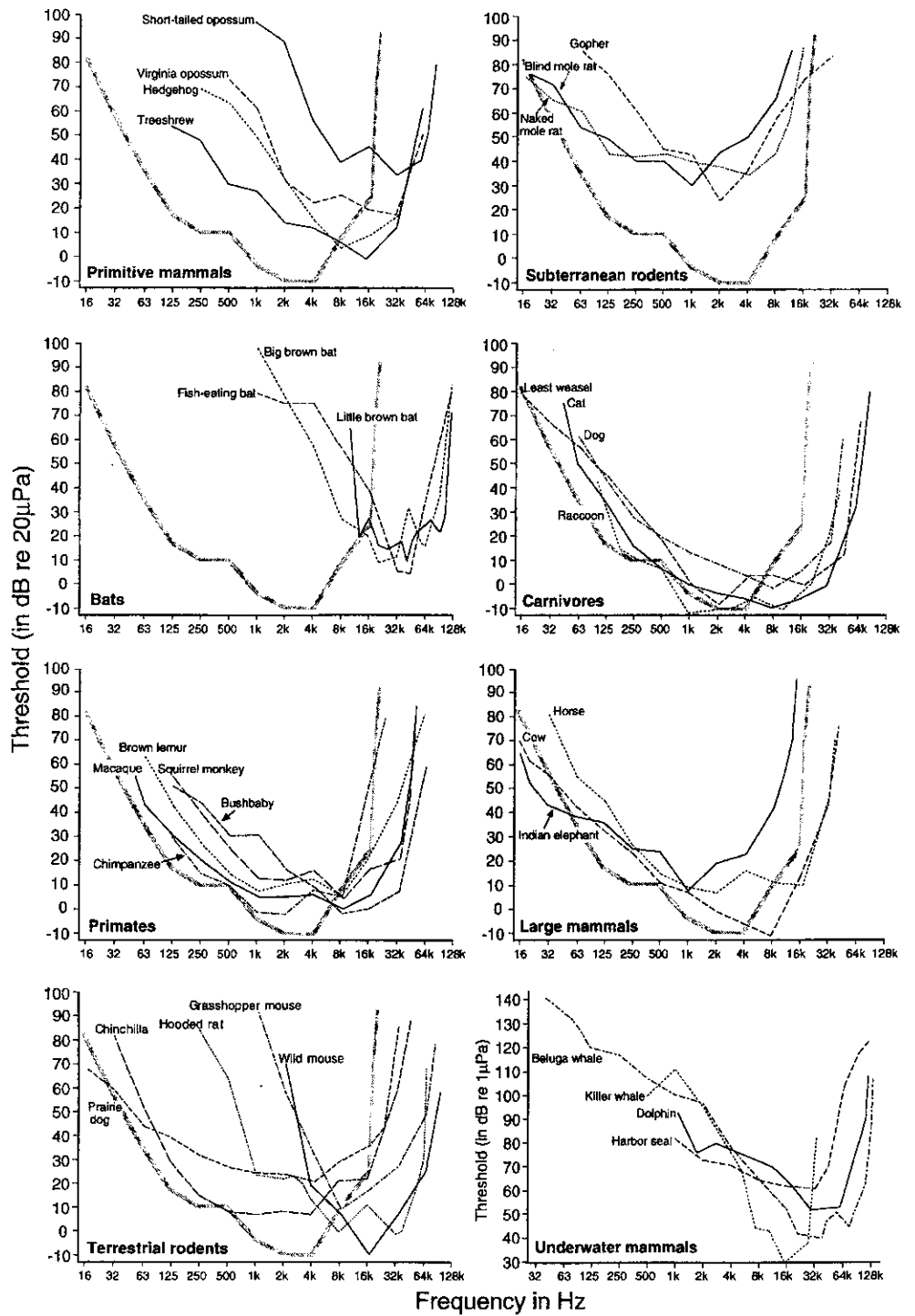
Figure 2. Audiograms of representative mammals. A human audiogram (shaded line) is shown for comparison in each figure except the underwater mammals. See Fay (1988) for references to individual audiograms. Note that the underwater audiograms use a different reference level.
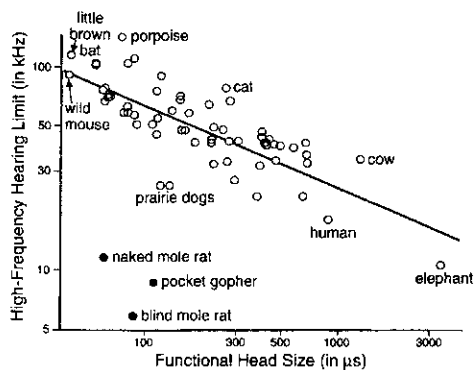
Figure 3. Relationship between functional head size and high-frequency hearing.

useful in enhancing an animal's ability to pick out signals embedded in a noisy world, but also provides an important cue for localizing sound. Indeed, the pinnae provide the main cues for localizing sound off to the side and for determining whether a sound source is in front or behind. However, the effectiveness of the pinna depends on the wavelength of the sound relative to the size of the pinna. Because low frequencies are not attenuated by the pinnae, it is necessary for animals to hear high frequencies in order to use pinna cues. Just how high they must hear depends on the size of the animal's head and pinnae. Thus, small mammals need to hear higher frequencies than larger mammals, so that their pinnae may provide usable locus cues.

The existence of a relationship between the size of an animal's head and high-frequency hearing is illustrated in Figure 3 (Masterton et al., 1969). In this figure, head size is defined as the "functional" distance between the two ears, where functional distance is the time it takes for sound to travel around the head from one ear to the other. As can be seen, mammals with small heads and close-set ears are able to hear higher frequencies than species with large heads and, presumably, larger pinnae ($r = -0.78$, excluding subterranean species). That mammals use their high-frequency hearing to localize sound is indicated by the fact that removing frequencies above 10 kHz can degrade the ability of an animal to use binaural spectral difference, pinnae locus cues, or a combination of the two (R. S. Heffner & H. E. Heffner, 1992a).

It should be noted that subterranean mammals have departed from the mammalian plan (the pocket gopher, blind mole rat, and naked

mole rat in Figure 3). Not only have these animals lost the ability to hear high frequencies, but they have also lost virtually all ability to localize brief sounds (see "Localization of Sound"). Evidently animals that have adapted to the one-dimensional world of an underground habitat have little use for sound localization and are thus released from the selective pressure to hear high frequencies.

Low-Frequency Hearing. There is currently no satisfactory explanation for the 9-octave variation in low-frequency hearing (H. E. Heffner & R. S. Heffner, 1992). We do know that high- and low-frequency hearing are positively correlated, which suggests that there is a trade-off so that animals with good high-frequency hearing often have poor low-frequency hearing and vice versa. However, there are exceptions to this relationship, with some mammals possessing good low- and high-frequency hearing (e.g., cats and marine mammals) and others not hearing as low as predicted from their high-frequency hearing (humans and elephants).

Localization of Sound

The ability to localize sound varies depending on the relative location of the sound source and the type of sound being localized. Animals are more accurate making left-right discriminations across the midline than front-back or vertical discriminations (R. S. Heffner, H. E. Heffner & Koay, 1995). In addition, complex sounds such as clicks and broad-band noise are easier to localize than narrow-band noise, while pure tones are the most difficult of all. Indeed, this latter fact appears to be exploited by some animals, since their tonal calls make it more difficult for predators to localize them (Brown & May, 1990).

The acuity for left-right localization has been determined for over 36 species representing 12 different orders of mammals (Figure 4). Using noise stimuli too brief to be scanned or tracked, these studies have found large species differences, with thresholds ranging from around 1° (e.g., elephants and humans) to more than 20° (e.g., gerbils and cattle), with subterranean rodents being unable to localize brief sounds at all (R. S. Heffner & H. E. Heffner, 1992a).

In the search for the source of this variation, a number of factors have been considered. Among these are the size of an animal's head (an indicator of the relative magnitude of the bin-
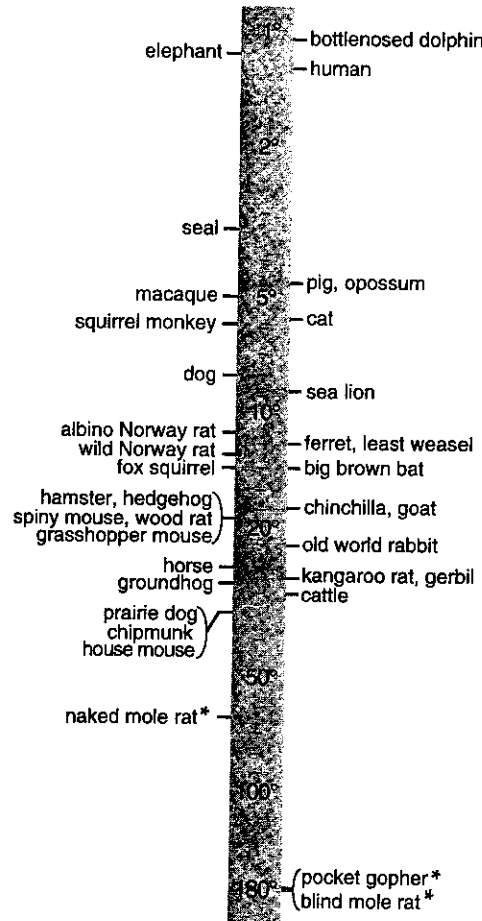
Sound-Localization Thresholds

Figure 4. Sound-localization thresholds of mammals. All mammals were tested with brief sounds (clicks or 100 msec noise bursts) with the exception of the subterranean rodents*, who could not localize brief sounds.
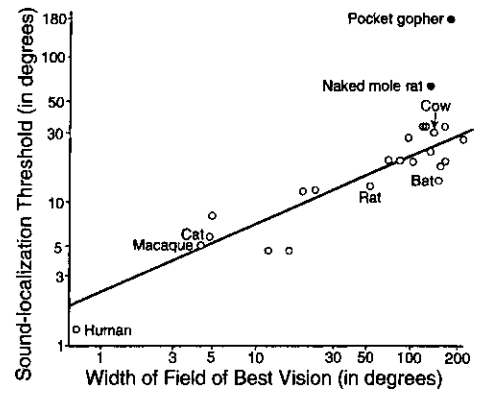

Figure 5. Relationship between the width of the field of best vision (as determined by ganglion cell densities) and sound-localization thresholds for mammals. Species with narrow fields of best vision have better sound-localization acuity than species with broad fields of best vision. Note that the blind mole rat and pocket gopher, which have lost both the ability to hear high frequencies and to localize brief sounds, had to be tested with sounds of longer duration. Excluding these animals from the correlation raises the coefficient from 0.86 to 0.93.

a primary role of sound localization is to orient the eyes to the source of a sound. Thus, in order to capture a sound source visually, species with narrow fields of best vision require greater localization accuracy than do species with broader visual fields.

Identification of Sound

The response of animals to meaningful sounds has been studied in the field using playback techniques (McGregor, 1992) and in the laboratory by training animals to discriminate or categorize natural sounds. One line of research has examined the ability of primates to perceive their vocal communications. An example is the demonstration that the playback of the vervet monkey alarm calls for "leopard," "eagle," and "snake" results in appropriately different responses; for example, the monkeys run to trees when they hear the "leopard" alarm call but look down when they hear the "snake" alarm (Seyfarth, Cheney & Marler, 1980). Laboratory studies have also been used to investigate the categorization of natural sounds by animals. An example is the classification of alarm calls by vervet monkeys, which are initially trained to discriminate their alarms calls and then tested on their ability to generalize to novel calls (Owren, 1990).

aural locus cues) and the possibility that certain life-styles, such as predator/prey and nocturnal/diurnal, might be associated with this variation (R. S. Heffner & H. E. Heffner, 1992b, 1993). The only factor that can account for the variation in sound localization acuity, however, is a visual parameter: the width of an animal's field of best vision, that is, the horizontal size of its fovea or visual streak. The width of the field of best vision is strongly correlated with sound-localization acuity (r = 0.86). Animals with narrow fields of best vision (such as cats and monkeys) have better localization acuity than those with broader fields of best vision (such as horses and rats). This correlation suggests that

Birds

Birds differ from mammals in that they (1) lack an external ear (although some species possess a fold of skin that partially encircles their ear canals and some owls have a feathered facial ruff that acts like a pinna), (2) have a single-ossicle middle ear, and (3) possess a straight cochlear duct, that is, inner ear (Knudsen, 1980; Manley & Gleich, 1992). Although birds have the best hearing of nonmammalian vertebrates, they do not hear above 12 kHz and their ability to localize sound is generally not as good as that of mammals.

Detection of Sound

Behavioral audiograms are available for 23 species of birds representing 7 different orders, although many are incomplete, covering only part of a species' hearing range (Dooling, 1992; Fay, 1988). Compared with mammals, the variation in hearing in birds is small (Figure 6). The 60-dB high-frequency hearing limit of birds varies by about an octave, from 6 kHz for the mallard duck to around 12 kHz for the barn owl. Of those birds tested, the low-frequency cutoffs range from 100 Hz for the bullfinch to 250 Hz for the canary. However, some birds may have unusually good low-frequency hearing, which they may use for navigation, and there is evidence that the 60-dB low-frequency cutoff for the pigeon is 5 Hz (Kreithen & Quine, 1979). The best frequency of hearing for birds is around 3 kHz. However, birds are generally not as sensitive as mammals, the barn owl being one of the few exceptions.

Localization of Sound

Although a number of studies have measured the ability of birds to localize sound in the horizontal plane, it is difficult to compare results because of procedural differences between studies (H. E. Heffner & R. S. Heffner, 1992). In particular, different studies have used various stimuli (such as noise, tones, and birdcalls), all with good reason but with the result that the thresholds are not comparable. Comparisons are further complicated by the use of different definitions of threshold.

The most accurate birds are raptors that use their hearing to locate prey. The barn owl and short-eared owl have thresholds of 1–2° and the marsh hawk has a threshold of 2°. To
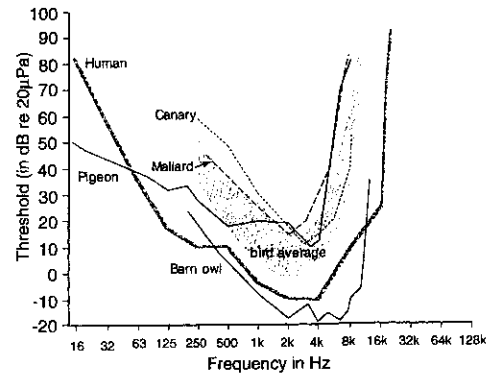

Figure 6. Average and representative audiograms of birds, with a human audiogram (shaded line) shown for comparison. Average bird audiogram (±1 standard deviation) is shown by shaded area. Adapted from Dooling (1992), p. 547.

attain such accuracy, these species have evolved a pinnalike facial ruff which enables them to use "pinna" cues, although they lack the high-frequency hearing of mammals. Hawks, however, lack a facial ruff, and the red-tailed hawk and American kestrel have somewhat larger thresholds of 8–12° (Rice, 1982).

Other birds are much less accurate: the localization thresholds for songbirds for brief noise bursts typically range from 20° to 30°, and thresholds of around 100° have been reported for parakeets (Park & Dooling, 1991). Although a localization threshold of 4° has been obtained for the pigeon using heart rate conditioning, it should be replicated using operant conditioning techniques before one accepts the conclusion that pigeons are as accurate as raptors.

Most birds appear to use both the binaural time- and intensity-difference cues, with the more accurate raptors also using "pinna" cues. In addition, birds have an interaural canal connecting the two middle ears, which is believed by some to enhance the binaural time cue. However, the primary function of this canal may be to equalize pressure between the two ears, since the middle ears of birds contain baroreceptors (von Bartheld, 1994).

Identification of Sound

The response of birds to meaningful sounds has been studied in the field using playback techniques and in the laboratory by training birds to discriminate or categorize natural sounds, particularly the calls of their own and

other species. For example, field studies have been used to determine the degree to which different species of swallows recognize and approach the sound of their own offspring and to examine the response of male song sparrows to the songs of other males (Beecher & Stoddard, 1990). Laboratory studies have investigated the categorization of vocalizations by various songbirds and have used reaction time as a measure of the degree to which a bird perceives two calls or songs to be different (Dooling, 1992).

Reptiles

The middle and inner ears of reptiles are much more diverse than those of birds or mammals. For example, whereas most reptiles possess an eardrum that is flush with the surrounding skin, a few have a recessed membrane and others do not have an eardrum at all (Wever, 1978). Anatomical and electrophysiological studies suggest that the ears of reptiles are inferior to those of birds and mammals but superior to those of fishes and amphibians in terms of sensitivity, frequency range, and discriminative capability. However, there is virtually no behavioral information on the hearing abilities of reptiles.

Among reptiles (lizards, snakes, turtles, alligators, and crocodiles) the only behavioral measure of hearing has been an audiogram of the red-eared turtle *(Pseudemys scripta)* (Patterson, 1966). As shown in Figure 7, the turtle is relatively insensitive and does not hear above 1 kHz. Electrophysiological data suggest that snakes also have poor sensitivity, with their high-frequency hearing limited to around 1 kHz. Lizards and crocodiles, on the other hand, appear to be more sensitive and may possess better high-frequency hearing, with an upper limit near 5 kHz (Köppl & Manley, 1992; Wever, 1978).

Reptiles can probably localize sound, although there are no data on this. Similarly, they may respond to meaningful sounds, a conclusion suggested by the fact that some species (e.g., geckos and crocodiles) emit vocalizations. However, virtually all attempts to train reptiles to respond to sound have failed (Wever, 1978), although they can be conditioned to visual stimuli (e.g., Burghardt, 1977). In addition, they show few, if any, unconditioned responses to sound. It appears that reptiles do not make as
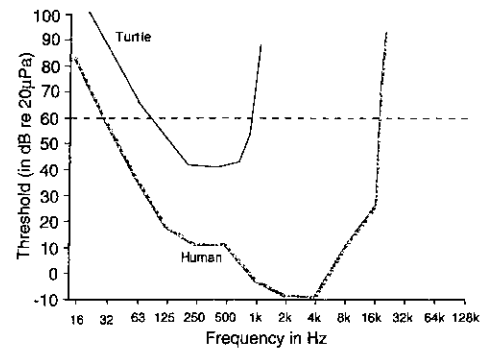
Figure 7. Behavioral audiogram of the red-eared turtle. A human audiogram (shaded line) is shown for comparison. Adapted from Patterson (1966), p. 457.

wide a use of hearing as do most other vertebrates.

Amphibians

The inner ears of the three extant orders of amphibians—Anura (frogs and toads), Urodela (newts and salamanders), and Apoda (worm-like animals that burrow underground)—are not believed to be ancestral to the reptilian ear, which differs markedly from them (Wever, 1985). Among amphibians, only the anurans appear to be well adapted to hearing airborne sounds. The fact that frogs and toads make extensive use of vocalizations in locating mates has made it possible to study their unconditioned response to a variety of sounds. Thus, gravid females will approach the sound of a male of their species (phonotaxis), and unconditioned responses may be obtained from a calling male by presenting sounds that either evoke an antiphonal response or else cause the male to slightly alter the timing of its call (McGregor, 1992; Narins, 1992). In addition, the hearing ability of frogs has been studied through use of the reflex-inhibition technique (Megela-Simmons, Moss & Daniel, 1985). As a result, more is known about the hearing of frogs than of reptiles.

It may be noted that in addition to receiving sound through their tympanic middle ear, anurans and most salamanders have an opercularis system which connects the otic capsule to the forelegs and is believed to play a role in the detection of substrate vibrations. Frogs also possess other nontympanic pathways for

sound reception, including the lateral body wall and lungs (Hetherington, 1992).

Detection of Sound

Although a number of behavioral audiograms have been obtained for frogs, most rely on unconditioned responses, which tend to underestimate sensitivity (see Fay, 1988). More-sensitive audiograms, obtained using the conditioned reflex-inhibition technique, are available for the bullfrog and green tree frog (Megela-Simmons et al., 1995). As shown in Figure 8, the green tree frog has a slightly wider hearing range, while the bullfrog has better sensitivity. Thus, the hearing of frogs is inferior to that of birds and mammals but may surpass that of turtles (cf. Figures 7 and 8).

Localization of Sound

The sound-localization ability of frogs has been studied by placing an animal in a testing room, playing a vocalization from a loudspeaker, and then recording the accuracy of the frog's head or body orientation or its jump. Although testing is usually done in two dimensions, frogs will jump onto vertical stakes, which allows their vertical localization ability to be estimated. Accuracy is expressed in terms of directional error. Typical average errors are 16° for the green tree frog (Hyla cinerea) and 23° for a miniature dendrobatid frog (Colostetus nubicola) (Rheinlaender & Klump, 1988). The elevation thresholds are about double the two-dimensional thresholds. Although most species appear to be too small to use binaural time and intensity cues, their eardrums are linked together by wide eus-

tachian tubes and the mouth cavity. This makes it possible for a sound to reach the inner as well as the outer surface of the eardrum, turning the ear into a "pressure difference" receiver, and this is believed to make the ear more directionally sensitive (Eggermont, 1988).

Identification of Sound

Playback studies are more commonly used with frogs than with other vertebrates, including birds (Fritzsch, Ryan, Wilczynski, Hetherington & Walkowiak, 1988; McGregor, 1992). These studies have recorded the reactions of male and female frogs to the calls of frogs from different populations or to synthetic calls that vary along physical parameters such as rate, rise-time, and duration (Gerhardt, 1989; Ryan, Perrill & Wilczynski, 1992). Such studies have found that females prefer calls of lower frequency (which are produced by large males); male frogs, on the other hand, show a greater increase in the aggressive nature of their vocalizations when they are presented with lower-frequency calls (Wagner, 1989).

Fish

Fish have true hearing, and some use vocalizations in courtship, mating, and aggressive interactions (Popper & Fay, 1993). The inner ears of fish consist of one or more of the otolith organs (the saccule, utricle, and lagena), which in terrestrial vertebrates have a vestibular function. Each of these organs contains hair cells which serve to detect sound. The pathway for sound transmission to the ear varies between species. Some fishes, called "hearing specialists," have evolved a mechanical coupling between their swim bladder or other type of gas-filled bubble and their inner ear (e.g., via Weberian ossicles). Other "nonspecialist" fish lack such a coupling, and some have no swim bladder. Thus, there is much diversity in the peripheral auditory structures of fish as well as in their inner ears. Of the three superclasses of fish (jawless fishes, cartilaginous fishes, and bony fishes), the bony fishes constitute the largest group of living fishes and the one whose hearing has been most widely studied.
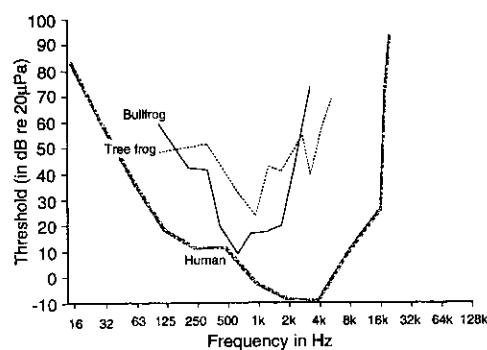

Figure 8. Behavioral audiograms of the bullfrog and green tree frog. A human audiogram (shaded line) is shown for comparison. Adapted from Megela-Simmons et al. (1995), p. 1240.

Detection of Sound

Fish are relatively easy to train, and behavioral audiograms are available for over 50 species,

including sharks (Fay, 1988; Klump, Dooling, Fay & Stebbins, 1995). The general pattern that emerges is that the hearing specialists possess greater sensitivity and higher-frequency hearing (up to 3 kHz) than the nonspecialists. This is indicated in Figure 9, which shows the behavioral audiograms for five species of fish. As can be seen, the goldfish and the soldierfish, whose swim bladders are connected to their ears, are the most sensitive of the 5 species and the only ones that hear above 1 kHz. The lemon sole and squirrelfish, whose swim bladders are not connected to the ears, are of intermediate sensitivity. Finally, the oscar, which lacks a swim bladder, is the least sensitive. In summary, fish hear between 30 Hz and 3 kHz, with the exact range and sensitivity depending on the degree to which a species has evolved a specialized apparatus for transmitting sound to the inner ear. Why some fish have evolved greater sensitivity than others is unknown.

Localization of Sound

Although there are few behavioral studies of fish's sound localization, at least some fish are capable of localizing sound (Popper & Fay, 1993). For example, codfish are able to localize with an accuracy of 10° to 20° in both azimuth and elevation and are also able to discriminate between sound sources that differ in distance. Because so few species have been examined, it is not known if systematic differences exist between species. In addition, the cues used and the neural mechanisms underlying directional hearing in fish are not yet known.

Identification of Sound

Many fish produce sound and some use it for courtship, with males being the usual producer. By observing either the approach behavior of a female or an answering call, playback studies using the goby and toadfish have indicated that changes in duration and in the rate of repetition are critical, while the fundamental frequency of a call may be varied considerably without affecting the response (Hawkins & Myrberg, 1983).

Insects

The sense of hearing is well developed in insects, and their use of sound is widely studied. Be-
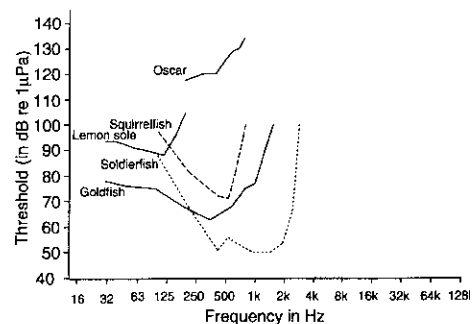

Figure 9. Behavioral audiograms of five species of fish. Adapted from Popper & Fay (1993), p. 18.

cause hearing has evolved independently in many groups, there is a wide variety of different ears. Among insects, the transducer itself varies from hairlike antennal structures that detect particle movement to tympanal organs more like our own eardrum. Insects with tympanal organs (such as crickets, locusts, katydids, cicadas, moths, and butterflies) generally have better sensitivity and are able to hear higher frequencies than other insects. The location of the hearing organs is also varied and includes the thorax, various segments of the abdomen, the base of the wings, a vein of the forewings, the front legs, labial palps, the ventral midline, and the antennae. Although all the receptors consist of some form of hair cell, they vary greatly in number from a single cell in some moths to more than 1,000 cells in mosquitos and cicadas (Michelsen & Larsen, 1985).

The auditory abilities of insects have been studied through neural recordings and by the observation of unconditioned responses, although the operant conditioning of honeybees to sound has also been reported (Kirchner, Dreller & Towne, 1991). The unconditioned responses consist of approaching a sound (positive phonotaxis), turning away from a sound (negative phonotaxis), and modifying a communication call in response to a sound (Gribakin, Wiese & Popov, 1990; Pollach & Hoy, 1989; Simmons, Wever & Pylka, 1971; Weber & Thorson, 1989).

Detection of Sound

The responses of insects to sounds are highly stereotyped, and their hearing appears to have evolved to solve the specific tasks of locating a mate or prey, avoiding bats, or both. An example of insects that use sound for courtship are
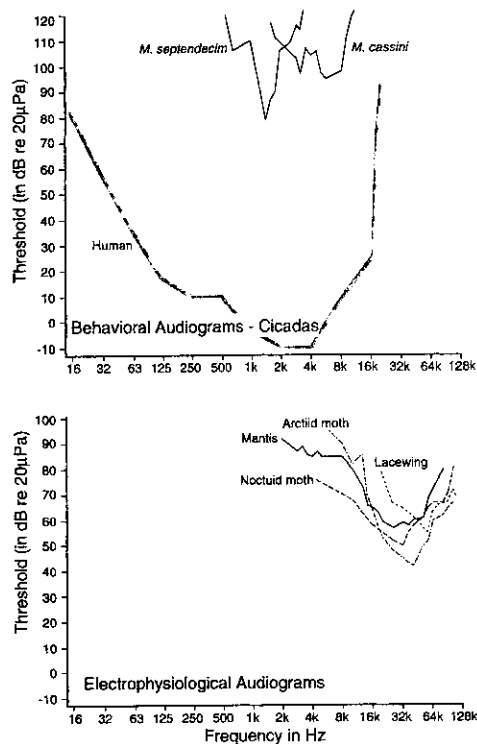
Figure 10. Top: Behavioral audiograms of two species of cicadas, with a human audiogram (shaded line) shown for comparison. Male cicadas were tested by noting whether they produced a call in response to a tone. Adapted from Simmons et al. (1971), p. 212. Bottom: Electrophysiological audiograms of four species that hear high frequencies. Adapted from Yager & Hoy (1989), p. 487.

two species of cicadas whose behavioral responses to sound are shown in the top of figure 10. These species, which are found together, have different peaks of hearing sensitivity, which match the different frequencies of their courtship calls. Moreover, their calls are quite loud, reaching levels that are deafening for humans and that are thought to act also as a repellant to bird predators (Simmons, Wever & Pylka, 1971).

Bats have been a major source of selective pressure on the hearing of nocturnal flying insects, which have evolved the ability to detect bat echolocation calls and take appropriate action. The ability to detect the high-frequency echolocation calls of bats has been observed in many insects, including beetles, green lacewings, locusts, mantids, katydids (bush crickets), tachinid flies, crickets, and moths (Hoy, 1992; Robert, Amoroso & Hoy, 1992). Both neural

and behavioral audiograms indicate that many species are able to hear up to 100 kHz, with their best hearing in the range of 20–60 kHz, the level at which bat echolocation signals contain their maximum energy (Figure 10, bottom).

Many insects use hearing for both courtship and bat avoidance, which results in an audiogram with peaks of sensitivity in both the low frequencies (for mating calls) and high frequencies (for bat echolocation calls). A classic case is the cricket *(Teleogryllus oceanicus)*, which can be tested in tethered flight by observing steering responses to tones (Nolen & Hoy, 1986). The female of this species shows movements towards a loudspeaker for low frequencies, which signal a potential mate, and movements away from the speaker for high frequencies, which signal a nearby bat (Figure 11, top). Intense high frequencies, which signal a closely approaching bat, elicit evasive movements, whereas responses to midrange frequencies (around 10 kHz) depend on the parameters of the stimulus: they do not generate avoidance unless they are quite loud, and they are attractive only if they are presented with a temporal pattern similar to the social calls.

Insects appear to use hearing to solve problems on an ad hoc basis, as illustrated by the existence of sexual dimorphism in hearing. For example, the males of certain species of mantids, which fly and must evade bats, are sensitive to high frequencies while the females are flightless and lack high-frequency hearing (Yager & May, 1990). Another example are parasitoid flies of the genus *Ormia*: the female flies are attracted to singing male crickets and deposit their maggots on or near them (Robert, Amoroso & Hoy, 1992). As a result, the female flies are more sensitive than the males to the frequencies of the cricket's calling song (see bottom of Figure 11).

Localization of Sound

The sound-localization ability of insects is studied by exploiting the approach response to courtship calls and the avoidance response to simulated bat calls. Detailed studies of approach behavior have been made by recording the movements of an animal on a spherical treadmill, and avoidance behavior has been observed by measuring the direction of the steering response of tethered flying insects (Pollack & Hoy, 1989; Rheinlaender & Römer, 1990; Weber & Thorson, 1989). Studies have shown that grasshoppers, crickets, katydids,
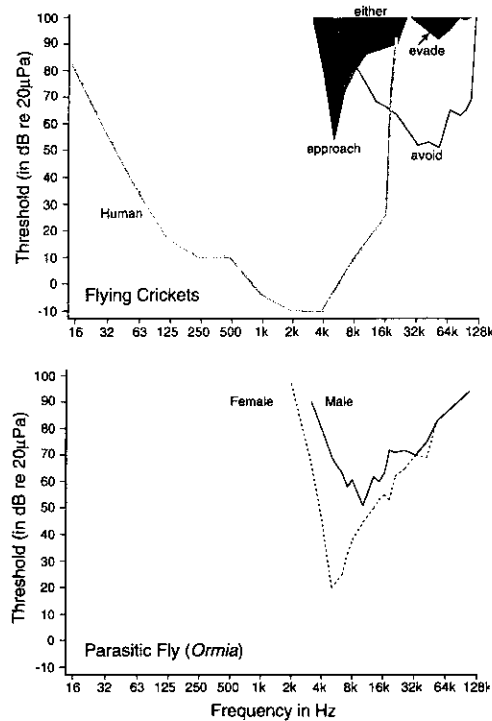
Figure 11. Top: Composite behavioral audiograms obtained from tethered, flying crickets (Teleogryllus oceanicus), with a human audiogram (shaded line) shown for comparison. Crickets show approach, avoidance, either approach or avoidance, or evasive behavior depending on the frequency, intensity, or temporal characteristics of the tone. Adapted from Nolen & Hoy (1986), p. 436. Bottom: Electrophysiological audiograms of male and female parasitoid flies of the genus Ormia illustrating sexual dimorphism. Females are more sensitive than males to the calling song of its cricket host, which attains its maximum energy between 3–6 kHz. Adapted from Robert et al. (1992), p. 1136.

and moths are able to localize sound; that is, they show appropriate movement to the left or right when a sound is presented more than 10° to 30°off midline—the actual threshold depending on the spectrum and duration of the stimulus as well as the species. However, insects appear simply to lateralize sound to the left or right and apparently cannot localize sound within a hemifield (Rheinlaender & Römer, 1990). Because both sides of their tympanic membranes receive sound, it is believed that like frogs, insects localize by using their ears as pressure-difference receivers (Lewis, 1983).

However, not all insects are able to localize sound. In particular, the praying mantis shows no evidence of a directional response to

ultrasound in tethered flight (Yager & May, 1990). It should be noted that both of its tympana are located together in a deep ventral cleft and are separated by less than 150 μm, thus giving it a "cyclopean" ear (Yager & Hoy, 1989).

Identification of Sound

Playback techniques are widely used to study the perceptual responses of insects by assessing the effectiveness of different sounds in eliciting an approach or avoidance response. Studies using these techniques have shed light on the ability of crickets to discriminate the calls of their own species from those of others, the relative effectiveness of different parts of a call, the modification of the response to one sound by the simultaneous presentation of a second sound, and the role of the frequency, intensity, and temporal characteristics of a sound (Gribakin, Wiese & Popov, 1990; Pollack & Hoy, 1989; Weber & Thorson, 1989).

Concluding Remarks

This survey of hearing has indicated the diversity of hearing among the different groups of animals and gives some idea of the selective pressures that have shaped the ability of animals to respond to sound. In the case of insects, the selective pressures have been dealt with in a relatively simple manner: approach a potential mate (or prey) and avoid a predator (bats). Mammals, on the other hand, have evolved the ability to use hearing to respond to sound sources in more sophisticated ways, as illustrated by the communication calls of monkeys and by human language. What is also illustrated is that there is no trend toward "better" ears. Animals have evolved the ability to hear well enough to ensure their survival, no more. Should an animal move into an environment in which certain features of hearing are no longer necessary for survival, it will rapidly relinquish those features, as in the case of subterranean rodents that have lost their ability to hear high frequencies and to localize sound.

References

Beecher, M. D. & Stoddard, P. K. (1990). The role of bird song and calls in individual

recognition: Contrasting field and laboratory perspectives. In W. C. Stebbins & M. A. Berkley (Eds.), *Comparative perception, Vol. II: Complex signals* (pp. 375–408). New York: John Wiley.

Brown, C. H. & May, B. J. (1990). Sound localization and binaural processes. In M. A. Berkley & W. C. Stebbins (Eds.), *Comparative perception, Vol. I: Basic mechanisms* (pp. 247–284). New York: John Wiley.

Burghardt, G. M. (1977). Learning processes in reptiles. In C. Gans (Ed.), *Biology of the reptilia, Vol. 7: Ecology and behaviour A* (pp. 555–681). New York: Academic Press.

Dooling, R. J. (1992). Hearing in birds. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 545–559). New York: Springer-Verlag.

Eggermont, J. J. (1988). Mechanisms of sound localization in anurans. In B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington & W. Walkowiak (Eds.), *The evolution of the amphibian auditory system* (pp. 307–336). New York: John Wiley.

Fay, R. R. (1988). *Hearing in vertebrates: A psychophysics databook*. Winnetka, IL: Hill-Fay Associates.

Fritzsch, B., Ryan, M. J., Wilczynski, W., Hetherington, T. E. & Walkowiak, W. (Eds.). (1988). *The evolution of the amphibian auditory system*. New York: John Wiley.

Gerhardt, H. C. (1989). Acoustic pattern recognition in anuran amphibians. In R. J. Dooling & S. H. Hulse (Eds.), *The comparative psychology of audition* (pp. 175–197). Hillsdale, NJ: Lawrence Erlbaum.

Gribakin, F. G., Wiese, K. & Popov, A. V. (Eds.). (1990). *Sensory systems and communication in arthropods*. Basel: Birkhäuser.

Hawkins, A. D. & Myrberg, A. A., Jr. (1983). Hearing and sound communication under water. In B. Lewis (Ed.), *Bioacoustics: A comparative approach* (pp. 347–405). New York: Academic Press.

Heffner, H. E. & Heffner, R. S. (1992). Auditory perception. In C. Phillips & D. Piggins (Eds.), *Farm animals and the environment* (pp. 159–184). Wallingford,
U.K.: CAB International.

Heffner, R. S. & Heffner, H. E. (1992a). Evolution of sound localization in mammals. In D. B. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 691–715). New York: Springer-Verlag.

————. (1992b). Visual factors in sound localization in mammals. *Journal of Comparative Neurology, 317*, 219–232.

————. (1993). Degenerate hearing and sound localization in naked mole rats *(Heterocephalus glaber)*, with an overview of central auditory structures. *Journal of Comparative Neurology, 331*, 418–433.

Heffner, R. S., Heffner, H. E. & Koay, G. (1995). Sound localization in chinchillas, II: Front/back and vertical localization. *Hearing Research, 88*, 190–198.

Hetherington, T. E. (1992). The effects of body size on the evolution of the amphibian middle ear. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 421–437). New York: Springer-Verlag.

Hoy, R. R. (1992). The evolution of hearing in insects as an adaptation to predation from bats. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 115–129). New York: Springer-Verlag.

Kirchner, W. H., Dreller, C. & Towne, W. F., (1991). Hearing in honeybees: Operant conditioning and spontaneous reactions to airborne sound. *Journal of Comparative Physiology A, 168*, 85–89.

Klump, G. M., Dooling, R. J., Fay, R. R. & Stebbins, W. C. (Eds.). (1995). *Methods in comparative psychoacoustics*. Basel: Birkhäuser.

Knudsen, E. I. (1980). Sound localization in birds. In A. N. Popper & R. R. Fay (Eds.), *Comparative studies of hearing in vertebrates* (pp. 289–322). New York: Springer-Verlag.

Köppl, C. & Manley, G. A. (1992). Functional consequences of morphological trends in the evolution of lizard hearing organs. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 489–509). New York: Springer-Verlag.

Kreithen, M. L. & Quine, D. B. (1979). Infrasound detection by the homing pi-

geon: A behavioral audiogram. *Journal of Comparative Physiology A, 129,* 1–4.

Lewis, B. (1983). Directional cues for auditory localization. In B. Lewis (Ed.), *Bioacoustics: A comparative approach* (pp. 233–257). New York: Academic Press.

Manley, G. A. & Gleich, O. (1992). Evolution and specialization of function in the avian auditory periphery. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 561–580). New York: Springer-Verlag.

Masterton, R. B. (1992). Role of the central auditory system in hearing: The new direction. *Trends in Neurosciences, 15,* 280–285.

Masterton, B., Heffner, H. & Ravizza, R. (1969). The evolution of human hearing. *Journal of the Acoustical Society of America, 45,* 966–985.

McGregor, P. K. (Ed.). (1992). *Playback and studies of animal communication.* New York: Plenum.

Megela-Simmons, A., Moss, C. F. & Daniel, K. M. (1985). Behavioral audiograms of the bullfrog *(Rana catesbeiana)* and the green tree frog *(Hyla cinerea). Journal of the Acoustical Society of America, 78,* 1236–1244.

Michelsen, A. & Larsen, O. N. (1985). Hearing and sound. In G. A. Kerkut & L. I. Gilbert (Eds.), *Comprehensive insect physiology, biochemistry, and pharmacology, Vol. 6: Nervous system: Sensory* (pp. 495–556). New York: Pergamon Press.

Narins, P. M. (1992). Biological constraints on anuran acoustic communication: Auditory capabilities of naturally behaving animals. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 439–454). New York: Springer-Verlag.

Nolen, T. G. & Hoy, R. R. (1986). Phonotaxis in flying crickets, I: Attraction to the calling song and avoidance of bat-like ultrasound are discrete behaviors. *Journal of Comparative Physiology A, 159,* 423–439.

Owren, M. J. (1990). Acoustic classification of alarm calls by vervet monkeys *(Cercopithecus aethiops)* and humans *(Homo sapiens),* I: Natural calls. *Journal of Comparative Psychology, 104,* 20–28.

Park, T. J. & Dooling, R. J. (1991). Sound localization in small birds: Absolute localization in azimuth. *Journal of Comparative Psychology, 105,* 125–133.

Patterson, W. C. (1966). Hearing in the turtle, *Journal of Auditory Research, 6,* 453–464.

Pollack, G. S. & Hoy, R. R. (1989). Evasive acoustic behavior and its neurobiological basis. In F. Huber, T. E. Moore & W. Loher (Eds.), *Cricket behavior and neurobiology* (pp. 340–363). Ithaca, NY: Cornell University Press.

Popper, A. N. & Fay, R. R. (1993). Sound detection and processing by fish: Critical review and major research questions. *Brain, Behavior and Evolution, 41,* 14–38.

Rheinlaender, J. & Klump, G. (1988). Behavioral aspects of sound localization. In B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington & W. Walkowiak (Eds.), *The evolution of the amphibian auditory system* (pp. 297–305). New York: John Wiley.

Rheinlaender, J. & Römer, H. (1990). Acoustic cues for sound localisation and spacing in orthopteran insects. In W. J. Bailey & D. C. F. Rentz (Eds.), *The tettigoniidae: Biology, systematics, and evolution* (pp. 248–264). New York: Springer-Verlag.

Rice, W. R. (1982). Acoustical location of prey by the marsh hawk: Adaptation to concealed prey. *The Auk, 99,* 403–413.

Robert, D., Amoroso, J. & Hoy, R. R. (1992). The evolutionary convergence of hearing in a parasitoid fly and its cricket host. *Science, 258,* 1135–1137.

Ryan, M. J., Perrill, S. A. & Wilczynski, W. (1992). Auditory tuning and call frequency predict population-based mating preferences in the cricket frog, *Acris crepitans. The American Naturalist, 139,* 1370–1383.

Seyfarth, R. M., Cheney, D. L. & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behavior, 28,* 1070–1094.

Simmons, J. A., Wever, E. G. & Pylka, J. M. (1971). Periodical cicada: Sound production and hearing. *Science, 171,* 212–213.

Stebbins, W. C. (1983). *The acoustic sense of animals.* Cambridge, MA: Harvard University Press.

von Bartheld, C. S., (1994). Functional morphology of the paratympanic organ in

the middle ear of birds. *Brain, Behavior, and Evolution, 44,* 61–73.

Wagner, W. E. Jr. (1989). Graded aggressive signals in Blanchard's cricket frog: Vocal responses to opponent proximity and size. *Animal Behavior, 38,* 1025–1038.

Weber, T. & Thorson, J. (1989). Phonotactic behavior of walking crickets. In F. Huber, T. E. Moore & W. Loher (Eds.), *Cricket behavior and neurobiology* (pp. 310–339). Ithaca, NY: Cornell University Press.

Wever, E. G. (1978). *The reptile ear.* Princeton, NJ: Princeton University Press.

————. (1985). *The amphibian ear.* Princeton, NJ: Princeton University Press.

Yager, D. D. & Hoy, R. R. (1989). Audition in the praying mantis, *Mantis religiosa* L.: Identification of an interneuron mediating ultrasonic hearing. *Journal of Comparative Physiology A, 165,* 471–493.

Yager, D. D. & May, M. L. (1990). Ultra-sound-triggered, flight-gated evasive maneuvers in the praying mantis *Parasphendale agrionina,* II: Tethered flight. *Journal of Experimental Biology, 152,* 41–58.