mutation are all critical to understanding the origins and maintenance of animal signal diversity.

8. Animal communication systems can be classified in several ways. One axis focuses on the **modality** (light, sound, chemicals, touch, hydrodynamics, or electricity) used to create signal stimuli, the **medium** (air, water, or solids) through which the signal propagates, and the preadaptations for that modality and medium that are present in each taxon.
9. A second axis for signal classification focuses on the alternative kinds of information that signals might provide. Since the sender knows more about its own status than any other animal, many signals provide information about sender conditions. Such information may include sender identity, sex, age, dominance status, and location. In some cases, the sender can provide information about the receiver that the latter cannot know on its own. Finally, the sender may provide receivers with information about other parties, such as predators or approaching conspecifics, or about objects, such as food.
10. A third method of classifying signals focuses on the mechanisms by which signals are kept honest when sender and receiver have a conflict of interest. **Index signals** are constrained in ways that make it impossible for a sender to be deceitful. **Handicap signals** impose higher costs or lower benefits on deceitful senders. Receivers can punish deceitful senders using **conventional signals**, and in aggressive contests, confident senders can confirm their self-assessment by making themselves vulnerable with **proximity signals**. Where there is minimal conflict of interest between sender and receiver, no honesty guarantees are needed.
11. A fourth axis classifies signals into one of four contextual categories that differ in the relevant payoffs that each party receives following communication exchanges. Usually, a species' signal repertoire can be divided into its **aggressive signals**, **mating signals**, **social integration signals**, and **environmental signals**. Different species may have more or fewer signals in each category, but most species have at least a few signals of each type.
12. Animals may use signals that mix categories both within and across the above classifications. **Multimodal signals** utilize two or more modalities at once, and each modality may invoke a different honesty guarantee. Birds often combine acoustic and visual displays, whereas insects combine visual and chemical components. Animals may also provide information about multiple conditions in the same signal: a frog's call can indicate the caller's body size and its species in the same signal. Finally, the same signal may be used in multiple contexts: the songs of many birds are designed both to repel male competitors and to attract potential female mates.
13. All communication requires the same seven steps. For the sender, this consists of (1) generating an initial stimulus, (2) modifying it to ensure proper pattern, and (3) coupling it to the propagation medium. These three sender steps are followed by (4) propagation in the medium, which usually results in some distortion of the released signal, depending on its design, the modality, the medium, and the distance between sender and receiver. The final three steps occur at the receiver and are the reverse of those undertaken by the sender: (5) coupling the propagated signal from the medium into the receiver's sense organs, (6) modifying it as necessary to improve detectability and resolution, and finally (7) identifying and classifying the perceived signal. Variations among species at each step contribute to the overall patterns of signal diversity seen in animals.

Further Reading

Good introductions to the evolution of animal behavior in general can be found in Alcock [1] and Dugatkin [13]. Signal classification and associated evolutionary processes are discussed by Hauser [33] who provides an in-depth review of the physiological preadaptations for signal evolution; Hailman [26], who classifies signals according to the complexity and redundancy of coding rules; and Searcy and Nowicki [77], and Maynard Smith and Harper [53], who review current thinking about conflicts of interest, honesty guarantees, and signal evolution.

COMPANION WEBSITE
sites.sinauer.com/animalcommunication2e

Go to the companion website for Chapter Outlines, Chapter Summaries, and References for all works cited in the textbook. In addition, the following resource is available for this chapter:

Web Topic 1.1 ***Animal communication and science education***
Because most students naturally like animals, and animal communication integrates so many disciplines, the topic can be used as an entry point for science education in middle and high school curricula. Here we provide some background and relevant links.

Web Topic 1.2 ***Information and communication***
Some scientists feel that the role of information provision should be downplayed in definitions of animal communication. A few even recommend elimination of the term when applied to animal interactions. Here, we outline the case for information as a useful and even key concept in understanding the evolution and diversity of animal signals.

Chapter 2

Sound and Sound Signal Production

Overview

Most humans are born into a world in which sound communication is a dominant activity. While we tend to take the mechanisms that allow vocal exchanges for granted, the production of useful sound signals presents significant hurdles, and most animals dispense with sound communication altogether. In this chapter, we outline the basic physical constraints within which we, and animals, must operate if we are to communicate with sound, and describe some of the techniques that different species use to mitigate and even take advantage of these constraints.

Properties of Sound

The media of sound communication

In contrast to the vacuum of outer space, every cubic meter of our planet is filled with matter. Matter consists of atoms that are largely bound together into molecules. When animals want to communicate with each other, their signals must pass through some type of intervening matter. We call the matter linking sender and receiver the **medium** of the communication process. Different media impose different constraints on the kinds of signals that senders can create and receivers can detect and process. For sound, the different states of matter constitute quite different media.

STATES OF MATTER We can initially categorize a medium according to whether it is a **fluid** or a **solid**. In turn, we can divide fluids into **gases** and **liquids**. To understand the differences, note first that all molecules on the Earth are moving at least slightly. A number of types of motion are possible, including internal vibrations within each a molecule, molecular rotations, or translational movements of a molecule from one location to another. The total energy in all such movements is the **kinetic energy** of the molecule. The **temperature** of a medium is a measure of the average kinetic energy of its molecules.

Molecules and atoms can be attracted to each other through a number of forces. Whereas kinetic movements tend to separate molecules, the attractive forces bring them closer together. When the kinetic energy of molecules is high relative to the attractive forces between them, the matter occurs as a gas (such as air). Air molecules occur at low densities, which means they can travel considerable distances before they collide with another molecule. When they do collide, they bounce and do not stick to each other. In a liquid (such as water), the attractive forces between molecules are high relative to kinetic energies; molecules thus remain much closer together and at higher densities than air. A water molecule can move, but not very far, before it collides with another, and water molecules tend to cohere (stick together) when they do collide. Air and water are both considered fluids because they can assume any shape. In contrast to fluids, solids tend to retain their shape when perturbed. The attractive forces in a solid are so much stronger than the kinetic energy of the molecules that molecules can make only tiny translational movements. Internal vibrations may also be limited by the proximity of nearby molecules, and molecular rotations are usually prevented by the strong linkage between neighbors.

PRESSURE If we were to map the translational movements of individual air or water molecules, we would see that the directions moved in any small neighborhood were random. Suppose we place a small square surface inside such a neighborhood. When a molecule collides with that surface, it exerts a small force on it. Over a short period, many different molecules will collide with that surface, exerting a combined force on it. This total force divided by the area of the surface is known as the **ambient pressure** of the medium. Since molecular movements are random, similar numbers of collisions occur over time in any given direction. We would record the same pressure whether we aimed the surface upward, to the side, or even diagonally. Pressure is nondirectional.

In a neighborhood with a higher density of molecules than our first sample, there would be more molecules available to collide with the square, and the net force, and thus the measured pressure, would be higher. Similarly, if we examined another neighborhood with the same density of molecules as the first sample but at a higher temperature, the higher kinetic energy per molecule would result in a greater force per collision, and again, a higher recorded pressure. Ambient pressure is thus positively correlated with both molecular density and temperature.

The nature of sound

GENERATING SOUNDS Suppose we insert a large flat circle of a hard material into a fluid medium such as air or water. After the molecules settle down to their usual random movements, we can use the disk to measure the ambient pressure in the medium. Once we have this measurement, we rapidly move the flat side of the disk forward by one centimeter (**Figure 2.1**). As the front side of the disk moves forward, it pushes all the air molecules in front of it forward as well. This creates a higher-than-average density of molecules (a **condensation**) on the front side of the disk, and a lower-than-average density of molecules (a **rarefaction**) on the back side of the disk. The condensation layer of molecules will show a pressure that is higher than the ambient pressure we measured earlier, and the rarefaction layer will show a lower-than-ambient pressure.

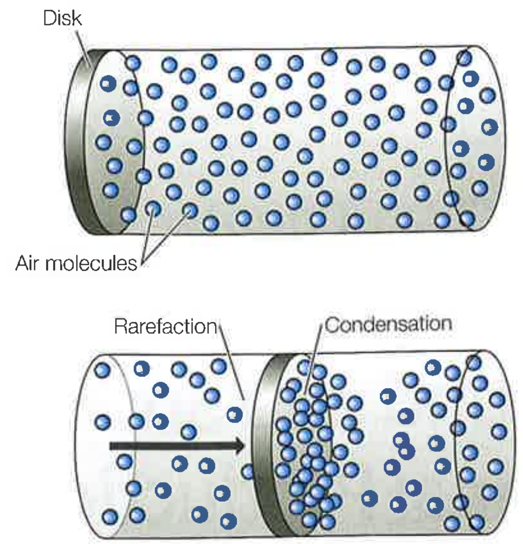


FIGURE 2.1 Generation of a sound by movement of a disk in an air-filled tube If the disk is immobile, air pressures will be identical throughout the tube. As we move the disk suddenly to the right, we collect air molecules and create a condensation ahead of it. At the same time, we create a rarefaction behind the disk. The disturbances created on each side of the disk are then transferred to successive layers of molecules further away from it even though individual molecules do not move very far. We will have created a propagating sound.

In addition to altering local pressures, the movement of the disk transfers additional kinetic energy and a relatively cohesive forward direction of motion to each of the molecules in the condensation. These molecules move forward and collide with the next layer of molecules. These collisions transfer both the forward direction and extra kinetic energy to the molecules in the second layer, while bouncing the first layer back toward the disk. This process continues to transfer the condensation to successively distant layers while individual molecules move no further than the 1-cm displacement caused by the disk movement. Behind the disk—the area of rarefaction—a similar process takes place. In this case, molecules just outside the rarefaction encounter more collisions from molecules farther from the disk than from those close to it. They thus get bounced into the rarefaction and fill it up. However, this leaves a rarefaction layer behind them, and this causes the next layer to move into that zone and fill it up. In this way, the rarefaction also radiates away from the disk.

The net effect of moving the disk forward is to generate two disturbances (a condensation and a rarefaction), both of which radiate away from the source over time. While the molecules closest to the disk are forced to move distances much larger than they would have traveled given no disk movement, successive layers of molecules acquire the forward kinetic energy not from the solid disk but from collisions with other molecules. Their subsequent direction of movement will be a combination of the random movement they would have undergone after any normal collision plus

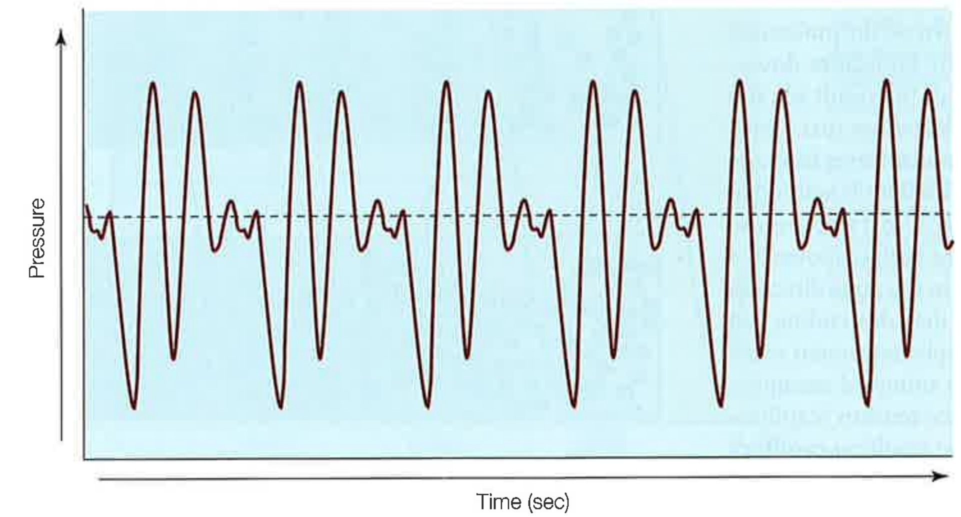


FIGURE 2.2 Waveform of English-speaking human child saying the word *are* It is easy to see that even though there is considerable variation in successive peaks of this waveform, there is a clear pattern that repeats every fourth peak. This signal is thus periodic.

the forward motion of the disturbance. As a result, molecules farther from the disk pass on the forward disturbance, but their actual net displacement gets smaller and smaller with distance from the disk. Eventually at long distances from the disk, it is only the disturbances that change location, and not individual molecules. A radiating disturbance in the pressure of a medium is called a **sound**.

Web Topic 2.1 ***Measuring sound pressure***
Microphones are used to measure the variations in pressure caused by a propagating sound. Specialized types of microphones exist for sound propagation in air, water, and solid substrates. These microphones work by converting pressure variation into electrical signals that can then be measured, stored, and characterized.

GENERATING WAVES IN A FLUID A single sudden disturbance in the pressure of a medium generates an **impulse** sound. What if, instead of creating a single impulse, we repeatedly move the disk back and forth along some fixed axis? Let us further ensure that the movement of the disk is **periodic**: that is, that it repeats the same motion over and over. This will generate successive condensations and rarefactions on both sides of the disk. Instead of a single radiating layer of condensations around the sound source, we now have a series of successive condensation (and intervening rarefaction) layers. The inner layers reflect the most recent disk movements and the outer layers reflect earlier movements.

If we use a fixed microphone to record the successive condensations and rarefactions as they radiate past us, we can generate a graph of pressure versus time. Depending on the way we move the disk back and forth, this graph might appear as in **Figure 2.2**. Because the pressure measurement in this graph rises and falls around the ambient pressure average, we say that the sound propagates as **waves**, and the graph of pressure versus time is thus called the sound's **waveform**. In our example, the shared direction of movement that molecules pass on to each other as the disturbance spreads is the same direction in which the condensations and rarefactions are moving. When molecular movements and sound disturbances travel in the same direction, we say that the sound consists of **longitudinal waves**. This is the primary process for sound propagation inside large volumes of fluids such as air and water (**Figure 2.3A**).

Web Topic 2.2 ***Visualizing sound waves***
The best way to understand the differences between different types of sound waves is to view an animation that shows how the molecules move as the sound propagates. We list a number of websites where you can watch visualizations of most of the basic acoustic processes described in this chapter.

GENERATING WAVES IN A STRING If we tie a rope to a tree, add just a bit of tension, and make a small flip in our end, a wave of displacement will move down the rope until it hits the tree. This is another example of a propagating wave. Note that each segment of the rope does not move toward or away from the tree, as would the molecules propagating a longitudinal wave, but instead oscillates along a line perpendicular to the rope axis. A similar type of oscillation is generated in the strings of a guitar or harp when they are plucked. This oscillation is called a **transverse wave** (**Figure 2.3B**). Light signals are propagated as transverse waves of electromagnetic energy. As we shall see, spiders and some insects communicate by sending transverse waves along strands of silk, and some fish species pluck tightened tendons like guitar strings to make sounds.

GENERATING WAVES ON A WATER SURFACE Unlike air, water is a relatively sticky medium: water molecules are strongly attracted to each other. Below the surface of a body of water, the forces experienced by each water molecule include the downward pull by gravity and the attractive forces from all directions exerted by nearby molecules. At the surface, gravity continues to pull down on the molecules; but now, attractive forces only pull the molecules downward and to the sides. Unless disturbed, the result is a flat surface with a strong surface tension. When we toss a rock into a pond, the ripples radiate out as circular waves from the impact point. These waves propagate with both longitudinal and transverse components (**Figure 2.3C**). In a ripple moving from left to right, a molecule near the surface moves in a clockwise trajectory, rising and moving in the same direction as the ripple when the crest passes, and then descending and moving opposite to the direction of ripple movement while in the trough (see Web Topic 2.2 for an animated example). When ripples are close together, surface tension (capillarity) dominates ripple behavior, and the resulting **capillary waves** radiate more slowly as the distance between them is increased [39, 119, 161, 230]. When the ripples are far apart (at least 1.7 cm or more), gravity affects the ripple behavior more than surface tension does. The resulting **gravity waves** radiate more quickly from the source as the distance between ripples is increased.

GENERATING WAVES IN A SOLID In a solid, molecules cannot move very far before they collide with adjacent molecules. As a result, one often finds both longitudinal waves (also called compression waves) and transverse waves (also called shear waves) propagating inside a solid at the same time. In cylindrical solids such as plant stems, a third category, called **bending waves**, may also be present. These are similar to transverse waves but propagate in more complicated ways [254]. One may also find waves propagated on the surfaces of solids. These are similar to the ripples described above for water surfaces, except that surface molecules in solids move in an elliptical counterclockwise trajectory as the sound propagates from left to right (**Figure 2.3D**). In **Rayleigh waves**, the transverse component moves on a vertical line perpendicular to the surface, (see animation at Web Topic 2.2), and in **Love waves**, the transverse component is a side-to-side motion parallel to the surface. As one moves into the interior of a solid, the elliptical trajectories of molecules near the surface gradually lose their longitudinal component and become entirely transverse.

The characterization of sounds

Sound is a propagated disturbance in the density and pressure of a medium. This means that characterizing any given sound requires that we specify both how sound pressure might vary at a fixed location over time (temporal properties) and how sound pressure might vary over space at any given time (spatial properties). We take up each of these perspectives in turn.

BASIC TEMPORAL PROPERTIES OF SOUNDS We now return to the use of a moving disk to generate sound waves in air or water, only this time we place a single microphone at some moderate distance from the disk to record pressure variations at that site over time. Let us begin with a sound source that moves in a simple **sinusoidal pattern**. This is the movement pattern that we would record if we tracked the oscillating position of a child on a playground swing or a bouncing weight suspended from a spring. In each case, the object being tracked moves rapidly in one direction, gradually slows down, and then reverses direction and moves the other way, building up speed as it passes the midpoint, and then gradually slows down to reverse its movement again. If we move our disk in such a sinusoidal way, it will generate successive condensations and rarefactions in the medium that will pass by our microphone. A graph of the corresponding pressure recorded by the microphone over time would appear as in **Figure 2.4**.

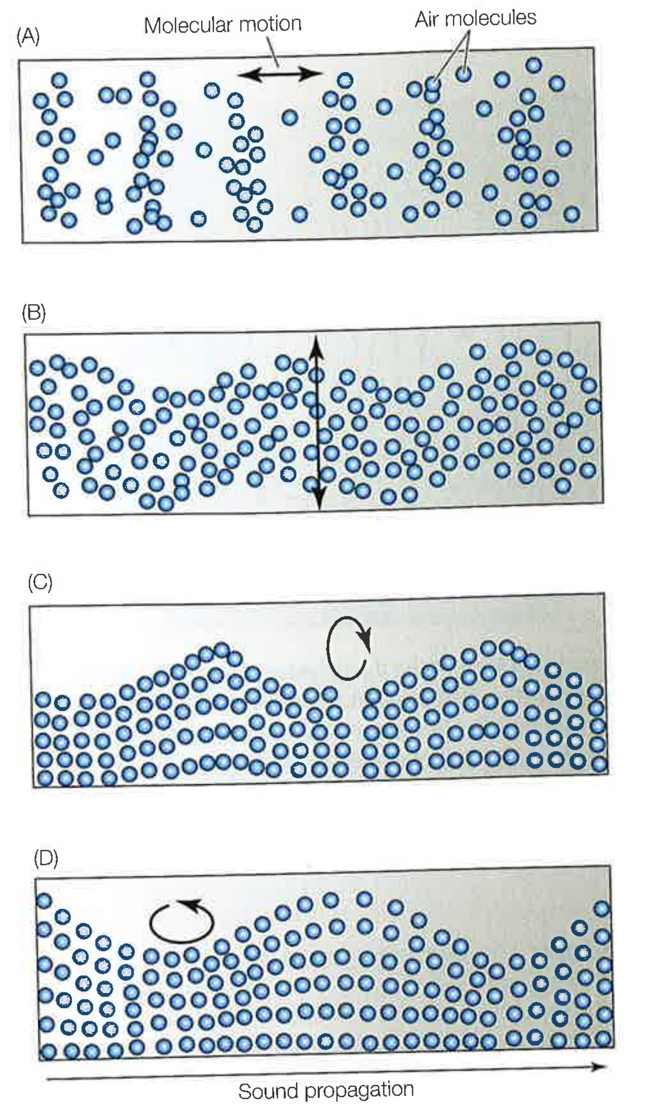


FIGURE 2.3 Types of propagating sound waves In all examples, sound propagates from left to right, and the dark arrows indicate the trajectory of motion of propagating molecules. (A) Longitudinal waves such as one finds in air or water far from any boundaries. Molecular motion is parallel with the direction of sound propagation. (B) Transverse waves as in a vibrating guitar string. Molecular motion here is perpendicular to the direction of sound propagation. (C) Surface waves on a body of water. Surface molecules propagate the ripples by moving in a clockwise (relative to direction of propagation) elliptical trajectory. (D) Rayleigh waves on the surface of a solid substrate. Molecules on the surface move along a counter-clockwise elliptical path. Love waves (not shown) are similar to Rayleigh waves except that they move the substrate side to side in a transverse motion, whereas Rayleigh waves move the substrate up and down. In solids, one may find any combination of these wave types as well as additional types such as bending waves.

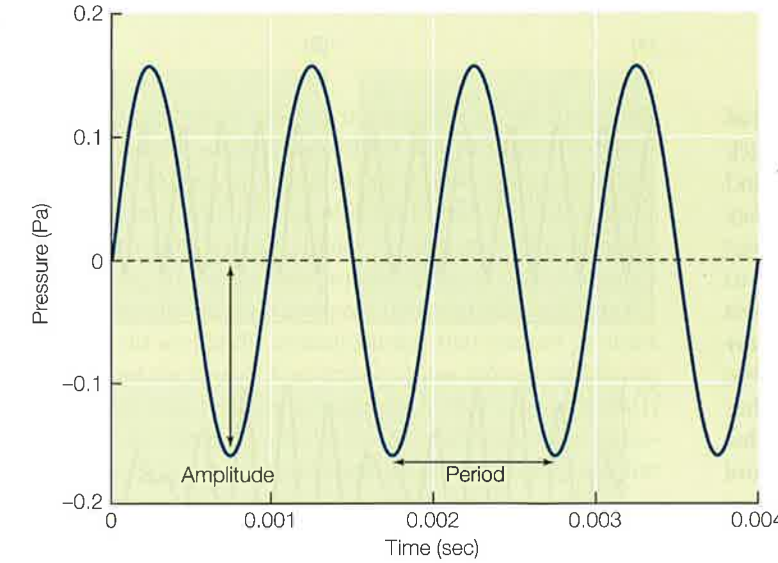


FIGURE 2.4 Time recording of varying pressure due to passage of sinusoidal sound waves past a microphone Amplitude is a measure of the deviation of the passing sound pressures relative to the ambient level (here marked as 0). A typical songbird would produce a sound amplitude of about 0.16 Pa recorded 1 m away. The period is the amount of time it takes to record one complete cycle of the sound. Here, the period is about 0.001 sec. The frequency of the sound is the reciprocal of the period and in this example would be about 1000 Hz.

There are several obvious measures we could make on this graph to characterize the sound. We see that the pattern of pressure variation repeats in a regular fashion. One obvious measure that we could extract from the graph is the interval we have to wait before the same part of the sound wave repeats. This interval, measured in seconds, is called the **period** of the wave. We could also measure how many complete cycles occur per second, which is called the **frequency** of the sound. Because wave frequencies are important measures throughout physics, the fundamental unit of frequency, one cycle per second, has been named the **Hertz** (abbreviated **Hz**), after the German physicist Heinrich Hertz. In practice, we need to measure only period or frequency, since one is the reciprocal of the other. For example, if we find the period of a sinusoidal wave to be 0.001 seconds (or 1 msec), the frequency can easily be computed as 1/0.001 = 1000 Hz (or 1 kHz). The only other time measurement we might want to make on this graph is *when*, relative to some reference time, the wave achieves a specific part of the cycle, such as a peak or valley. This is known as the **phase** of the wave. Phase is not very important when there is only a single frequency present in a sound. But as we shall see, it can become very important when multiple sine waves are present in the same sound or at the same location.

In addition to the time measurements, this graph allows us to measure the degree to which the passing sound waves differ from ambient pressure levels. One obvious measure is the difference between the peak (or valley) pressure and the ambient pressure (shown as the midline of the graph). This difference is one measure of the **amplitude** of the sound wave, measured as a standard unit of pressure, the **Pascal** (abbreviated **Pa**). While the difference between the peak and ambient pressure is a useful amplitude measure for single sine waves, it may not be very representative for more complicated sounds. The most common alternative is a weighted average of the differences between each part of the wave and the ambient level called **RMS** amplitude. Details can be found at Web Topic 2.3. Finally, whether one measures peak or RMS amplitude, most publications on sound will not report these absolute values, but instead will report the ratio between the measured amplitude and a reference sound. The most common reference is the pressure difference between the measured sound and the softest sound an average human can hear (called SPL). Because humans can hear over a very wide range of amplitudes, these ratios can get very large. The practical solution is to use the logarithm of the ratio, properly scaled, to report amplitudes. This relative unit of amplitude is called the **decibel** (abbreviated **dB**). See Web Topic 2.3 for details on computing amplitudes in dB. However measured, the amplitude of a sound signal is usually referred to as its **sound pressure**.

Web Topic 2.3 ***Quantifying and comparing sound amplitudes***

A variety of methods are available for measuring and comparing sound amplitudes. Here we define some of these methods, show how they are computed, and discuss when each might be most useful.

One might wonder why we don't use ambient pressure as the reference point and then refer to different sound levels as the percentage change from ambient pressures. There are several reasons why this is not done. The first is that ambient pressures change with altitude, the weather, local exposure to sunlight or wind, and many other factors. Having a fixed reference standardizes sound measurements. The second reason is that the change in pressure created by a passing sound wave is extremely small. Even a sound with an amplitude so high that it reaches the pain threshold in humans would only change local pressures by 0.02% as it passed. This is another reason why the instruments for measuring ambient pressure and sound pressures require quite different designs.

An additional temporal measure of sound propagation that will be important in later chapters is **particle velocity**. Velocity is defined as the distance an object moves per unit time. If we focus on an infinitesimal volume of fluid as a sound propagates, this "particle" of fluid will move back and forth at the same frequency as the sound. At low-fluid densities, this particle will be able to move some distance before it turns around and moves back in the other direction; at higher densities, it will encounter more resistance to its movements and the displacement will be less. Since the frequency is the same in both media, the time available for movement in a given direction has to be the same. Thus, the particle velocity in the lower-density medium will be higher than that in the higher-density medium. We shall see that this has important implications for how animals emit and capture ambient sounds.

TEMPORAL PATTERNS OF SOUNDS: INTERFERENCE AND BEATS The prior example considered a sound source moving in a sinusoidal manner. What if the movement of the disk is best described as the sum of two sine waves? Alternatively, what if our microphone responds simultaneously to sine waves radiated from two different nearby disks? In either case, any medium molecule near the microphone is going to be receiving kinetic energy and directions of motion from two different sine waves at the same time. What would we record? In fact, what we record is simply the sum of the pressures predicted at each moment for the two waves. Suppose the two sine waves have exactly the same frequencies and amplitudes. If they arrive at the medium molecules near the microphone so that they are in exactly the same part of their cycle, we say that they are **in phase**. When both peak at the same time, the total pressure at the microphone is twice what it would be if only one sine wave were present. Now consider the opposite possibility that the two waves are completely **out of phase**: when one has its peak near the microphone, the other is in its valley. The condensation caused by one wave will be countered by the rarefaction caused by the other. The result will be no deviation from ambient sound pressures at all: the two waves simply cancel each other out. When two sine waves with the same frequencies and amplitude are in phase, we say that they experience **positive interference**; when they are out-of-phase, they experience **negative interference**.

What if the two sine waves do not have the same amplitude or frequency? They can still interfere with one another. As the two waves become more dissimilar in amplitude, the higher-amplitude wave will dominate the combination and the second wave will have a decreasing effect on the first (whether positive or negative). If they have the same amplitude, but differ slightly in frequency, then the behavior of the sum is a bit more complicated. At first, one may have its peaks when the other is having its valleys and the interference will be negative, reducing the amplitude of the sum. However, after several more cycles, the wave with a higher frequency will begin to catch up with the other wave, they may interfere more positively, and the amplitude of the sum will increase. The higher-frequency wave then moves ahead of the slower one again, and they return to the out-of-phase state.

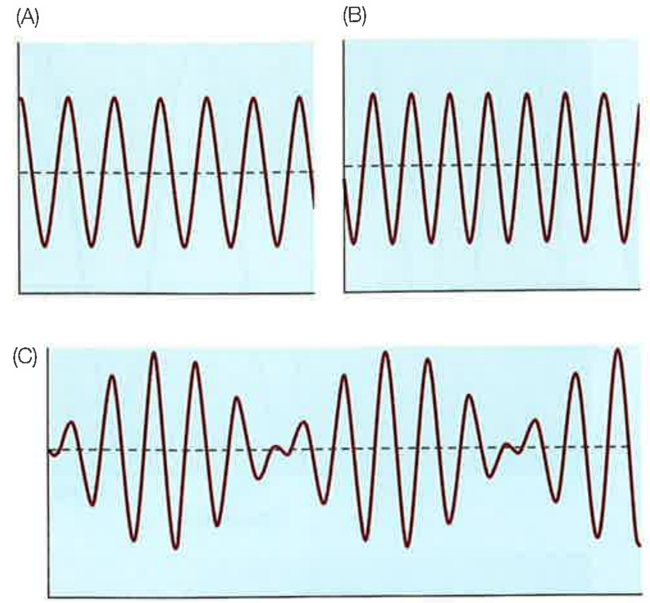


FIGURE 2.5 Generation of beats (A) Waveform of pure sinusoidal tone at 1 kHz. (B) Waveform of pure sinusoidal tone at 1.2 kHz. (C) Waveform of combination of first two tones producing beats. Combination waveform is periodic but nonsinusoidal; the pattern repeats at a rate equal to the frequency difference between the original two pure tones (1.2 kHz – 1.0 kHz = 200 Hz).

The summed result of two waves with slightly dissimilar frequencies is a sine wave whose frequency is the average of the two components, and whose amplitude rises and falls with a regular pattern (**Figure 2.5**). The frequency of this rise and fall in amplitude equals the difference between the frequencies of the two original sine waves, and the resulting variations in amplitude are called **beats**. An animated example can be found at Web Topic 2.2.

TEMPORAL PATTERNS OF SOUNDS: COMPLEX WAVEFORMS In practice, it is very difficult for most physical systems (or animals) to produce a sinusoidal sound in air or water. The waveform recorded at a single microphone will not be sinusoidal but some other more complicated pattern. To complicate this further, many animal sounds are not really **periodic**: the same waveform pattern is not present throughout the entire sound, and so we see a series of different waveforms during the course of the sound signal. How can we possibly measure and compare such sounds?

Luckily, several mathematicians, particularly J. B. J. Fourier (1768–1830) and J. P. G. L. Dirichlet (1805–1859), showed that most periodic and continuous waveforms can be decomposed into an infinite sum of simple sine waves. Because the amplitudes of the high-frequency components tend to be very small, (see Web Topic 2.4 for reasons), we really need to consider only a limited range of low-frequency sine waves to adequately characterize most periodic signals. This characterization would specify the frequency, amplitude, and relative phase of each component of the sound signal, measures that we already know how to make. Because most animal ears perform this kind of **Fourier analysis** on

sound signals before sending information to the brain, this approach also provides an excellent way to compare sounds similarly to the way an ear would do it. Even better, most animal ears ignore the relative phase information except when two components are very similar in frequency. This allows us to focus largely on the component differences in frequency and amplitude when we compare two animal sound signals.

How do we handle animal sounds that are not periodic throughout the signal? Fortunately, most animal signals can be divided into consecutive segments that are sufficiently periodic that we can perform a separate Fourier decomposition on each segment and then string the results together to see the overall pattern. The cost of this segmentation is that the ability to discriminate between adjacent frequencies declines as segments get shorter. But in practice, we can usually find a suitable segmentation of a complex sound that tells us most of what we need to know.

The most common way to characterize animal sound signals is with a **spectrogram** (also called a **sonogram**). This is a plot with time on the *x*-axis running from left (earlier) to right (later), and frequency on the *y*-axis (running from low frequencies near the origin and extending upward). Each point in the plot corresponds to a specific time segment within the signal and a particular band of frequencies. If the Fourier decomposition indicates a high amplitude for frequencies in a given band at a given time, the plot shows one extreme of color or darkness; but if that band of frequencies is not present or is at low amplitude at that time, the plot shows an opposite color or darkness at that point. A variety of computer programs are now available (many for free) that generate spectrograms quickly and effectively. Since where the segmentation cuts are made is arbitrary, several sophisticated techniques are used to smooth out these plots so that junctions between adjacent segments are not visible. Some programs also allow the user to extract and view the Fourier composition of any segment that they wish to examine. Such a plot is called a **power spectrum** or **section**.

As an example of this approach, consider a single call of a male túngara frog (*Engystomops pustulosus*). The overall waveform of this call is shown in **Figure 2.6**. We can see that the call is fairly explosive, with a rapid onset at high amplitude and then a gradual diminution in amplitude during the call. Variation in amplitude during the course of a signal is called **amplitude modulation.** If we expand the waveform

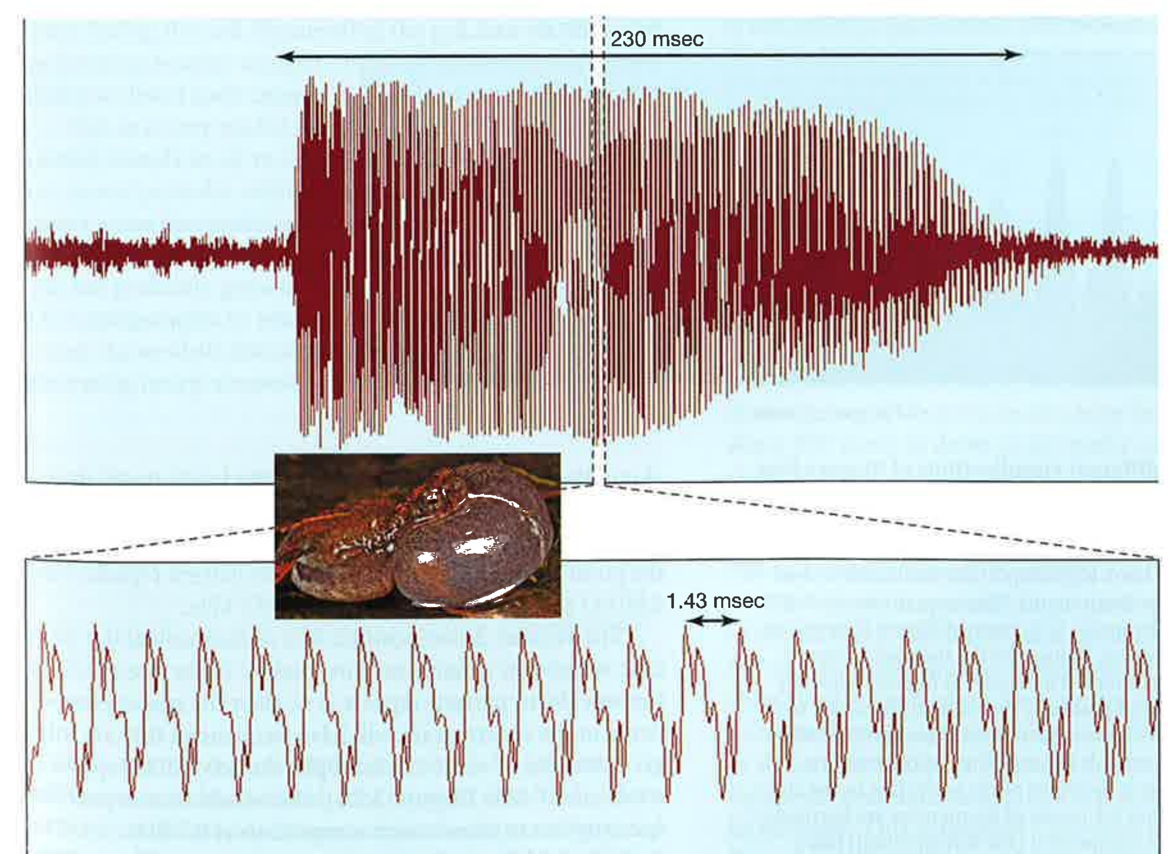


FIGURE 2.6 Waveform of single call by male túngara frog (*Engystomops pustulosus*) Both plots show varying sound pressure relative to ambient pressure (middle line) on the vertical axis and time on the horizontal axis (events on left occurred prior to events on right). The waveform in the dashed section of the top plot is expanded along the time axis in the lower plot to show the wave details. Inset shows a male túngara frog with his throat sac filled with air while calling.

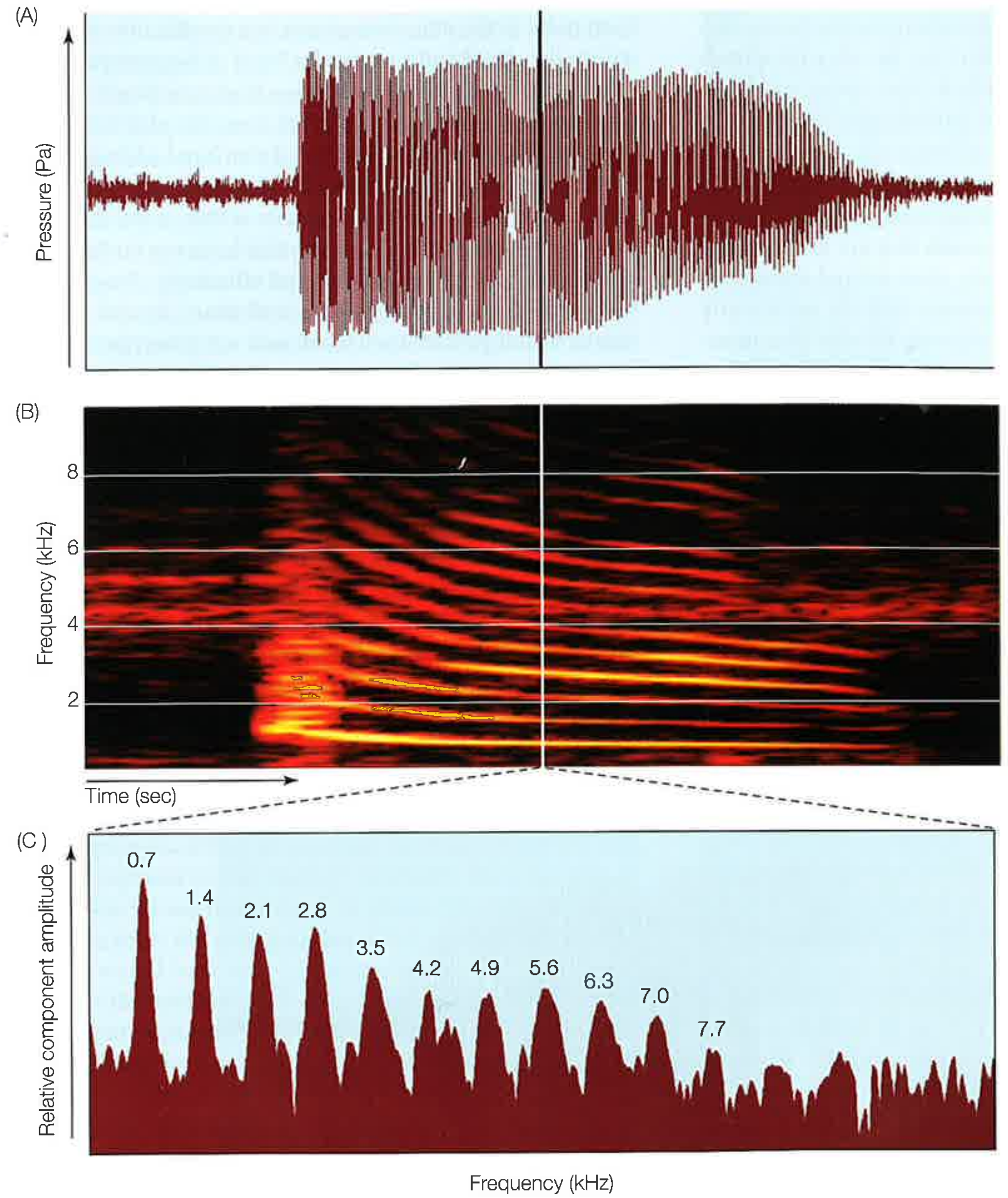


FIGURE 2.7 Three different visualizations of túngara frog call (A) Waveform (same as in Figure 2.6). (B) Spectrogram of same sound aligned and on same time scale as waveform in (A). Brighter (yellow) colors in the spectrogram indicate that a given frequency at that time has a high amplitude, and darker colors indicate low-amplitude components. Spectrogram shows that the beginning of call is quite noisy, with many different frequencies contributing to this portion. Subsequently, the major components are evenly spaced bands. These start at higher frequency values early in the call and gradually decrease in frequency over the course of the call. We note also a band of background noise between 4–5 kHz that extends through the entire recording. (C) A power spectrum slice at the point of the white line in the spectrogram. This shows that the bands of frequencies are harmonically related: the lowest component (the fundamental) has a frequency of about 0.7 kHz, and all higher frequency bands are integer multiples of this frequency. Note that the component amplitudes tend to decrease with frequency. This pattern of harmonically related bands is very common in the spectrograms of animal sound signals.

along the time axis at any point after the initial onset, we see that it is not a simple sine wave, but is periodic within short segments: the same basic shape repeats at regular intervals. At the point shown in Figure 2.6, the wave pattern repeats every 0.00143 seconds or at a rate of about 0.7 kHz.

The Fourier decomposition of a nonsinusoidal but periodic waveform is fairly easy to predict: if the rate at which the waveform pattern repeats is *w*, then the major components in the spectrogram will have frequencies that are integer multiples of *w*. In our example, the waveform repeats at a rate of 0.7 kHz (**Figure 2.7A**). We would thus expect the spectrogram to show major components at 0.7 kHz, 1.4 kHz, 2.1 kHz, 2.8 kHz, and so forth. As we can see in **Figure 2.7B**, this is exactly what we find. This spectrogram shows evenly spaced bands throughout the course of the call. The power spectrum for the segment indicated by the vertical white line in the spectrogram is shown in **Figure 2.7C**. Here we plot the relative amplitude of each frequency component on the vertical axis against the frequencies of possible components. We see that there is a series of peaks in this plot with each peak corresponding to the band at that frequency in the spectrogram. If we measure the frequency at the top of each peak, we find that these are all integer multiples of 0.7 kHz, the repeat rate for the waveform. Frequencies that are integer multiples of a reference frequency are called **harmonics** and the entire suite of them is called a **harmonic series**. The reference frequency is called the **fundamental**, the component at twice the reference is called the **second harmonic**, and so on. For most animal sounds, all harmonics will be present. In cases where the repeating wave pattern is very symmetrical, only the fundamental and the odd-numbered harmonics are present; however, this happens only rarely with animal sounds.

In the spectrogram in Figure 2.7B, we see that the fundamental and the harmonics all seem to decrease in frequency as the call proceeds. This is because the repeat rate of the basic pattern actually slows down during the call, and thus the frequency components must all decrease accordingly. We hear this as a slightly descending pitch during each frog's call. Variation in frequency composition during the course of a signal is called **frequency modulation**. Note that if we had performed the Fourier decomposition on the entire sound, we would not be able to detect these slow frequency modulations during the call. Segmenting the call into sections and performing Fourier analysis on each provides us with some ability to detect such changes during the course of a signal.

This is a very useful example because the majority of animal sounds in air or water are nonsinusoidal waves but are almost periodic within short segments. We should thus expect to see harmonics in the spectrograms of such animals' signals. Where we see only single pure frequencies, the animal has probably gone to a lot of work to filter out all but a few components in what was initially a harmonically rich sound. As we shall discuss later, animals have an easier time generating nearly sinusoidal sounds in solid media.

Web Topic 2.4 ***Fourier analysis of animal sounds***
Here we provide an introduction to the logic behind Fourier decomposition of animal sounds, including links to several excellent software packages for creating spectrograms and introductions on how to use these packages. We also provide links to sites where one can use such methods to compare archived animal sounds.

SPATIAL PATTERNS OF SOUNDS: THE SPEED OF SOUND As we have seen, a sound disturbance is passed from molecule to molecule at successive distances from the source. The speed with which a layer of molecules can hand off the pressure disturbance to the next layer, and thus the speed at which the sound propagates in that medium, depends on two properties of the medium (**Figure 2.8**). The first property is the density of the medium. This is a function of the mass of the molecules (larger masses result in higher densities), and the average distance between the molecules (more tightly packed molecules result in higher densities). All other factors being equal, the speed of sound is inversely related to medium density. This is because it takes longer for an activated layer to get the next layer moving if the second layer has many molecules in it or if those molecules have large masses. Water is about 800 times as dense as air; and a solid, such as steel, is about 8 times as dense as water. Based on density alone, we might expect sound speed to be highest in air, intermediate in water, and least in solids. In fact, the reverse is true. This is due to a second factor that must be considered.

The second factor affecting sound speed is the **stiffness** of the medium. For fluids such as air and water, stiffness is the relative resistance to compression: water resists being compressed much more than air does. For solids, stiffness refers both to incompressibility and to the solid's resistance to distortion in shape. All other properties held constant, the speed of sound in a medium is positively correlated with its stiffness. This is because a pressure disturbance passing through a stiff medium spends less time in compression and distortion than a disturbance moving through a non-stiff medium does. Water is about 10,000 times as stiff as air, and steel is about 100 times as stiff as water. Although the differences in density bias the speed of sound in these media in one

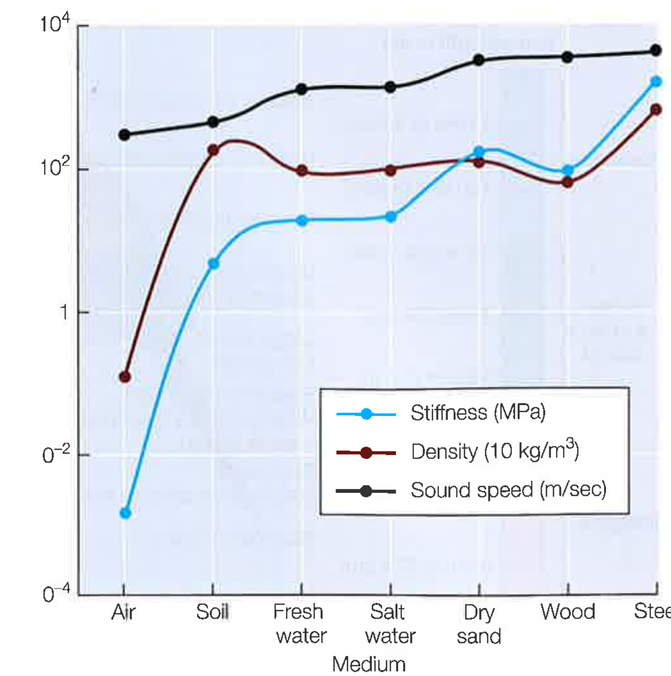


FIGURE 2.8 Stiffness, density, and speed of sound in some sample media Stiffness is measured as bulk modulus for fluids and Young's modulus for solids (Mpa), density in tens of kg/cubic meter, and sound speed in m/second. The speed of sound increases with stiffness, but decreases with medium density. Because both measures tend to increase together as one switches between media, the range of sound speeds is much less than might be expected given independent variation in stiffness and density.

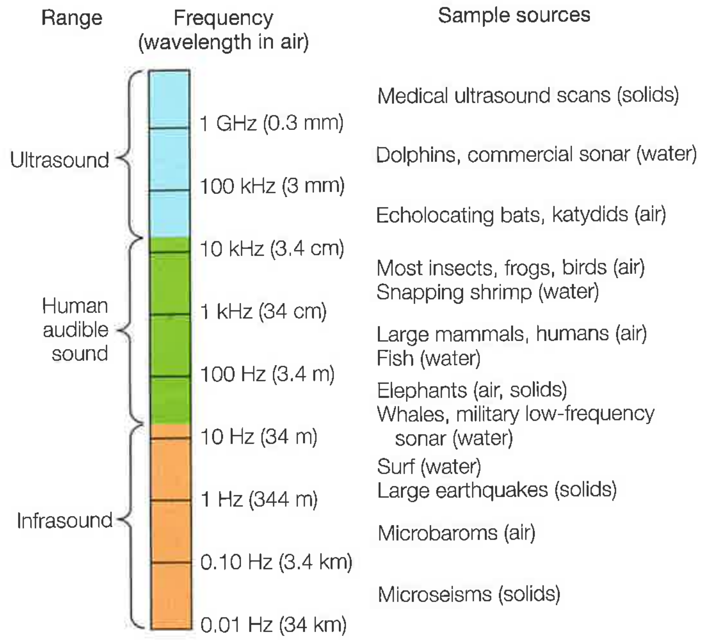


FIGURE 2.9 The acoustic spectrum The plot shows the sound frequencies used by different animals, including humans; the wavelengths of those frequencies in air; and whether the resulting sounds are propagated in air, water, or solid substrates. Note that wavelengths for a given frequency in water will be 4.4 times as long as those in air, and those in solids roughly 14–15 times as long as those in air. Microbaroms are low-frequency airborne sounds created by large-scale movements of the ocean that compress or rarefy the layer of air above. Microseisms are low-frequency vibrations propagated in the Earth from distant earthquakes, volcano action, fault movements, and explosions.

direction, the differences in stiffness more than compensate. As a result, the speed of sound is about 344 m/sec in air, 1500 m/sec in water, and 5100 m/sec in a bar of steel. Actual sound speeds will differ a bit from these values depending on local temperatures, ambient pressures, and the composition of the medium. Humidity can change the speed of sound in air, and salinity can alter the speed of sound in water. Although the speed of sound is independent of frequency within fluids like air or water, it can be very frequency-dependent inside solids and at boundaries between media. For example, the speed with which ripples spread on the surface of a pond will vary depending on the frequency being propagated. Sounds in solids can also show frequency-dependent propagation speeds.

SPATIAL PATTERNS OF SOUNDS: WAVELENGTH The speed of sound plays a major role in determining the spatial pattern of a sound. Consider a sound wave with a frequency of 1 kHz in air. It will take 0.001 seconds (the period) to generate one complete cycle of this sound. By the time the sound source has finished generating this single cycle, the leading edge of the wave will have radiated 0.34 m (about 1 foot) away from the sound source. If we had created this same 1-kHz sound in water, the initial part of the wave would be 1.5 m away from the final part. The spatial length of a single cycle of a sound wave in a particular medium is known as its **wavelength**.

Because it takes longer to create a sound with a longer wavelength, we see that the wavelength and frequency of a sound are inversely related: high frequencies have small wavelengths, and low frequencies will have large wavelengths (**Figure 2.9**). Wavelength will also depend critically on the speed of sound of the medium. A given frequency of sound in water will have a wavelength about 4.4 times as long as that same frequency in air because of the difference in the speeds of sound in the two media. Sounds in solids will have wavelengths 14–15 times as long as the same sounds in air. Why does wavelength matter? As we shall see later, it is difficult for most animals to generate an intense sound with a wavelength more than twice their body size. Given the effects of different speeds of sound, this constraint will be greater for aquatic animals than for terrestrial ones.

SPATIAL PATTERNS OF SOUNDS: DOPPLER EFFECTS Consider a male bird that is flying toward its perched mate and emitting a call in flight (**Figure 2.10**). As successive waves radiate from its beak toward its mate, the male follows in the same direction. This means that the leading edge of a wave will travel a shorter distance by the time the trailing edge is emitted than would be the case if the caller were not moving. The wavelengths of all frequencies in the male's call will thus be shortened because of his motion toward his mate. Because successive peaks and valleys of the sound waves arrive at the female's ear with reduced delays, she perceives his call as being shifted to higher frequencies. If the male were flying away from the female, then the wavelengths of his emitted sounds would lengthen, and she would perceive his call as being shifted to lower frequencies. The same effects would be created if the male were to call from a perch and the female receiver were to fly toward or away from him during his calling. If both birds were to fly in the same direction, then the changes in wavelengths and frequencies would cancel out. Shifts occur only when the sender and receiver have different relative motions.

The change in propagated frequencies when either the sender or the receiver is moving relative to the other is called a **Doppler shift**. The magnitude of the shift in sound frequencies depends on the ratio of the speed of the moving individual to the speed of sound in the relevant medium. Birds and bats are among the fastest fliers in terrestrial environments. Their speeds rarely exceed 10 m/sec, although a stooping falcon might achieve a speed of nearly 50 m/sec. In air, a perched receiver attending to a call emitted by a sender flying directly toward or away from the receiver at 10 m/sec will experience a Doppler shift of about 3% in all song frequencies. The speed of movement of most animals sending and receiving sound signals in air—and thus the Doppler shifts they experience—will be less than this, and animals typically ignore the slight shifts in frequency. Foraging bats

FIGURE 2.10 Doppler shift when calling sender is moving relative to receiver Calling bird is flying from left to right. This causes successive waves in its emitted call to crowd together in front of it and spread out behind it. A receiver to the right of the flying bird will hear all components in the flyer's call at slightly higher frequencies. A receiver positioned behind the flying bird will hear the call at slightly reduced frequencies.

are an exception. They emit calls and listen for echoes from possible food targets. Slight shifts in the frequencies of the outgoing sound and returning echoes provide information to the bat on its speed relative to an edible target. We discuss this strategy further in Chapter 14. In water and solids, the speed of sound is so much higher than the velocities of moving animals that Doppler shifts are much less likely to be biologically relevant. See an animation of Doppler shifts at Web Topic 2.2.

SPATIAL PATTERNS OF SOUNDS: NEAR FIELD VERSUS FAR FIELD We noted that near a sound source, medium molecules get moved over distances larger than they would normally travel if no sound were being propagated. However, as a disturbance radiates away through successive layers of molecules, the distances traveled by the molecules quickly become little more than they would have been without a disturbance present. This does not mean that molecular movements are the same whether a sound is being propagated or not. What differs during sound propagation is that adjacent molecules in a layer will all have a component of their movement in the same direction and in sufficient concert that they increase pressure in the next layer. It is not *how far* they move, but *where and when* they move that distinguishes the movements of molecules that are propagating sounds from their movements when no sound is present.

The zone around the sound source where the distances that propagating molecules travel are greater than usual is called the **near field** of the sound, and the outer zone where molecular translocations return to normal is called the **far field** of the sound (**Figure 2.11**). In acoustics, the outer boundary of the near field is usually defined as a distance of 1/6 of a wavelength from the source or 1/3 the diameter of the source, whichever is larger. However, it should be remembered that the transition is actually gradual and not

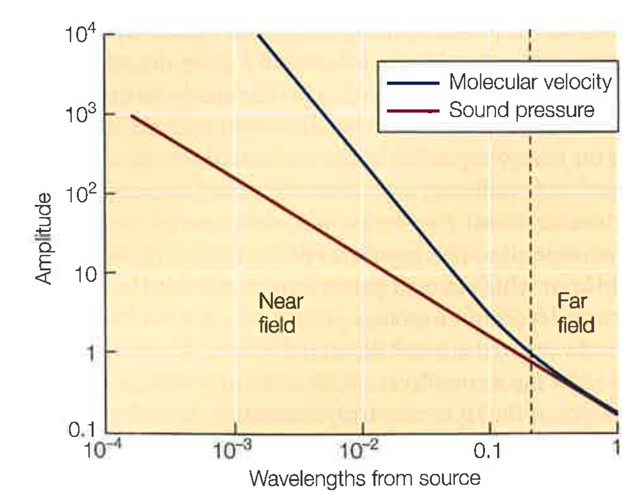


FIGURE 2.11 Plot of sound pressure and molecular velocity as a function of the distance (in wavelengths of the sound) from a point source Pressure values have been standardized relative to the characteristic acoustic impedance of the medium. Both pressure and velocity decrease with distance from the source, but velocity begins at a much higher value close to the source and decreases more rapidly with increasing distance. Although the two eventually converge at about one wavelength's distance. Although the transition is clearly gradual, the convention is to consider the region between the source and the distance marked with the dashed line the near field of the sound, and all greater distances the far field.

sharp, so this guideline is only approximate. In practice, a distance of 1/3 of a wavelength from the source or 2/3 the diameter of the source is required before near field effects become negligible. The ability of a receiver to detect a sound signal may depend significantly on whether it is located in the near or the far field of a sound source. A receiver in the near field could perceive the sound through some delicate sensor that is dragged by the tidal movements of the surrounding medium. In the far field, it is unlikely that tidal movements of the medium will be sufficient to cause stimulation of the sensor. In this situation, the receiver can at best try to monitor variations in pressure. Even this strategy can be challenging: by the time a sound propagates into the far field, the pressure variations due to the sound may only be about 0.02% or less of the ambient pressure of the medium.

The propagation of sound

One cannot hear a sound once one gets far enough away from the source. Sound signals get fainter with distance and eventually drop below the level of ambient noise. To understand this process, we now examine the various factors that erode a sound disturbance as it propagates and thus limit the range over which the sound can be detected by a receiver.

SPREADING LOSSES Each time a sound source moves, it must expend energy to push the adjacent medium molecules ahead of it. The stiffer and denser the medium, the more energy the sound source has to expend to move the molecules a given distance. Because most animal sound sources move repeatedly to produce waves, the best measure of this process is the amount of energy expended per unit time. This is known as the **power** spent by the sound source. By forcing adjacent medium molecules to move in a given direction, the sound source transfers some of its kinetic energy to the molecules. This transfer is never very efficient: in animals, less than 1% of the energy expended by the sound source ends up in the pressure wave radiating away from the sound source [119].

A sound source first transfers kinetic energy to the first layer of molecules. This layer then passes this energy on to the second layer which in turn passes it on to the third layer. The successive layers of molecules propagating a sound are concentrically arrayed around the sound source: the first layer is enclosed by the second layer which is, in turn, enclosed by the third layer. If the layers are truly concentric, then it must be the case that an outer layer constitutes a larger surface area and consists of more molecules than an inner layer. It follows that as the sound radiates away from the sound source, the initial kinetic energy supplied to the first layer gets spread out over more and more molecules as it moves to successively more distant layers (Figure 2.12). The amount of energy each molecule acquires will thus decrease with distance from the sound source. As the kinetic energy per molecule decreases, the difference between the peak sound pressure and the ambient pressure must also decrease. This **spreading loss** causes the pressure of a sound signal propagating into three dimensions to decrease with the reciprocal of the distance

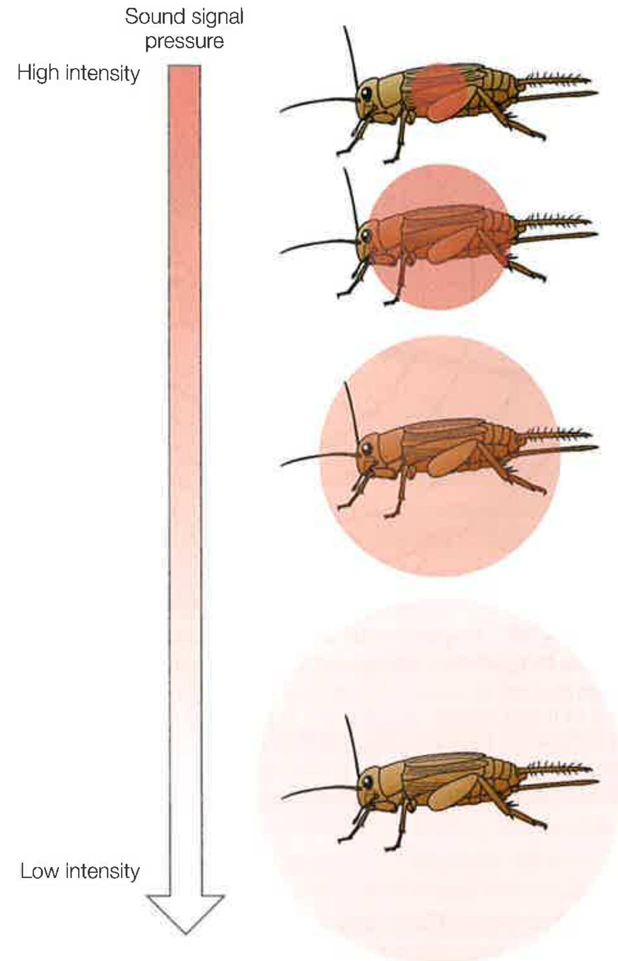


FIGURE 2.12 Spreading losses in a sound signal's pressure as it propagates away from its source Reddish spheres show the location of the leading portion of a single call element at successive times after the cricket made the sound. Because the same initial energy is spread over larger and larger spherical surfaces as the sound radiates away from the source, the pressure at any point on a larger and later sphere is less than that on a smaller and earlier one.

between the sender and the receiver. Because spreading losses arise simply from geometrical considerations, they occur at the same rate for all frequencies.

Water striders and other aquatic insects signal by sending ripples outward on the surface of the water. In this case, the sound energy is largely spread in two dimensions instead of three. This reduces the rate of spreading loss; in fact, pressure decreases with the square root of the distance from the source for sound waves moving on a surface. Tree hoppers and spiders that live on thin-stemmed plants can communicate by introducing sound waves into the plant tissues. Receivers that are some distance away from the sender detect these waves as they pass under their feet. Because such stems and branches are essentially one-dimensional media, there is *no* spreading loss as these sounds propagate [32].

HEAT LOSSES In addition to spreading losses, sound energy can be lost each time that molecules collide with each other. Such losses are largest when a molecule collides with another that has different physical properties. For example, air is largely composed of oxygen and nitrogen molecules. When one layer of these molecules is moved forward by a propagating sound wave and collides with the next layer, most (though not all) of the kinetic energy is passed on to the next layer, since nitrogen and oxygen gas molecules have similar properties. If, however, there are water vapor molecules in the next layer, they may convert the kinetic energy passed to them by nitrogen or oxygen molecules into internal vibrations and molecular rotations. This reduces some of the translational kinetic energy needed to sustain the sound wave and eventually converts it to heat (random movements of the molecules). The amount of heat loss in air is a complicated function of frequency, temperature, and relative humidity. At a temperature of 20° C, heat losses are maximal at relative humidities of 4–20% for frequencies of 1–10 kHz, respectively, and less for lower and higher humidities. As the frequency is increased, the relative humidity at which peak heat losses occur also increases. In seawater, dissolved salts such as magnesium sulfate and boric acid are very dissimilar to water molecules and thus have a similar effect on sound propagation. Here too, attenuation depends on frequency, temperature, dissolved salt concentrations, and pressure.

Since **heat losses** (also known as **excess attenuation**) occur with each successive collision between layers of molecules propagating the sound, their effect is cumulative. The drop in sound pressure during propagation due to heat losses alone will thus be roughly proportional to the distance between sender and receiver. Also, since adjacent layers collide more frequently when propagating a high-frequency sound wave than when propagating a low-frequency one, high frequencies lose more sound energy to heat losses than do low frequencies. In most media, heat losses increase with the square of the sound frequency. This means that the maximum distance over which two animals can communicate by sound will be shorter if they use high frequencies than if they use low frequencies. We discuss this principle in more detail in Chapter 3.

The type of medium significantly affects the rate of heat losses (Figure 2.13). For example, a 1-kHz sound propagating 500 m in fresh water will lose about 0.001% of its energy due to heat losses. The same sound propagating the same distance in seawater would lose 0.5% of its initial energy, and in air the heat losses would reduce the signal amplitude by 44%. Sounds are detectable at much greater distances in water than in air. Excess attenuation is very complicated in solids, in part because most solids have bounded surfaces that also affect sound propagation. We take up such boundary effects in the next sections.

ACOUSTIC IMPEDANCE When a layer of medium molecules propagating a sound pushes against the adjacent layer, the latter will resist being compressed and distorted.

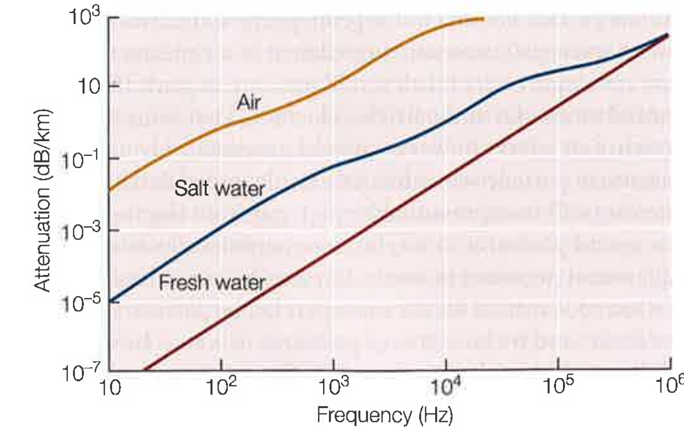


FIGURE 2.13 Heat losses of propagating sound as a function of frequency and medium Heat losses need to be combined with spreading losses and any scattering effects to compute actual sound pressures at a distance from a source. As a rough rule, heat losses increase with the square of the frequency in all media. Deviations from this rule depend on humidity and temperature effects in air, and dissolved salts and temperature in water. Note that for a given frequency in the range typically used by animals for communication, heat losses in salt water are about 100 times as high as those in fresh water, and those in air are 100 times as high as those in salt water. (After [323].)

This resistance by the medium to having its current behavior altered is called its **acoustic impedance.** When a large volume of medium is far from sound sources and also from objects consisting of different media, its acoustic impedance is approximately equal to the product of its current density and speed of sound. This product is called the **characteristic acoustic impedance** of the medium. Since the speed of sound depends largely on the stiffness of the medium, characteristic acoustic impedance is essentially the product of medium density and stiffness. Both factors will make it harder for a given sound pressure to move a given volume of medium. In fact, the higher the characteristic acoustic impedance of a medium, the shorter the distance that one layer of medium can move the next when propagating a sound. As we noted earlier, water is about 800 times as dense as air, and also has a sound propagation speed that is 4.4 times as high. As a result, the characteristic acoustic impedance of water is about 3500 times as great as that of air. Most solids, such as wood, have characteristic acoustic impedances 5000 times as great as that of air. This has very important implications for how sound propagates in each medium, and what happens at boundaries between different states of matter.

We have seen that the energy imparted to a medium by a sound source becomes spread over larger and larger areas of medium as the sound propagates away from the source (spreading losses). It follows that the amount of energy per unit area of medium, known as the **intensity** of the sound, must decrease as the distance from the source increases. Sound intensity is equal to the product of the sound pressure and the particle velocity of the propagating sound wave. The low characteristic acoustic impedance in air means that it does not require very much sound pressure to generate substantial molecular and particle velocities. That same sound pressure in water, however, would generate only a small increase in particle velocities. As a result, a sound of a given intensity will be represented by high particle velocities and low sound pressures in air, but low particle velocities and high sound pressures in water. Put another way, the energy of a sound is carried for the most part by the particle velocities in air, and by local sound pressures in water. In solids, which usually have higher characteristic acoustic impedances than either air or water, the energy in sound waves is almost entirely conveyed by the sound pressure, and molecules are barely able to move at all.

In practice, the actual acoustic impedance for sound propagation is often different from that predicted by the medium's characteristic acoustic impedance value. For example, consider a tube with walls consisting of some solid material and a hollow filled with air. When sound waves propagate along the air-filled hollow of the tube, the air molecules in the center of the tube largely encounter only other air molecules, while those at the boundary of the hollow space will also collide with the incompressible and unmoving molecules that make up the tube wall. This will create a drag or friction that resists the passage of the sound waves close to the tube wall. The acoustic impedance will be closest to the characteristic value for air in the center of the hollow but higher at its margins. Overall, the average acoustic impedance inside a tube filled with air will be higher than that for an unbounded volume of air at the same temperature and humidity. Similarly, the acoustic impedance of air close to the surface of a body of water will be higher than the acoustic impedance of air high above this surface: air molecules close to the surface will not be able to move as freely as those with no water molecules nearby. Conversely, the acoustic impedance for water near a pond's surface will be lower than that deeper into the pond since water molecules on the surface will meet much less resistance to movement upwards than they would if surrounded on all sides by water molecules. While we can easily compute the characteristic acoustic impedance for a medium using its density and sound speed, we often have to modify this value up or down when considering that same medium near a boundary with another medium.

REFLECTION AND REFRACTION What happens when sound traveling in one medium encounters a boundary with another medium? The answer depends critically on the relative acoustic impedances of the two media at the boundary. Because sound energy is conveyed largely by molecular velocities in air, but by high sound pressures in water, a sound wave traveling in one of these media will face a difficult time crossing a boundary into the other medium. Instead, nearly all of the incident sound energy will be **reflected** back into the initial medium at the surface of the boundary (Figure 2.14). The angle of travel of the reflected waves will be determined by

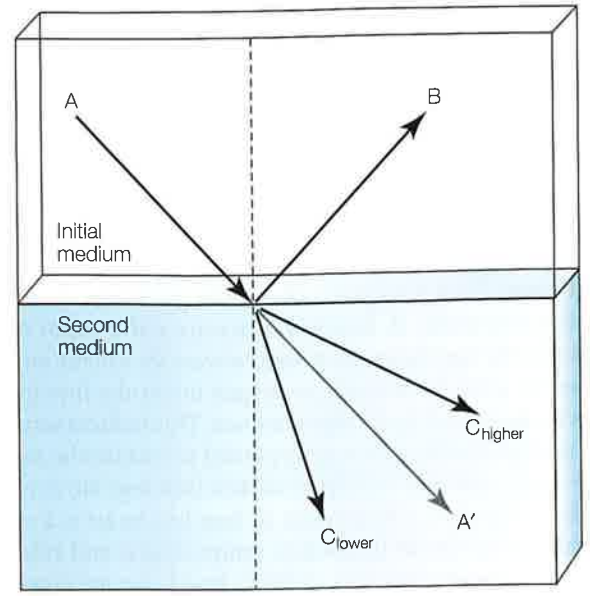


FIGURE 2.14 Reflection and refraction of sound at a boundary between two media In this example, sound initially traveling in the white medium along line A strikes the surface of the blue medium at an angle. If the acoustic impedances of the two media differ, some of the incident sound energy will likely be reflected from the surface and back into the white medium along line B. Note that the angles of the incident and reflected sound waves are the same relative to the boundary surface. If the acoustic impedances of the two media are not too different, some incident sound energy may also be transmitted through the boundary and into the blue medium. If the speed of sound (C) in the blue medium is higher than that in the white medium, the transmitted sound will be refracted (bent) away from the dashed line perpendicular to the surface as shown in line C_{higher}. If the blue medium has a slower sound speed, the transmitted sound's trajectory will be refracted toward the dashed perpendicular line as shown in line C_{lower}.

the angle of the incident waves. For example, if the incident sound waves were traveling from left to right at an angle of 30° relative to the surface of the boundary, then the reflected waves would also travel from left to right at an angle of 30° relative to the surface. Depending on the two media and the incident angle of the sound waves before reflection, the reflected sound waves may experience a phase shift: what were peaks in the incident sound wave can become valleys and vice versa in the reflected wave.

Reflections can have a major effect on sound propagation within a medium. For example, if two animals that are both in air are communicating by sound close to the ground, some of the sound waves arriving at the receiver will travel on a straight-line trajectory from the sender, but others will arrive at the receiver after being reflected off of the ground. If these are out of phase with the directly transmitted waves, the two can cancel and the receiver will hear nothing. Reflections within a small volume of medium such as inside a solid or small body of water can also produce very complicated interference patterns and thus modify the efficacy of sound communication significantly.

When the acoustic impedances of the two media are more similar than those of air and water, then some sound energy will traverse the boundary and continue propagating in the second medium. The direction of travel of the sound waves will likely be shifted: if the speed of sound is slower in the second medium, the travel direction of sound waves in the second medium will be bent closer to a line perpendicular to the surface than was the incident wave direction; if the speed of sound in the second medium is higher than the first, then the waves in the second medium will be bent upward so that their direction is more parallel to the surface than was the incident sound wave. This bending of the waves after crossing a boundary between media is called **refraction**. It is most likely to affect animal communication when sound is traveling in a single medium and encounters adjacent regions of medium with different temperatures, pressures, or compositions. Both water and air often exist in vertically stacked layers. These layers are usually insufficiently different in acoustic impedance to generate reflections, but are sufficiently different in sound speed to cause refraction. For useful animations demonstrating reflection and refraction, see Web Topic 2.2.

Web Topic 2.5 ***Reflection and refraction***

The fraction of sound energy reflected or refracted at a boundary is a complicated function of incident angle, relative acoustic impedances, and relative sound speeds. Here we present the equations for several different cases, and provide some real physical examples.

DIFFRACTION Consider a solid wall separating two large air-filled spaces. Sound traveling in one of the air-filled spaces will be reflected at the wall and no sound will appear on the other side. Suppose we then open up a circular window in the wall. Now some of the incident sound can pass through the hole and propagate in the second space. One might expect the sound field in the second space to be cylindrical in shape, given the circular shape of the hole. This is true only when the hole is large relative to the wavelengths of the incident sound. As the hole is made smaller relative to the sound wavelengths, the sound waves emerging from the hole will form a cone of sound. The angle of the cone increases as the relative size of the hole decreases, and for a small enough hole, emerging sound waves will radiate into all parts of the second space. The bending of sound waves after passing through or around an obstruction is called **diffraction**. Diffraction is a consequence of the wave nature of sound and explains why we can hear someone speaking around the corner of a building or detect a sound with both ears when the source is located on only one side of our heads. See an animated example at Web Topic 2.2.

SCATTERING A special case of reflection occurs when many objects consisting of one medium are distributed throughout a second one. Examples include trees and bushes sticking into the air space above the ground, and the air-filled swim bladders of fish scattered about in seawater (e.g., over a coral reef). If the acoustic impedances of the two media are sufficiently different, each object will constitute an individual reflector of incident sound waves. If the reflecting objects are situated between a sender and a receiver, this **scattering** of the sound during propagation can be another significant source of signal attenuation. The amount of scattering, and thus the amount of reduction in sound energy reaching the receiver, will depend on the abundance of such objects, their size relative to the wavelengths of the sound, and the location of the receiver relative to the source of sound and the objects. When wavelengths are much larger than the scattering objects, they simply bend around these obstacles, and very little sound energy is scattered. This is called **Rayleigh scattering** (Figure 2.15). As the wavelengths decrease in size, the fraction of incident sound energy that is scattered back toward the source gradually increases. Rayleigh scattering thus prevents higher-frequency components in a sound signal from reaching the receiver. Once wavelengths get down to about six times the size of the scattering objects, a more complicated behavior, **Mie scattering**, takes over. In this case, part of the incident sound energy arriving at a scattering object is directly reflected backward, whereas another part is diffracted around the object. Interference between the diffracted and reflected components can be positive or negative depending on the circumference of the object relative to the sound wavelengths and the relative location of the receiver. At even smaller wavelengths of sound, diffraction is negligible and all sound energy that strikes the object is reflected and lost to the receiver. See animation at Web Topic 2.2. We shall discuss the consequences of sound scattering in more detail in Chapter 3.

Sound Signal Generation

Sound signals begin with the production of some sort of vibration. There are dozens of ways that animals might generate a vibration, and nearly every mechanism has been used by at least one species. Given this, we might expect sound communication to be widespread among animal taxa. In fact, sound communication is largely restricted to arthropods and vertebrates, and even among these, modalities other than sound often predominate in their signaling repertoires. The major constraint that limits the use of sound for communication is not the generation of a vibration but the efficient coupling of that vibration into the propagating medium. In species that need to communicate over distances smaller than a body length, inefficient sound radiation can often be tolerated, and it is here that we see the widest variety of vibration mechanisms being used. However, animals that use sound to communicate over larger distances either use only those vibration sources that radiate efficiently or they feed the vibrations into secondary structures that are designed specifically for efficient sound radiation. In the following sections, we first examine the many ways in which animals

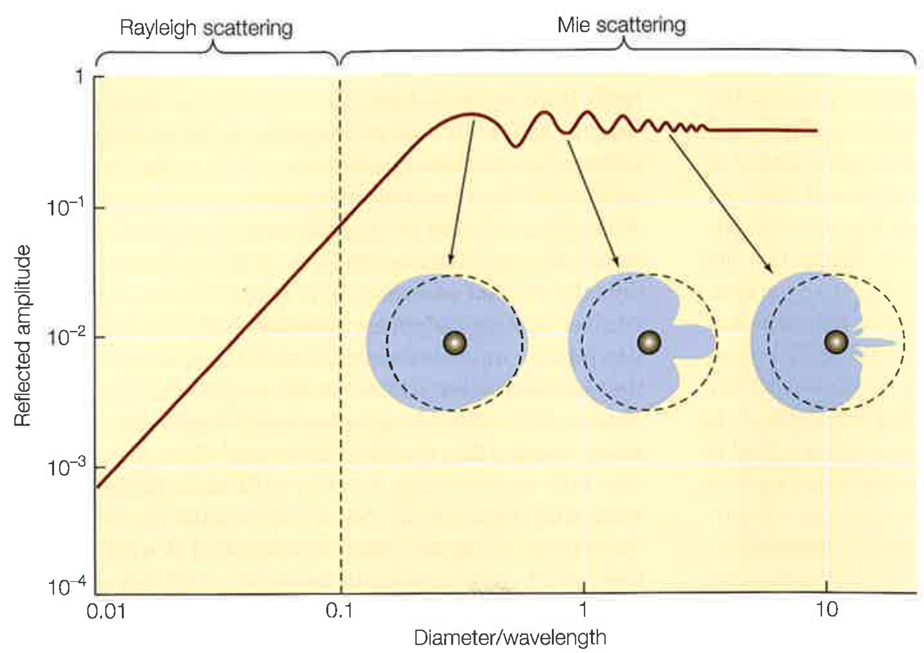


FIGURE 2.15 Sound scattering by a rigid sphere in a fluid medium Vertical axis is the ratio of reflected to incident sound pressure measured at a location about one-half wavelength away from the sphere along the line joining the sphere and the source. Horizontal axis indicates ratio of sphere diameter (here held fixed) to varying wavelengths of incident sound. At low ratios, sound waves sweep around the sphere and there is little reflection. Increasing the ratio (by decreasing the wavelengths) initially creates a smooth increase in reflected sound pressures, an effect called Rayleigh scattering. Above this ratio, reflection processes can become very complex, an effect called Mie scattering. For a sphere, reflection pressures rise and fall as the ratio is increased and eventually asymptote to a fixed value by a ratio of 6:1. While sound is reflected roughly equally in all directions for Rayleigh scattering, Mie scattering is increasingly asymmetric as the ratio is increased. Each blue plot shows the sum of incident and reflected sound pressure at the surface of the sphere for a given sphere/wavelength ratio; the sound source is located to the left of each plot, and the radius of the plot for any given angle around the sphere indicates the overall sound pressure in that direction. The dashed circle shows what that pressure would be if there were no sphere at that location. As the ratio increases, incident and reflected sound pressure add up positively in front of the sphere, whereas they interfere to form a "sound shadow" with lower-than-incident pressure on most of the rear side of the sphere.

generate vibrations and then look at the various devices that have allowed arthropods and vertebrates to improve the efficiency of sound radiation.

Producing vibrations

The production of a vibration usually entails an animal moving one part of itself relative to a nearby volume of medium or moving the nearby medium relative to some part of its body. There are four broad categories of movement that we encounter in animal sound production:

1. movement of a solid body part against another solid;
2. movement of a body part to create surface waves at a boundary between media;
3. movement of a body part to produce waves within a fluid medium; and
4. movement of a fluid medium against a body part.

We discuss each of these mechanisms in more detail below.

MOVING A BODY PART AGAINST ANOTHER SOLID There are several ways in which an animal can generate a vibration by moving a body part against another solid. The simplest method is **percussion**, in which the animal strikes two solid objects together with a rapid motion (**Figure 2.16**). The two most commonly used targets for percussion are nearby substrates and another body part. In arthropods, substrate percussion is known in crabs (Decapoda), stoneflies (Plecoptera), grasshoppers (Orthoptera), katydids (Orthoptera), crickets (Orthoptera), termites (Isoptera), booklice (Psocoptera), true bugs (Hemiptera), lacewings (Neuroptera), alderflies (Megaloptera), snakeflies (Raphidioptera), scorpion flies (Mecoptera), beetles (Coleoptera), caddis flies (Trichoptera), caterpillars (Lepidoptera), ants and wasps (Hymenoptera), and spiders (Araneae) [1, 15, 23, 62, 66, 92, 189, 243, 303, 331, 390]. Body parts used by arthropods to strike the substrate include the head, antennae, mouthparts, two or more legs, wings, the abdomen, or the entire body. Vertebrate examples of substrate percussion include head slaps against the substrate by benthic fish such as the mottled sculpin [399], vocal sac and foot drumming against the substrate in frogs [51, 232, 233, 269], rapid bill drumming of many woodpecker species against anything that will reverberate [90, 94, 196, 351, 406], beating a drumstick against a hollow

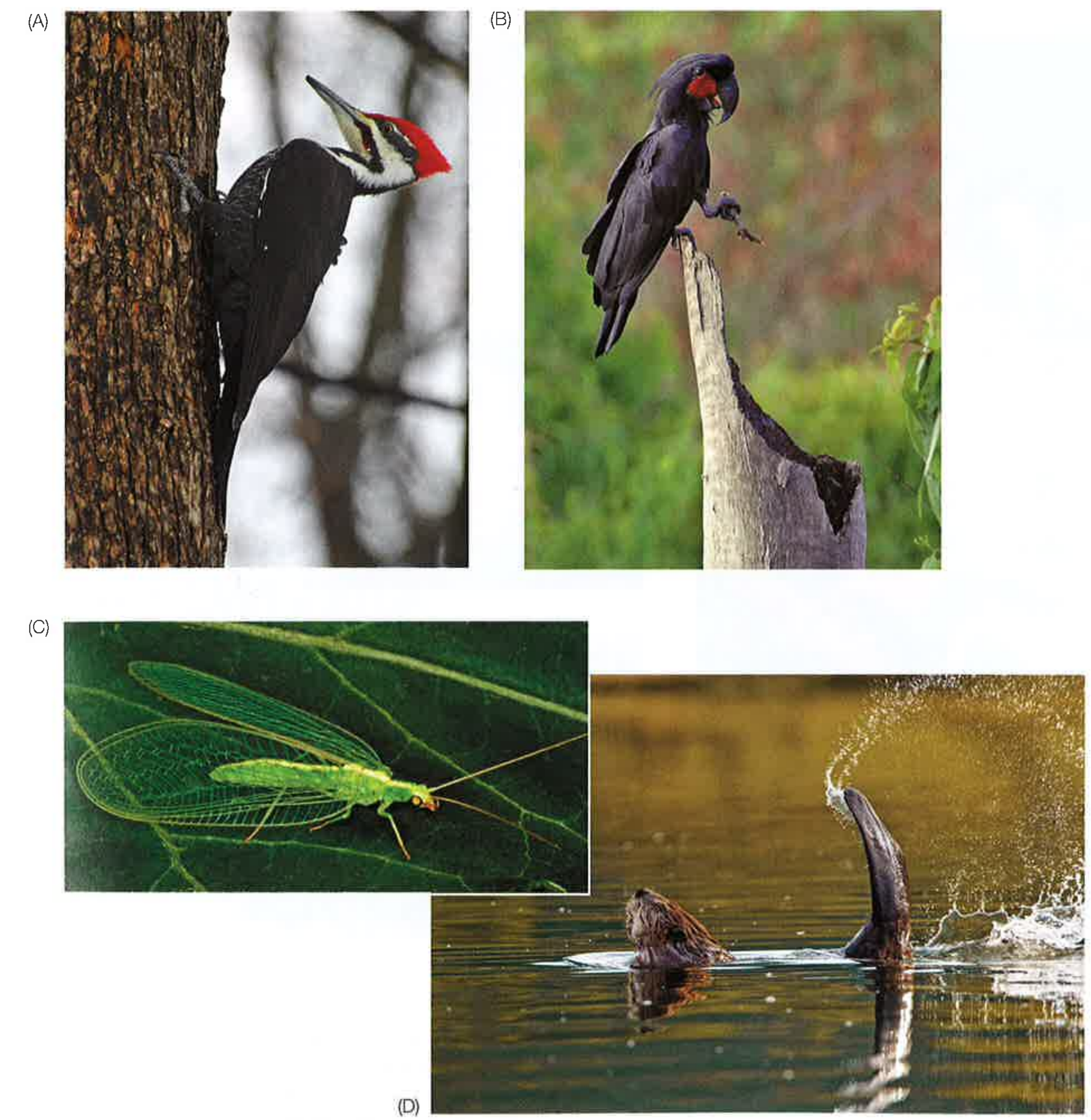


FIGURE 2.16 Vibration generation by drumming on external substrates (A) Like most members of their taxon, Pileated woodpeckers (*Dryocopus pileatus*) drum their beaks against tree trunks. Typical drums consist of 10–30 strikes at rate of 15/sec. (B) Male palm cockatoo (*Probosciger aterrimus*) holding the branch he used to drum against an advertised nesting cavity in a tree. (C) Lacewings (*Chrysoperla agilis*) vibrate their body and strike the vegetation substrate with a curved abdomen. (D) American beavers (*Castor candadensis*) strike the water's surface with their tails as an alarm signal to conspecifics.

log by male palm cockatoos [407], foot stamping by a wide variety of mammals [311], thumping of the head against burrow walls by mole rats [272], and the loud drumming against tree buttresses by chimpanzees [6, 7].

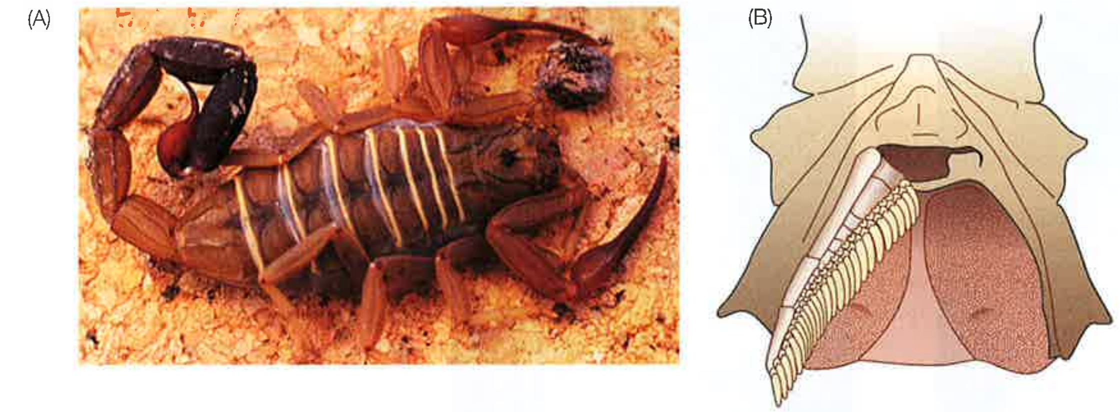
Mouthparts and wings are the most common anatomical tools for body–body percussive actions (**Figure 2.17**). Among vertebrates, many birds pop or snap their bills together as a threat; storks, herons, and the roadrunner perform more elaborate bill clacking as an integral part of their displays [347, 401]. Arthropods such as caterpillars and grasshoppers also click their mandibles to make sounds [92]. Wings can be struck against each other or against some other part of the body to produce sounds. Avian examples include owls [402], nightjars [252], manakins [42-45, 306], and flappet larks [38, 293]. Arthropod examples of wing clapping include grasshoppers [92] and whistling moths; the latter have hardened "castanets" on each wing to increase the intensity of the percussive sound

FIGURE 2.17 Vibration generation by striking body parts together (A) Male ruddy duck (*Oxyura jamaicensis*) drumming bill against water trapped in feathers and air-filled sac on breast. (B) White stork (*Ciconia boyciana*) performing bill clacking display at nest. (C) Male red-capped manakin (*Pipra mentalis*) striking wing against leg to make sound during courtship display. (D) Eastern diamond-backed rattlesnake (*Crotalus adamanteus*) coiled and rattling dry buttons on tail tip as a threat. Rattle is not in focus in the photo because it was vibrating back and forth at about 60 times/sec.

[2]. Rattlesnakes whip the hard multiple segments at the ends of their tails back and forth at a very rapid rate, resulting in a percussive staccato [76, 325, 411]. The displaying male stiff-tailed duck drums its bill against an inflated air sac on its breast [202, 203], and gorillas beat air-filled sacs on their breasts as a threat.

Instead of percussive striking, some species rub two solids together to produce more continuous vibrations. This is called **stridulation**. In the simplest case, simple friction between the two surfaces generates a repetitive cycle of sticking and slipping (see analysis of relevant physics in [119]). Fish such as grunts (Haemulidae) grind their pharyngeal teeth together, producing noisy vibrations with little periodic structure [50]. However, most stridulating species have accentuated this process by providing bumps, hairs, spines, ridges or ribs, on one or both of the rubbing surfaces. The most efficient system is a row of carefully spaced teeth on one surface (called a **file**) and a sharp edge or single tooth on the other (called a **plectrum**). The animal either moves the plectrum across the file or vice versa to generate a steady sequence of nonsinusoidal but relatively periodic vibrations. Thus spectrograms of stridulation signals can range from broadband smears across a wide range of frequencies (grunt tooth grinding) to stable harmonic series (orthopteran wing stridulation and catfish spine stridulation).

Given their hard exoskeletons and multi-jointed bodies, many arthropods (**Figure 2.18**) use stridulation to generate vibrations [99]. Almost every pair of juxtaposed or nearby body parts has been used for this purpose by some arthropod [92]. Insect examples include rubbing one segment of an antenna or leg against another segment of the same appendage, one wing against another wing, wings against legs, head against thorax, thorax against abdomen, legs against thorax, legs against abdomen, proboscis against thorax, etc. Crustaceans are a bit less inventive, but examples include rubbing



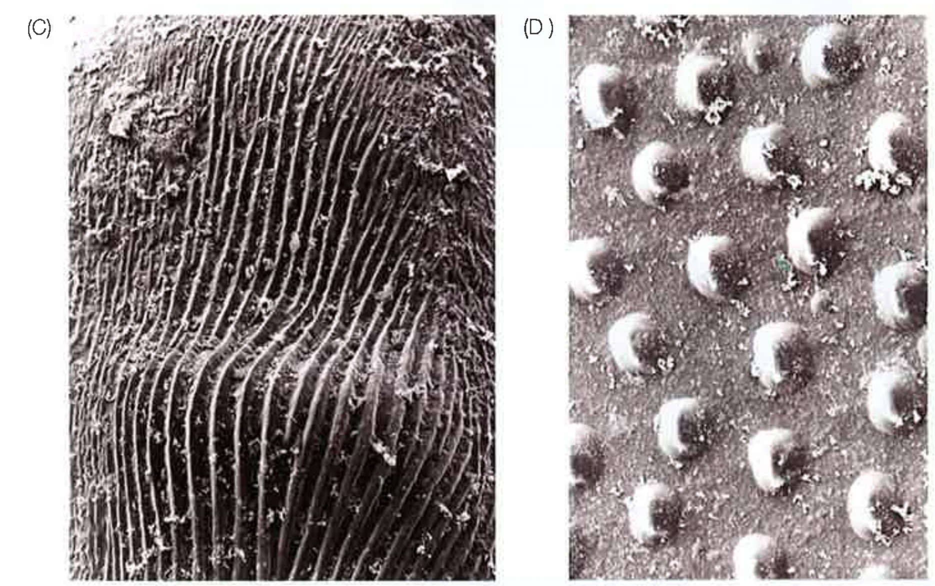


FIGURE 2.18 Example of arthropod stridulatory organ All members of the scorpion genus *Rhopalurus* are known to produce sounds. (A) Dorsal view of an adult *Rhopalurus abudi*. (B) Ventral view of *R. agamemnon* showing one of the paired toothed structures called pectines (singular *pecten*) that have both chemosensory and mechanosensory functions. The pecten on the left is shown in its normal position, while the other has been removed to reveal the dense field of bumps on the ventral side of the body. (C) *Rhopalurus* species have rows of fine ridges on the surface of each pecten tooth where it faces the body, and (D) an extensive field of small bumps on the opposing ventral surface. By moving the pectines appropriately, the pecten tooth ridges are dragged over the ventral surface bumps producing a steady stridulation. (After [236].)

antenna against cephalothorax, uropods against each other, one segment of a claw or leg against another segment of the same appendage, legs against carapace, claw against legs, and legs against legs. Spiders stridulate using pairs of mouthparts, legs against the body, or the cephalothorax against the abdomen. Scorpions use their claws and legs against each other or against the body, body segments against adjacent body segments, and some even use their sting as the plectrum against a file on a more basal segment of the tail. Other arachnids such as amblypygids, solpugids, and harvesters usually stridulate using mouthparts. Not surprisingly, millipedes and centipedes put their stridulation structures on adjacent legs. There is a very large literature on arthropod stridulation. Sample publications include studies on lobsters [290, 291], hermit, ghost, and fiddler crabs [1, 62, 195, 303, 331], orthopteran insects [82, 84, 103, 235, 264, 265, 298, 329], hemipteran insects [69, 242, 296, 322, 336, 418], beetles [77, 129, 193, 205, 237, 283, 284, 287], butterflies, moths, and caterpillars [75, 89, 117, 223, 409], caddis flies [197], ants and wasps [68, 158, 183, 189, 321, 382], spiders [23, 96, 98, 102, 201, 297, 308, 355, 379, 385], and scorpions [236].

Stridulation also occurs in vertebrates. Fish stridulate by grinding their teeth together [16, 50, 109, 222, 267], grating adjacent bones [73, 108, 378], or rubbing bony spines against adjacent bones, scales, or other spines [41, 105, 182, 335, 339]. Spine stridulation is used for sound production by hundreds of species of catfish [107, 217]. Some gekko lizards whip their tails so that adjacent scales rub and produce a rasping sound [130]. The elaborately barbed structure of bird feathers facilitates stridulatory rustling when plumes are rubbed or shaken together [147]. Male sage grouse rub the hard leading edge of the folded wings against rows of stiff breast feathers to produce swishing sounds during their display strut [188]. The small mammals called tenrecs can produce sound vibrations by rustling the spines on their back [55].

A third mechanism for vibration production involves the bending of a highly elastic plate of cuticle by body muscles until the plate buckles and snaps into a different configuration producing impulsive vibrations (**Figure 2.19**). The plate usually snaps back when the pressure on it is released, and this may produce an additional vibration. Such **buckling** is largely restricted to insects in the orders Hemiptera and

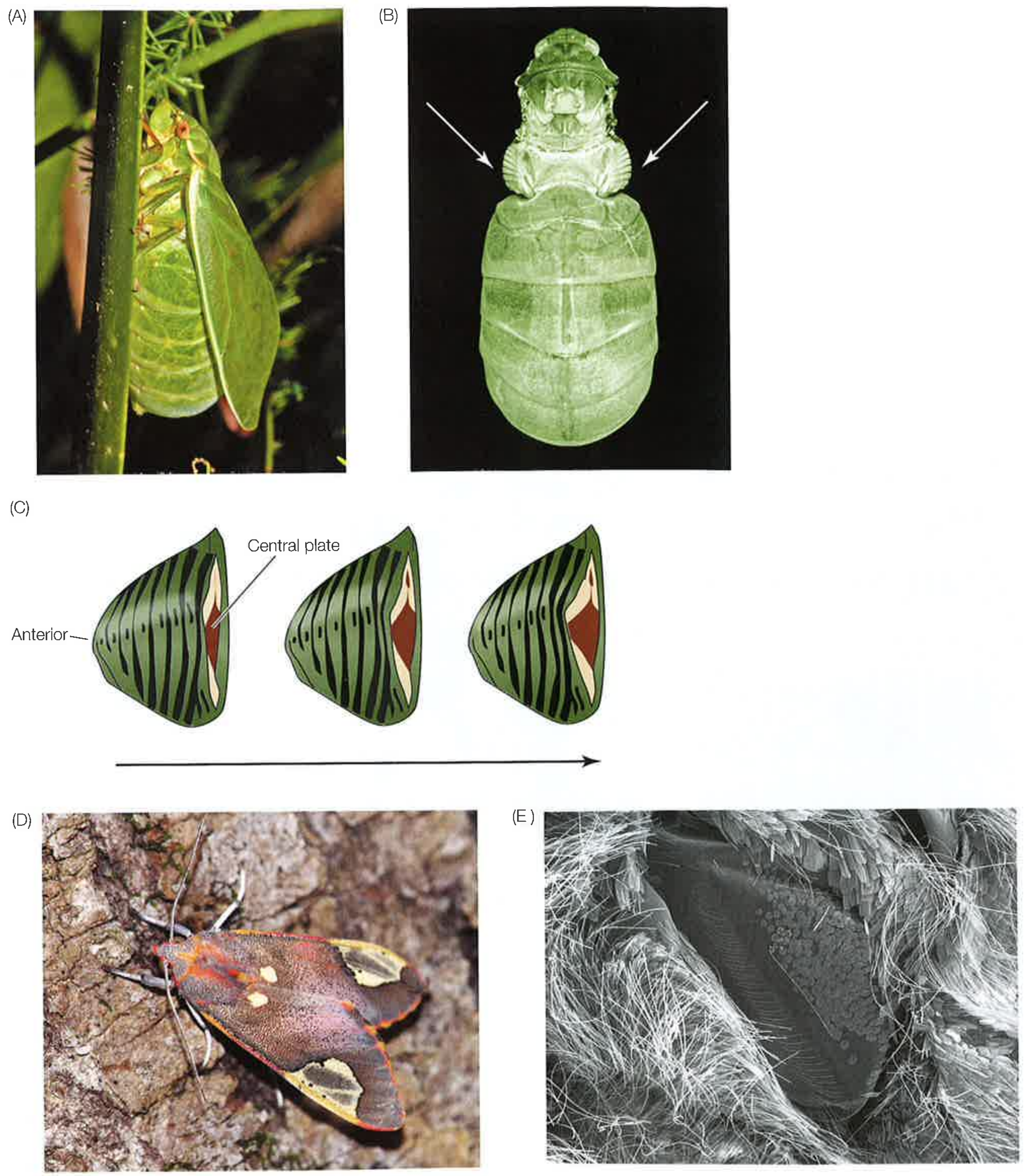


FIGURE 2.19 Insect tymbals (A) Bladder cicada (*Cystosoma saundersii*). (B) Dorsal view of male bladder cicada with wings removed to show ribbed tymbals on each side of body (arrows). (C) Successive stages in buckling of cicada tymbal (left to right). Each tymbal is viewed from the side with the anterior end on the left. Brown area is central plate. As plate is pulled towards anterior end by muscles, it, and then successive ribs, buckle and produce a sequence of sounds. (D) Arctiid moth (*Bertholdia trigona*) and (E) SEM photo of one of the tymbals located on its thorax. Note ridges along side of tymbal similar to ridges in cicada tymbal. Male moths use these tymbals to produce ultrasonic sounds that jam the sonar of attacking bats (see Chapter 14).

Lepidoptera. Auchenorrhynchan Hemiptera such as cicadas (Cicadidae), leafhoppers (Cicadellidae), froghoppers (Cercopidae), treehoppers (Membracidae), and planthoppers (Delphacidae) typically possess a convex cuticular plate called a **tymbal** covering an air space on each side of the abdomen [57, 66, 286]. Except for cicadas, tymbals are present in both sexes. Muscles rooted at the center of the body attach to each tymbal either directly or through a levered rod called an **apodeme**. As the muscles contract, a force is exerted on one portion of the convex tymbal plate until it suddenly pops into a concave state with a sudden generation of vibrations. Some cicadas have elaborated this scheme with a series of parallel ribs at successive distances from the apodeme insertion point. Instead of a single buckling of the entire tymbal, these ribbed tymbals buckle in steps, producing a longer series of initial vibrations [33, 35, 123, 178, 344, 354, 356, 416]. Cicadas typically buckle and relax the tymbals repeatedly at rates up to 100 times/sec. In some cicada species, the two tymbals are buckled repeatedly at this high rate but out-of-phase, producing even higher rates of buckling cycles [124, 231]. Tymbals also occur in Prosorrhynchan Hemiptera such as stink bugs (Pentotomidae), burrowing bugs (Cydnidae), and assassin bugs (Reduviidae) [390].

Lepidopteran tymbals are used to generate ultrasonic vibrations by a variety of nocturnal moths. Tiger moths (Arctiidae) have paired muscle-activated tymbals on the thorax; some owlet moths (Noctuidae), such as the Australian *Amyna natalis*, have tymbals on each forewing that are activated by twisting the wings; many waxmoths (Pyralidae) have tymbals at the base of each wing that are buckled by wing movements; and male *Symmoracma minoralis* (Pyralidae) have a single large tymbal on the ventral side of their abdomen [40, 75, 93, 160, 200, 268, 334, 346, 348, 349]. Many of these species have ribbed tymbals like those of the cicadas to produce longer bursts of vibrations. Neotropical butterflies in the genus *Hamadryas* (Nymphalidae) typically produce audible "cracking" sounds in flight. Although it was initially thought that this was due to percussion between the wings [263], recent work shows that a single wing can produce the sound and that some form of buckling vibration is the most likely source [408].

One group of fish, the croaking gouramis (Osphronemidae), has evolved a unique mechanism of sound production. Two enlarged tendons attached to each pectoral fin are stretched as the fin is moved in an anterior direction. The tendons are adjacent to bony processes of the fin rays that trap the tendons momentarily until further tension releases them with a snap. The effect is rather like the plucking of a guitar string. Each forward fin movement produces two short pulses of sound, and the two fins often move in opposite directions, producing long series of double pulses. Both sexes use these sounds when interacting with conspecifics [212, 213, 216, 221].

A final mechanism for generating vibrations using solids is **tremulation**. This involves rocking the entire body (or large parts of it) and transmitting the resulting vibrations into a solid substrate through the legs or some other appendage. It has been reported in insects in the orders Plecoptera, Orthoptera, Hemiptera, Megaloptera, Rhapidioptera, Neuroptera, Mecoptera, Trichoptera, Diptera, and Hymenoptera [14, 184, 390]. This is also the likely source of vibrations induced in plant stems by chameleons [21]. Such motions may also generate vibrations in the surrounding fluid medium (air or water), a mechanism that will be discussed in a later section.

Web Topic 2.6 ***Sample animal sounds***
Visit this website to hear examples of the kinds of animal vibrations discussed in this and following sections of the chapter. You will also be able to see the waveform and spectrogram of each example.

MOVING A BODY PART TO CREATE SURFACE WAVES As we have seen, the layer of medium closest to a boundary is likely to have somewhat different acoustic properties than a layer of the same medium farther from the boundary. Acoustic impedance is one property that is likely to vary in this manner. Various animal species have taken advantage of these differences to produce sound vibrations that then propagate on the boundary surface [230].

Some aquatic animals living on or near the surface of a body of water communicate by generating surface ripples that radiate away from the initial disturbance (Figure 2.20). Insect examples include Hemipteran water striders (Gerridae), which generate radiated ripples using vertical movements of the legs [403], and waterbugs (Belostomatidae), which pump the entire body up and down under water but

FIGURE 2.20 Calling signal of male water strider Repetitive motion of a male of this North American species (*Rhagadotarsus anomalus*) generates regular ripples that radiate out in concentric circles. The male is the tiny object at the center of the concentric ripples.

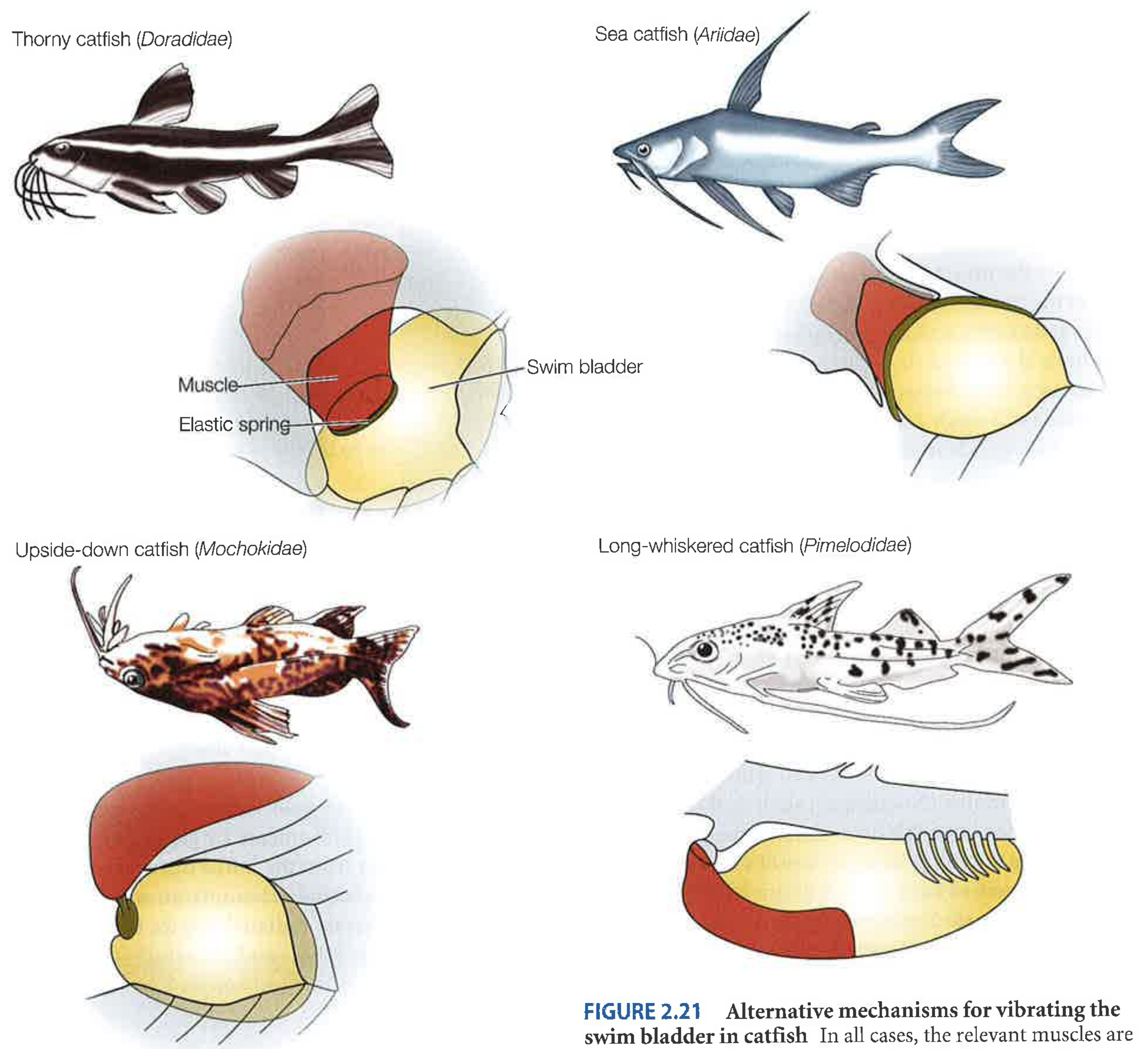


FIGURE 2.21 Alternative mechanisms for vibrating the swim bladder in catfish In all cases, the relevant muscles are rooted on one end to a structure other than the swim bladder. Examples from four catfish families are shown with details of representative swim bladder, relevant muscles, and elastic spring. (After [220].)

near the surface [214]. Male Siamese fighting fish signal to small fry feeding near the water's surface by pulsing water with their fins to generate surface ripples [215]. American alligators slap the water's surface with their heads [391], and a variety of whales and porpoises either perform tail slaps or leap out of the water and fall back to produce a massive splash [241, 395, 400]. It is not clear in either case whether the relevant vibrations are propagated at the surface or instead in the body of water as a whole.

Many of the percussive actions on substrates noted earlier are designed to create vibrations in the substrate instead of, or in addition to, vibrations in the nearby air or water. Where the wavelengths of the resulting vibrations are shorter than the thickness of the substrate, propagation will be limited largely to surface waves. Where wavelengths are larger than the thickness of the substrate (for example, when the substrate is a leaf or stem of a plant), the entire structure will propagate the vibrations. At intermediate wavelengths, both surface and interior waves may be propagated. We discuss these processes in further detail in the next chapter.

MOVING A BODY PART INSIDE A FLUID MEDIUM Many animals move a solid object to create vibrations and waves in their surrounding fluid medium. In some cases, these body parts are simply passing on vibrations generated elsewhere in the body. We take up this type of process in a later section. Here, we focus on movements of body parts that are the initial sources of sound vibrations in fluid media. There are at least four ways that animals initiate these sound vibrations.

The first method, **pulsation**, is to alternately contract and expand the surface of a closed but flexible object, so that medium is forced to move in concert with the surface. American lobsters [179] and mantis shrimp [292] expand and compress their cephalothoracic carapace in this manner. Most bony (teleost) fishes maintain buoyancy using a gas-filled sac called a **swim bladder** in the center of their bodies. Because the gas is more compressible than any fluid-filled tissue, the swim bladder can be compressed, stretched, or struck to produce relatively large vibrations over its surface. These are then radiated into the surrounding medium as sounds [52, 81, 104, 175, 176, 218-220, 288, 289, 377, 378].

In many fish, the relevant **sonic muscles** are attached to the back of the skull, the backbone, or the sides of the body and are used to move, stretch, or compress the swim bladder relative to that base attachment point. There is an amazing diversity of designs (**Figure 2.21**). In the simplest case—naked catfish (Pimelodidae), some rockfish (Sebastidae), and tiger perch (Terapontidae)—the muscles attach directly to the swim bladder. In thorny catfish (Doradidae), ocean catfish (Ariidae), and upside-down catfish (Mochokidae), an intervening bony plate or lever, called an elastic spring, is attached both to the swim bladder and to the muscles. Tension on the muscles pulls the elastic spring and the bladder in one direction, and muscle relaxation allows the elastic spring to snap the bladder back to its original position. In squirrelfish (Holocentridae), the muscles move flattened ribs that are attached to the sides of the swim bladder and thus compress and expand the swim bladder walls indirectly. The muscles in some rockfish (Sebastidae) connect first to the pectoral girdle and then terminate on ribs or vertebrae, allowing for overall contractions and expansions of the cavity containing the swim bladder. Piranhas (Characidae) have a flattened tendon enveloping the lower half of the swim bladder that can be pulled upward by muscles attached to one of the ribs. The reverse system is used in drums and croakers (Sciaenidae), which have a flattened tendon over the top of the swim bladder attached to muscles in the ventral body walls that can pull downward on the swim bladder. Cusk eels (Ophidiidae) and pearl fish (Carapidae) have one pair of muscles that stretches the anterior end of the swim bladder perpendicular to the body axis while a second set pulls the anterior end forward. Because the posterior end of the swim bladder is attached to vertebrae, these muscles stretch the anterior end of the swim bladder in two directions at once. Some mormyrid electric fish make sounds with muscles attached to the posterior end of the swim bladder [81]. Finally, the relevant muscles in toadfish and midshipman fish (Batrachoididae), sea robins (Triglidae), flying gunards (Dactylopteridae), dories (Zeidae), wasp fishes (Apistidae), cod and haddock (Gadidae), and other mormyrid electric fish are unattached to any skeletal component (**Figure 2.22**). This allows for rapid and repetitive excitations of the swim bladder at rates up to 300 contractions/sec in toadfish and midshipman fishes. Interestingly, the sonic muscles in toadfish and midshipman fishes are among the fastest-oscillating muscles known in vertebrate animals [106, 325]. The vibrations generated by these species are usually periodic but nonsinusoidal in waveform. The resulting spectrograms typically show a harmonic series with

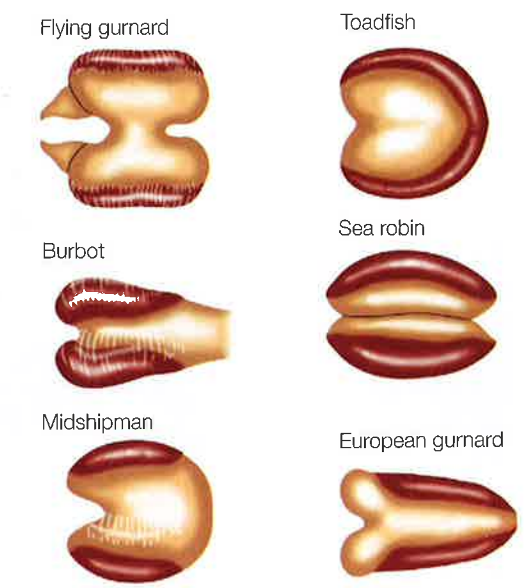


FIGURE 2.22 Examples of fish in which vibratory muscles are attached only to the swim bladder Swim bladders are drawn with anterior end to the left. Differences in geometry and shape reflect functional differences. For example, muscles (dark red) surround the sides and rear of the toadfish swim bladder, whereas they are found only on the sides of the midshipman's organ. This allows sufficient posterior flexibility for the midshipman to inflate its swim bladder before drumming. (After [220].)

a fundamental identical to the contraction rate of the sonic muscles [220].

A second mechanism, **fanning**, involves moving a flat solid object cyclically along a line perpendicular to its surface to produce a parallel movement of the nearby fluid medium. The wings of insects provide a classic example, as they may be vibrated (with or without flight) at rates up to several hundred Hz (**Figure 2.23**). In nearly all cases, little far-field sound is produced, but in the near field, air movements can be quite large and easily detected at distances of several centimeters by nearby receivers. Examples include the courtship dances of male *Drosophila* (Drosophilidae) [28, 32, 375, 376], large fruit flies (Tephritidae) [4, 48, 49, 240, 260] and sand flies (Psychodidae) [85, 86, 285]; the waggle dances of honeybees [256, 257]; and the wing-flicking displays of cave crickets (Phalangopsidae) [88, 177]. Male mosquitoes (Culicidae) are attracted to the near-field wing sounds of flying females, and females signal their interest by matching their wing-beat frequencies to that of the approaching male [146].

A third method, **fluid compression**, remains poorly understood but seems to involve such a rapid modification of local pressure in a fluid medium that it generates far-field sounds. In air, the rapid wing flicks of displaying male manakins produce loud snaps and pops that are easily heard in the far field [44, 45]. One possible mechanism is a sonic boom: this is produced whenever a solid object moves faster than the speed of sound in that medium, and is the cause of

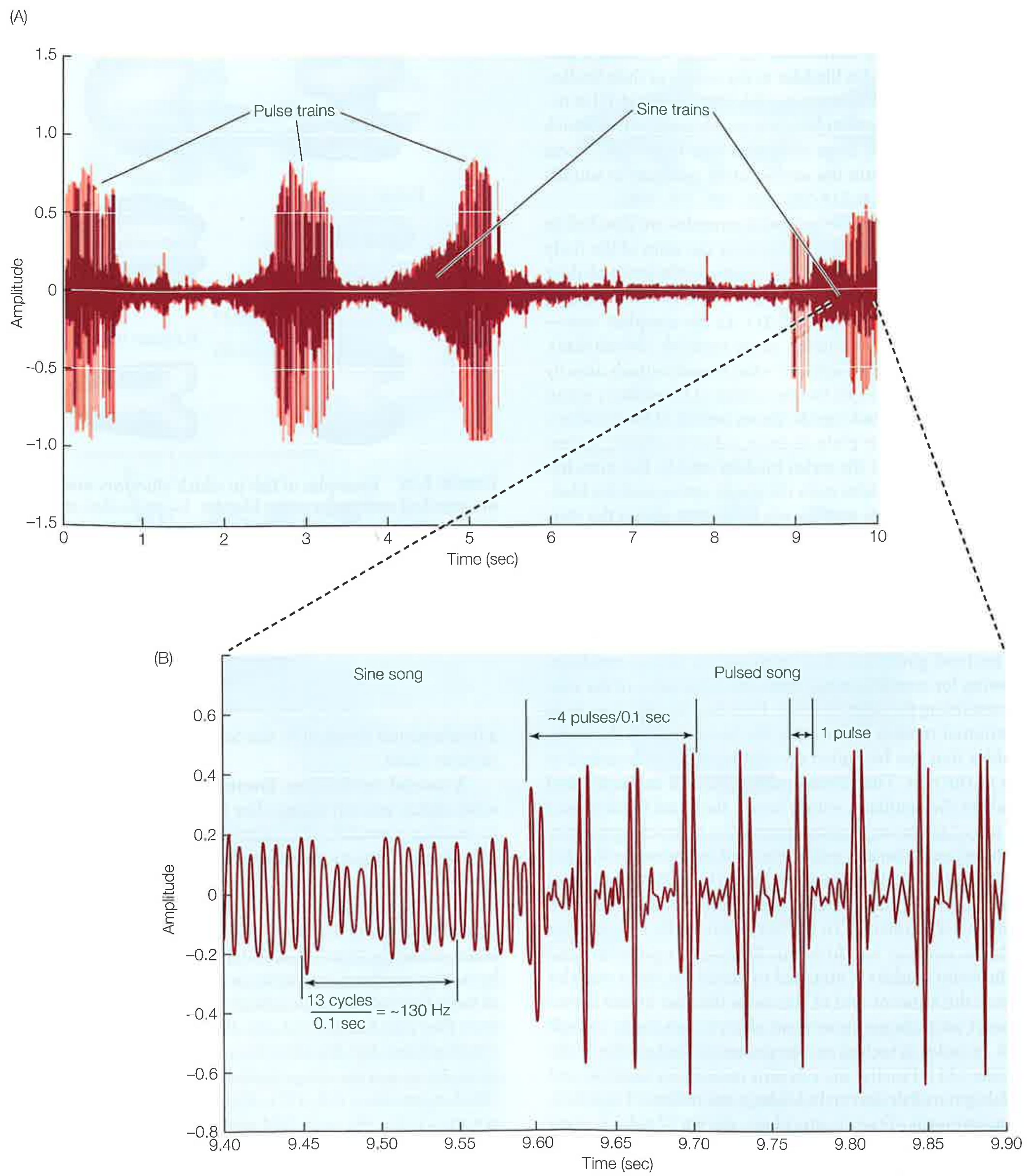
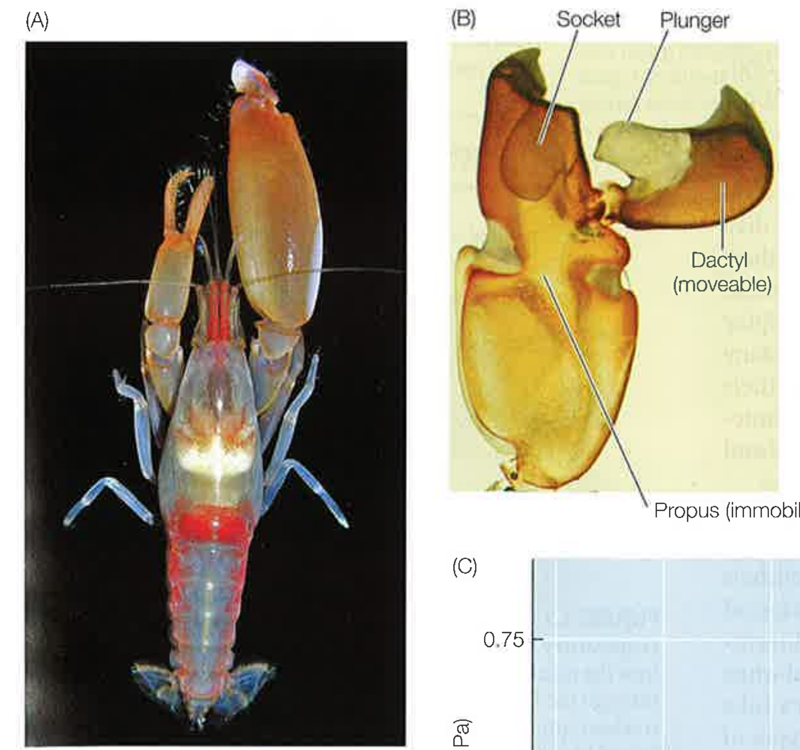


FIGURE 2.23 Near-field waveforms of sine and pulse songs generated by wings of courting male fruit fly (*Drosophila melanogaster*) Sine song is a nearly sinusoidal waveform with a repeat rate of about 130 Hz. Pulse song consists of sudden bursts of waves. The two kinds of songs are interspersed sequentially in normal courtship song. (A) Broad time scale showing 10 seconds of continuous courtship song. (B) Expanded portion of A showing 0.5-second portion. (After [204].)



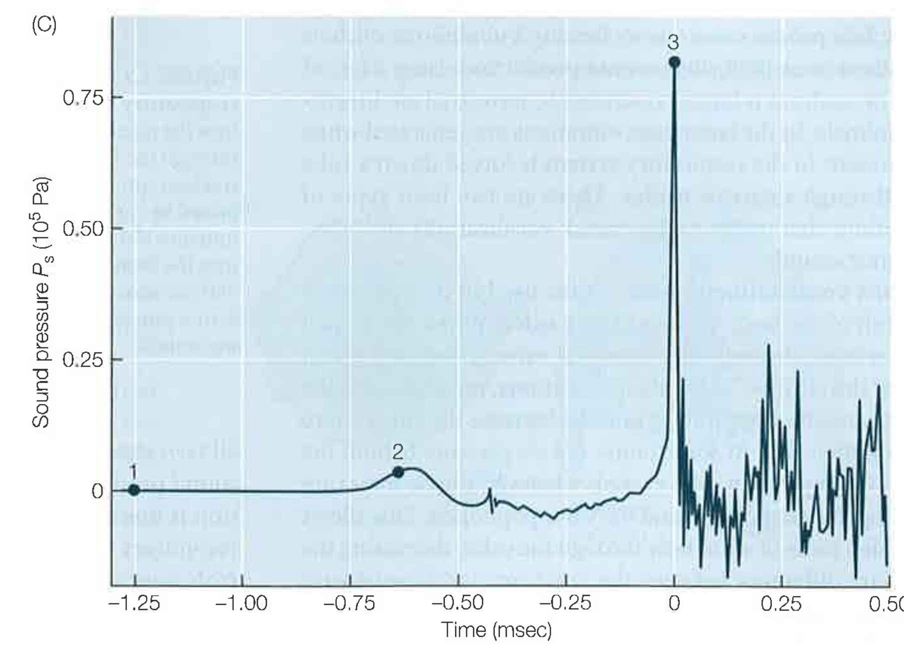


FIGURE 2.24 Snapping by snapping shrimp (*Alpheus* sp.) (A) Dorsal view of snapping shrimp with enlarged right claw. (B) Detailed view of enlarged right claw propus, and the moveable dactyl on which is a specially shaped plunger. Claw is currently open in the "cocked" position. (C) Plot of sound pressure amplitude relative to ambient levels versus time during one complete "snap" by the shrimp. After the claw is cocked (1), the plunger on the dactyl is moved extremely rapidly into a socket on the propus creating a cavitation bubble (2). Shortly thereafter, the bubble collapses (3), producing the large peak of pressure (the snap) and subsequent reverberations from nearby objects. (C after [387].)

the loud snap when one cracks a whip. Whether manakins can move the tips of their wings fast enough to produce a whip-crack remains unknown. Male ruffed grouse produce an accelerating series of low (40 Hz) thumping sounds by repeatedly bringing their partially extended wings toward each other very rapidly [8, 188]. High-speed films have eliminated the possibility of percussive effects in this behavior. The male sage grouse produces two loud "pops" during his strut display that are associated with a sudden expansion and oscillation of the two air sacs on his breast. While the pops might be generated in part by percussion between the two expanding sacs, it is also likely that each sac produces very rapid pressure changes near the sac surfaces [83]. Finally, very rapid movements in water can generate sufficiently extreme pressures around the moving object that nearby layers turn into a gas and form a bubble. The subsequent collapse of the bubble then generates a loud sound. This process, which can occur only in liquids, is called **cavitation**, and is the source of bubbles behind boat propellers. Snapping shrimp (Alpheidae) have an enlarged claw in which one of the two terminal segments can be locked, stressed, and then released very rapidly (Figure 2.24). The loud sound is the result of cavitation and not percussion [101, 387]. The shrimp use snapping as a defense against predators, to stun prey, during intraspecific contests, and to rally neighbors to eject intruders from a group territory [180, 209, 338, 381]. Because snapping shrimp are common throughout most of the world's oceans, they constitute the major source of high-frequency noise in most marine environments [10, 37, 56, 304, 309, 312].

The fourth mechanism, **streaming**, occurs when the signaler moves sufficiently rapidly through a fluid medium that the flow over its appendages generates vibrations. Several groups of birds produce whistling, winnowing, or humming vibrations while in flight. Among shorebirds, the woodcock

(*Scolopax minor*) has special feathers in the tips of its wings that can be spread to produce vibrations while in flight [299], whereas several species of snipe (genera *Gallinago* and *Coenocorypha*) have similar adaptations in their tails [53, 259, 383, 386]. Wing feathers specialized to produce flight sounds also occur in honeyeaters (Meliphagidae) [78], and several nighthawks in the genus *Chordeiles* perform an aerial dive display that ends with a booming sound when wing feathers are angled into the airflow [166, 258]. Hummingbirds also have specialized tail or wing feathers that generate display sounds during particular modes of flight [59, 60, 192]. Many pigeons and doves produce a whistling sound with their wings when startled into sudden flight, and this sound functions as an alarm signal attended to by both conspecifics and heterospecifics [72, 186].

MOVING FLUID MEDIUM OVER BODY PARTS Although some fish produce sounds by forcing bubbles out of their mouth or anus [393, 405], sound production using a forced flow of medium is largely restricted to terrestrial air-breathing animals. In the latter case, vibrations are generated when air present in the respiratory system is forced down a tube and through a narrow orifice. There are two basic types of vibrations that might be generated: vocalizations and aerodynamic sounds.

In a **vocalization system**, a tube used to move air into and out of the body is blocked by a valve. When the animal is breathing through this tube, the valve is kept open and out of the airflow. To produce vibrations, muscles close the valve, and other respiratory muscles increase the air pressure behind the valve. At some point, the air pressure behind the valve, (the upstream side) exceeds whatever muscle forces are holding the valve closed, and the valve pops open. This allows a sudden pulse of air to flow through the valve, decreasing the pressure difference between the upstream and downstream portions of the tube, and generating a suction on the valve lips called a **Bernoulli force**. The continued tension on the valve-closing muscles, the reduced pressure difference across the valve, the Bernoulli suction, and differential latencies in the movements of different masses in this system then cause the two lips of the valve to close and stop the airflow [87, 181, 380]. Upstream pressure starts to build up again, and the cycle repeats. Such a system will usually produce vibrations that are periodic but nonsinusoidal. A spectrogram of the resulting sound will show a harmonic series whose fundamental frequency is equal to the rate at which the valve pops open and closed. This rate will depend on the size, mass, and elastic properties of the valve lips, the muscle force used to close them, any tension applied to them by other muscles, and the pressure exerted by the upstream respiratory system prior to valve opening [119].

All terrestrial vertebrates have similar respiratory plumbing (**Figure 2.25**). Each of the two lungs is connected to a tube called a **bronchus**. The two bronchi join at some point to form a single tube called the **trachea**, which connects to the outside via the mouth and nasal cavities. Even though

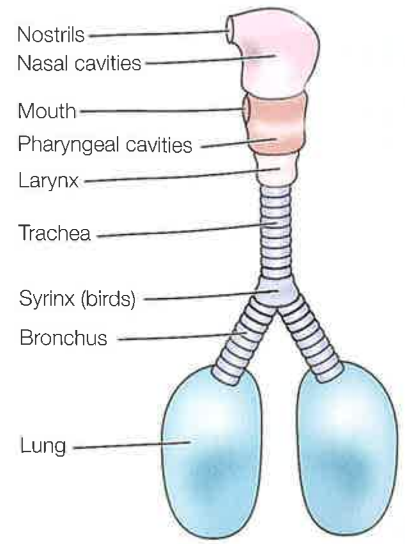


FIGURE 2.25 **The basic elements of a terrestrial vertebrate respiratory system** Air is inspired through the nostrils or mouth into the nasal or pharyngeal cavities, respectively. It then passes through the larynx (originally evolved to keep food out of the trachea) into the trachea, which consists of bone or cartilage rings joined by membranes. The trachea then joins the two bronchi (the junction elaborated into the syrinx in birds), which convey the air into the lungs. During sound emission, the reverse process occurs, with air moving through vibrating valves in the upper bronchi or syrinx junction (birds), or in the larynx (amphibians, reptiles, and mammals).

all terrestrial vertebrates share this basic design, their vocal sound production mechanisms are quite varied. This variation is due in part to different strategies for ventilating the respiratory system: those taxa with more sophisticated controls over ventilation are the ones most likely to produce vocal sounds, and the finer that control, the more complex the vocalizations.

Frogs and toads acquire air by expanding a throat sac while all other openings except the nostrils are closed. Once partially inflated, the sac is contracted, forcing air into the lungs. This is called **buccal pumping**. Air is expelled by the contraction of muscles in the body wall. Lizards and snakes, unlike frogs, have ribs and muscles that allow expansion of the thoracic cavity. Turtles' ribs are attached to their shells. Turtles, crocodiles, and alligators all have special muscles that move their viscera backward and forward to facilitate inhalation. Birds, like lizards and snakes, use muscles in their rib cages to expand and contract their thoracic cavities. Birds' lungs, unlike those of most other vertebrates, are not elastic and do not inflate or deflate with breathing. Instead, inhalation fills a set of air sacs that can subsequently pass the air through the lungs (**Figure 2.26**). This system stores large amounts of air needed for the high metabolic costs of flight. Mammals have augmented their thoracic musculature with a diaphragm that contracts to expand the thoracic cavity and draw air into the lungs. Whereas relaxed birds have relatively

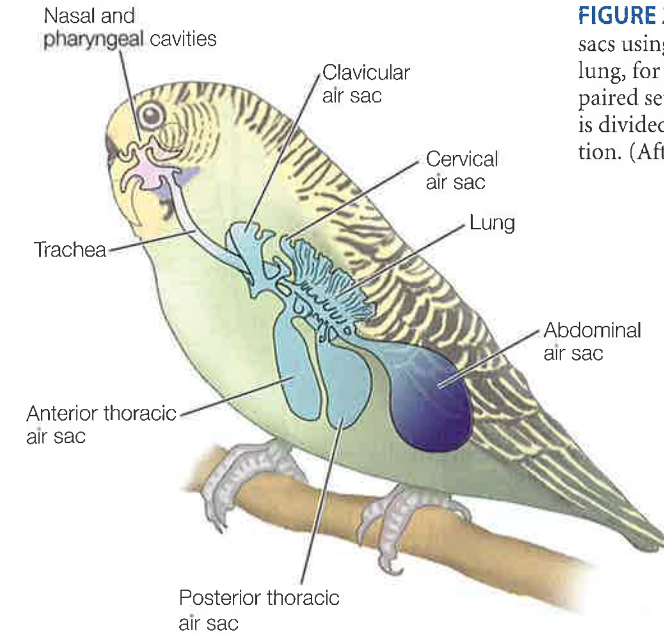


FIGURE 2.26 **Air sac system in birds** Diagram shows typical distribution of sacs using budgerigar (parrot) as example. There is a pair of sacs, one for each lung, for all but the clavicular air sac. Only one lung and one example of each paired set of sacs is shown in the figure. While there is a single clavicular air sac, it is divided into two lobes that encircle the syrinx and may be involved in vocalization. (After [100].)

full air sacs and must work to *exhale*, relaxed mammals have empty lungs and must work to *inhale*. The consequent differences in neuromuscular control of breathing may be partly responsible for the greater abundance of complex vocalizations in birds than in mammals.

All terrestrial vertebrates except birds position the valve for production of vocal vibrations at the top of the trachea [270]. This valve, called the **glottis**, likely first served functions other than vocalization. Possibilities include preventing food from entering the trachea, generation of internal pressures for egg laying or defecation, or prevention of air loss during diving [208]. When used to produce sounds, the glottal lips are called **vocal cords** (**Figure 2.27**). The glottis, along with its associated cartilages and muscles, is part of the **larynx**. In most vocalizing mammals and reptiles, sound vibrations are produced when the laryngeal muscles move the vocal cords into a laryngeal cavity at the top of the tracheal passageway. Upstream air pressure is then increased by contracting the muscles used for exhalation. At some point, the vocal cords begin to open and close, letting small puffs of air flow through the larynx. Additional muscles are often present that can vary tension on the vocal cords. This tension will help to determine the rate at which the vocal cords oscillate open and closed: increased tension usually leads to more rapid rates of vibration, and a spectrogram of the sound will thus show a higher fundamental frequency and a greater spacing between harmonics. Varying the tension during a call is often used to modulate both the fundamental and the harmonic structure in the resulting sound.

As might be expected given their relatively simple ventilation systems, many modern reptiles do not vocalize. Exceptions include some turtles and tortoises, most gecko lizards, and most crocodilians [130, 266, 319, 326, 328]. In contrast, the more sophisticated ventilation system in mammals has made vocalization extremely common in this group. The roars of lions, rumbles of elephants, lowing of cattle, screams of the tree hyrax, howls of monkeys, and human speech are all examples of vocalization sounds. In a variation on this theme, some bats have a very thin ribbon of tissue just downstream from the free margin of each vocal cord. These membranes, which are thinner than

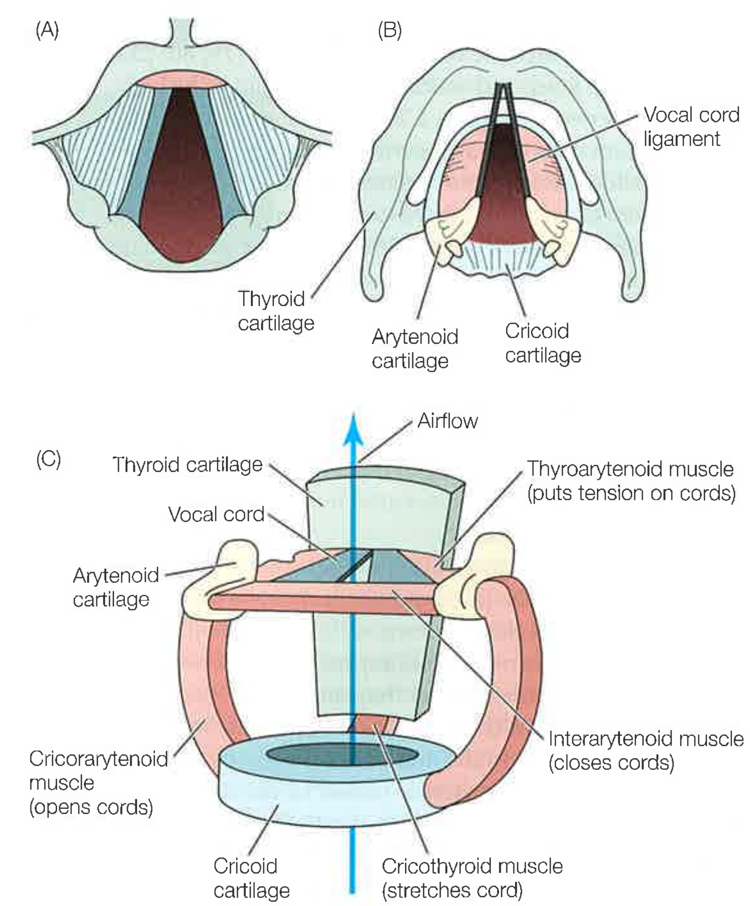


FIGURE 2.27 **Mammalian larynx** View from mouth of top of human larynx (A) and human larynx with soft tissues removed to show cartilages and ligaments (B). (C) Simplified diagram of essential working parts in mammalian larynx. Separate muscles open, close, and put tension on the vocal cords by moving them relative to attached cartilages. Cords are closed just prior to vocalization.

the vocal cord base, can vibrate independently and at much higher frequencies than the thicker part of the cords [164, 361]. Bats with these membranes typically echolocate by emitting short pulses of ultrasonic sounds in the dark and using the echoes to avoid obstacles and to locate food items (see Chapter 14). It has been proposed that the thicker bases of their vocal cords open and close to begin and end each pulse, and that airflow during the open phase causes the thinner membranes to vibrate independently at ultrasonic frequencies. Similar membranes are also known in some primates, cats, pigs, and llamas, but their function in these species is not yet clear [253].

Diving mammals present another special case. Because it is inefficient for these animals to release stored air when they are deep underwater, they need a way to trap and recycle air after it has passed through the vibratory valve during vocalization. Baleen whales (mysticete cetaceans) appear to generate vibrations in the larynx like other mammals, but pass the air into expandable nasal passages or a vocal sac attached to the larynx [9]. Toothed whales and porpoises (odontocete cetaceans), however, move air back and forth between nasal sacs situated between the larynx and the blowhole. A new valve, called **sonic lips**, has evolved in the passage between these sacs to produce the requisite vibrations [79, 80, 238, 239]. Seals, sea lions, and walruses also turn out to be highly vocal underwater (**Figure 2.28**). The loud and complex advertisement calls of male bearded seals (*Erignathus barbatus*), Weddell seals (*Leptonychotes weddellii*), ribbon seals (*Histriophoca fasciata*), and walruses (*Odobenus* spp.) are particularly striking [324, 345, 353]. Several of these species have special sacs attached to the trachea or the pharynx (the throat region between the larynx and the mouth), and the usual bony rings on one entire side of the trachea in the bearded seal have been replaced with a soft and expansible membrane [384]. These specializations contribute to underwater sound production, but the details are not yet understood. Tracheal sacs may provide air for long-duration vocalizations, and pharyngeal sacs, such as those found in frogs, may store air after vocalization for reuse.

Modern frogs and toads also produce sounds with a larynx at the top of their trachea, but like echolocating bats, most species use the glottis to turn airflow on and off. When on, the airflow passes over secondary membranes that are set into vibration and insert higher frequency components into the call (**Figure 2.29**). These membranes, unlike the ones in bats, are not attached to the margins of the glottis, but protrude into the airflow upstream (closer to the lungs) from the glottis [244–246, 337, 340]. In fire-bellied toads (*Bombina* spp.), the vibrating structures are thickened ridges on the sides of the larynx. These animals produce sounds on both inspiration and exhalation, and setting the ridges to vibrate with airflow in either direction requires symmetrical attachments. In contrast, common toads (*Bufo* spp.) have thin membranes, aimed downstream, that are set into vibration when the glottis pops open and airflow begins. In many toads, glottis oscillation is produced by mechanisms similar

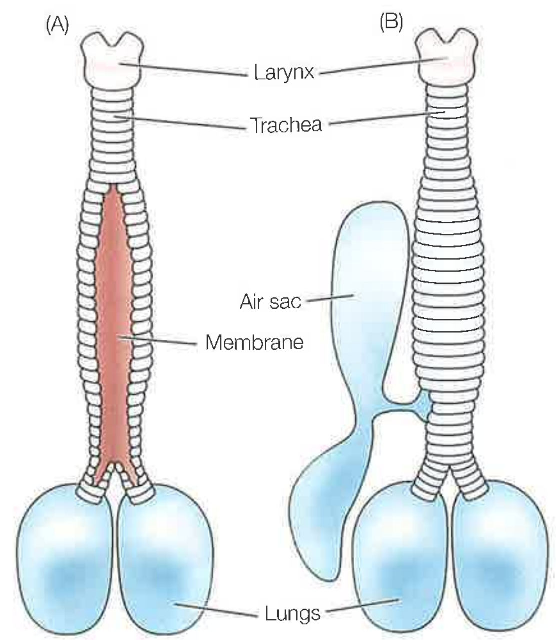


FIGURE 2.28 **Modifications of trachea for vocalization by phocid seals** (A) Incomplete tracheal and bronchial rings and associated membrane in bearded seal (*Erignathus barbatus*). (B) Tracheal air sac in male ribbon seal (*Histriophoca fasciata*). There is only one sac, located on the seal's right side. Females usually lack the sac and in males, it appears to get larger with body size or age. (After [384].)

to that in mammals: upstream pressure, airflow, elasticity, and muscle tension combine to produce repetitive glottal opening and closing at rates of several hundred Hz [244, 245]. When the glottis is open, the vocal membranes then oscillate at fundamental frequencies of 1–2 kHz. In some toads, the vocal membrane oscillations are nearly sinusoidal and display little energy at higher harmonics in spectrograms.

Amphibian genera with more complex laryngeal structures include common frogs (*Rana* spp.), cricket frogs (*Acris* spp.), and tree frogs (*Hyla* spp.), which have perpendicular ridges at the end of the vocal membranes (forming a T in cross section). The glottis is usually opened and closed by muscles in these species. When it opens, air pressure first pushes the flattened edges of the two vocal membranes together to close the airflow, and then forces them open again, setting them to vibrate [337, 340, 394]. The decrease in pressure and Bernoulli forces then pull them back together, and the cycle repeats as long as the glottis is held partially open. The result is a long call consisting of successive pulses of high-frequency vibrations [144]. The duration of the call (up to many seconds) is determined by how long the muscles hold the glottis open; the pulse rate (usually several hundred Hz) is set by the physical structure and properties of the vocal membranes and the airflow; and the vibration of the membranes when open (usually one to several kHz) is also determined by physical properties of the membranes and the

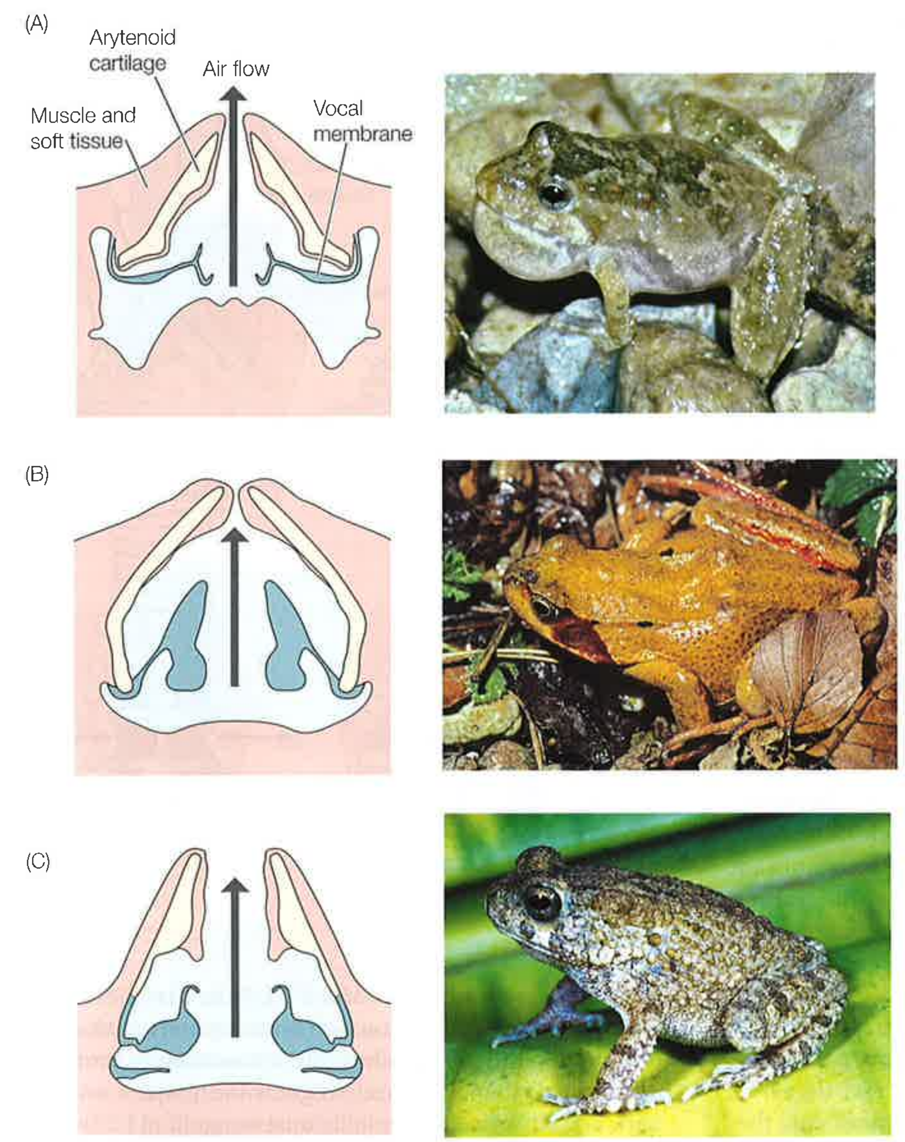


FIGURE 2.29 **Some common frogs and toads and their larynges** Glottal opening is at the top of each diagram, and arrow shows direction of airflow during vocalization. Blue area below the glottis indicates the tracheal and laryngeal air space; white area above the glottis is the pharyngeal cavity. (A) Cricket frog (*Acris crepitans*). Vocal membranes are T-shaped with a slight thickening at midpoint. (B) European common frog (*Rana temporaria*). T-shaped vocal membranes are considerably enlarged on their ends relative to cricket frog. (C) African toad (*Bufo regularis*). These vocal membranes are very enlarged before the filamentous tip and incorporate an ossicle that is heavy enough to depress the fundamental frequency considerably. Note that toads often have two pairs of vocal membranes, one upstream from the other. (After [145, 248, 340].)

airflow. Whether harmonics are present in spectrograms of the vibrations within a pulse depends on how sinusoidally the membranes can vibrate when not touching.

Many frogs and toads attach fibrous masses to the upstream side of the vocal membranes. These masses often lower the fundamental frequency of the membrane vibrations, and they can significantly affect the movement of the membranes and thus the presence or absence of harmonic structure in the sound [247, 248, 404]. In the túngara frog (*Engystomops pustulosus*), unusually large masses are present in cavities adjacent to the vocal membranes. Air flows not only between the edges of the vocal membranes, but also laterally through these cavities. The masses are also attached to the wall of the larynx and to the vocal cords in ways that allow them to vibrate at about half the fundamental frequency of the vocal cords. Male túngara frogs can vary laryngeal tensions and airflows either to prevent oscillation of the large masses, producing the obligatory "whine" component of the call, or to allow the masses to vibrate interactively with the vocal membranes, producing the facultative "chuck" component after the whine [91, 162, 198, 327].

Perhaps because they have such sophisticated neuromuscular control over exhalation, birds exhibit the most diverse and complex vocalization patterns. Unlike frogs, reptiles, and terrestrial mammals, birds do not have a sound-producing valve at the top of the trachea, but instead have one or more vibrating valves near the junction of the trachea and the bronchi. The specialized cartilages and muscles associated with these valves are called the **syrinx.** Normally, the trachea and bronchi of vertebrates consist of bony or cartilaginous rings linked by connective tissue to form tubes. Many birds create a vibration-producing valve in the syrinx by expanding the soft tissues linking the bony rings into large **tympaniform membranes** [5, 26, 207]. In some cases, these membranes are created using incomplete C-shaped rings in which the missing bony tissue is replaced with soft tissues. In other cases, several adjacent rings are converted into flattened and flexible elements that are embedded in the softer tissues. As a third option, the distance between a pair of adjacent rings is increased and filled with a much larger patch of membrane. However created, pulling the syrinx toward the head or tail, rotating particular rings, or expanding the air pressure in the interclavicular air sac that surrounds the syrinx can cause the tympaniform membranes to buckle into the center of the tube where airflow will set them vibrating. Avian syringes have classically been divided into three categories based on where these membranes are located.

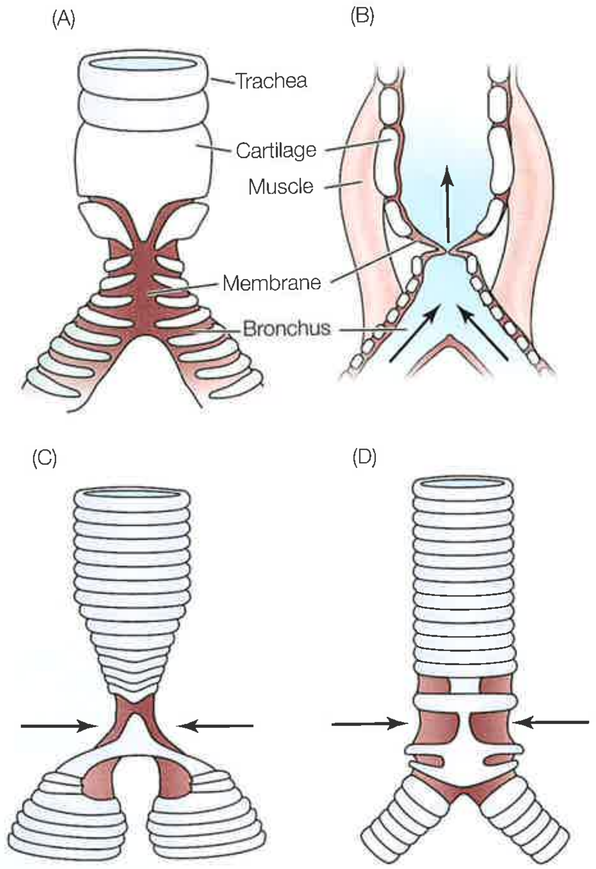


FIGURE 2.30 Example of bird tracheal syringes All figures are ventral views with mouth at top and lungs below. (A) Syrinx of blue-and-gold macaw (*Ara ararauna*). (B) Cross section of macaw syrinx showing lateral tympaniform membranes buckled into airflow (vertical arrows) by external muscles. (C) Syrinx of domestic chicken (*Gallus gallus*). Horizontal arrows indicate which membranes are buckled into tracheal cavity to create vibrating valve. (D) Syrinx of imperial pigeon (*Ducula latrans*). (After [26, 46, 207, 227].)

In birds with **tracheal syringes** the tympaniform membranes are located at the base of the trachea just before the junction with the two bronchi (**Figure 2.30**). Because these membranes form part of the outer wall of the trachea, they are called **lateral tympaniform membranes.** In many of these species, such as parrots and tyrannid flycatchers, but not pigeons and doves, the last 2–8 tracheal rings are fused into a single bony chamber called a **tympanum.** This appears to serve as a firm base against which the tension in adjacent membranes can be adjusted. In chickens and some relatives (Galliformes), doves and pigeons (Columbiformes), parrots (Psittaciformes), and some wading birds (Ciconiiformes), a tympaniform membrane exists on each side of the trachea just above the junction with the bronchi. In furnarioid suboscines (Passeriformes) such as woodcreepers, ovenbirds, gnateaters, antpipits, and antbirds, and in whistling ducks (genus *Dendrocygna*), a single tympaniform membrane is positioned centrally on the ventral side of the trachea. Physiological studies have demonstrated that these tracheal tympaniform membranes are indeed the source of vocal vibrations [46, 47, 95, 132–135, 138, 139, 153, 226, 227]. In pigeons and parrots, the tympaniform membranes are already partially buckled into the tracheal cavity during normal respiration. To create sounds, muscles move the syrinx toward the head, buckling the membranes further until they form a thin slit. Airflow through this slit generates the vocal vibrations, and adjacent muscles vary tension on the membranes to alter fundamental frequencies.

Birds with **bronchial syringes** have 1–2 tympaniform membranes on each bronchus below the junction of the trachea and bronchi (**Figure 2.31**). Examples include oilbirds, pauraques, and frogmouths (Caprimulgiformes), cuckoos, coucals, and guiras (Cuculiformes), penguins (Sphenisciformes), and some owls (Strigiformes). Oilbirds vocalize by relaxing the tension between the trachea and the syrinx, thus causing the lateral (external) tympaniform membranes in each bronchus to buckle into the bronchial cavity until each is very close to the corresponding medial (internal) tympaniform membrane. Airflow then generates vibrations in the tympaniform membranes [363, 371]. Note that these birds have a vibration generator on each bronchus and can theoretically produce two independent (i.e., not necessarily harmonically related) sounds at once. Penguins use unique combinations of the two sounds for individual recognition [12].

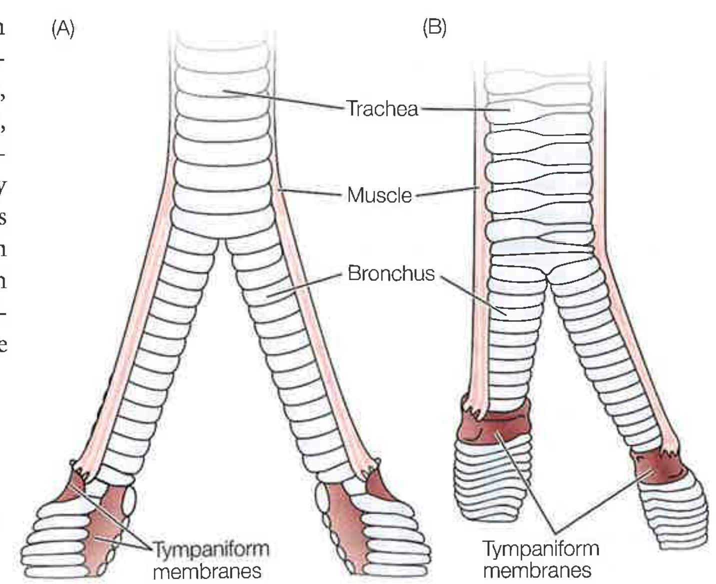


FIGURE 2.31 Example of bird bronchial syringes (A) Syrinx of ground cuckoo (*Carpococcyx renauldi*). (B) Syrinx of oilbird (*Steatornis caripensis*). Note that there are tympaniform membranes on both sides of each bronchus in both species. (A after [26]; B after [207].)

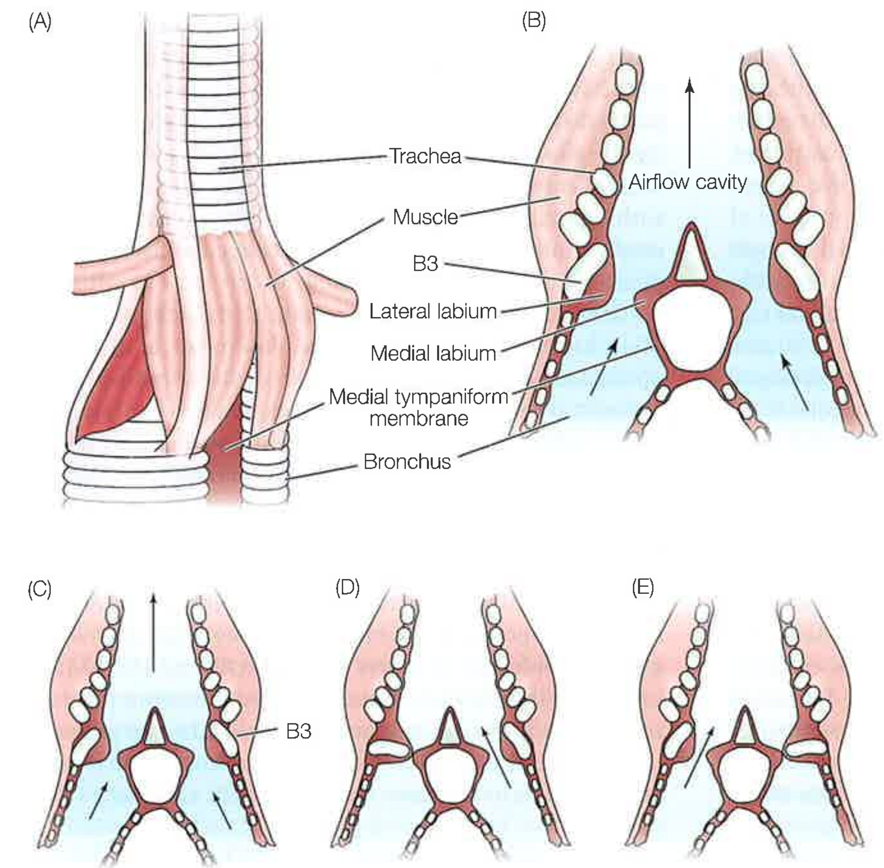


FIGURE 2.32 Example of bird tracheobronchial syrinx External view with relevant muscles attached (A) and cross section (B) of mockingbird syrinx when not vocalizing. Arrows show direction of airflow when exhaling and vocalizing. Medial and lateral labia are moved into airflow during vocalization by rotating third bronchial cartilage (B3). (C) Diagrammatic cross section of songbird syrinx when breathing, showing quiescent position of labia and B3 cartilages. (D) Configuration of songbird syrinx when producing high-frequency notes. Third bronchial cartilages (B3) are rotated forcing lateral labia into airflow. For high-frequency notes, left side is closed completely and right side pulses open and closed. (E) Configuration of songbird syrinx when producing low-frequency notes: right side is closed and left side pulses open and closed. (After [358].)

The majority of birds have **tracheobronchial syringes** in which the main expanses of elastic tissue are the **medial tympaniform membranes** located on the insides of each bronchus just below the junction of the trachea and the bronchus (**Figure 2.32**). Examples include ratites such as cassowaries (Struthioformes); most ducks and geese (Anseriformes); gulls and shorebirds (Charadriiformes); woodpeckers, barbets, and toucans (Piciformes); trogons, hornbills, and kingfishers (Coraciiformes); and perching birds (Passeriformes, with the exception of the furnarioid suboscines noted earlier). For many years, indirect evidence suggested that the medial tympaniform membranes were buckled into each bronchial cavity and set into vibration by concomitant exhalation [118, 139, 159, 352]. Subsequent work on songbirds (the Oscine Passeriformes) showed that vibrations are generated not by tympaniform membranes but by a pair of soft tissue pads, called the **lateral** (outside) and **medial** (inside) **labia**, located opposite each other in each bronchus [152, 155, 199, 226–228, 370]. A similar mechanism may operate with analogous structures in echolocating swiftlets [362]. In songbirds, each lateral labium is attached to a syringeal ring that can be rotated. Each medial labium is connected directly to the medial tympaniform membranes below it. Rotation of the ring behind a lateral labium and movement of the entire syrinx toward the head forces the two labia into the bronchial cavity. Such a syrinx thus has two independently vibrating valves (one in each bronchus). As with the other two types of syringes, vibrations generated by each valve are typically periodic but nonsinusoidal.

Web Topic 2.7 ***Animations of vocalizing birds***
Dr. Roderick Suthers and his team at Indiana University have pioneered our understanding about how the avian syrinx works. His lab has conveniently produced several animated clips demonstrating key steps in song production by northern cardinals and brown-headed cowbirds.

While all songbirds have labia and appear to use them to create vibrations, other taxa with a similar syrinx (e.g., gulls) appear to lack labia [132, 207]. All taxa with tracheobronchial syringes have medial tympaniform membranes, and it is possible that these contribute to sound production when labia are absent. Some species also show thinned membranes, (often called lateral tympaniform membranes but not to be confused with the lateral membranes in tracheal syringes), in the outer wall of the bronchi where songbirds would have a labium. Other species appear to have intermediate types of syringes in which tracheal lateral membranes extend down past the junction with the bronchi, and medial membranes that extend further toward the head than in songbirds [207]. Male sage grouse (*Centrocercus urophasianus*) have thin membranes on the external top sides of each bronchus and apparently can use these independently to produce two different and unrelated sounds at once [211]. An extreme case occurs in some geese and swans in which nearly the entire top section of each bronchus consists of membranous tissues. Sound production in geese is clearly an effective process, but the exact mechanisms remain to be studied.

Although both bronchial and tracheobronchial syringes allow for concurrent production of vibrations from two independent sources, the songbirds have taken most advantage of this opportunity [149–151, 154, 228, 274, 276, 278, 359, 366, 368–371, 373, 374]. With their sophisticated syringeal musculature, songbirds can move the labia into or out of the airflow at will. They can also use the labia to close off the airflow in a bronchus. This allows songbirds to produce rapid and complex songs by alternating between the two sides of the syrinx for successive syllables. Because the two sides of the syrinx are largely independent (except perhaps in very small songbirds; [277]), the successive syllables in a song can have quite different amplitude and frequency patterns. Many species have adopted a division of labor, producing low-frequency syllables on the left side of the syrinx and high-frequency syllables on the right. Male cardinals (*Cardinalis cardinalis*) combine these tricks by producing frequency-modulated syllables in which the first half is generated by one side of the syrinx, and the second half is added nearly seamlessly by the other side (**Figure 2.33**). In addition to using the two sides of the syrinx to produce successive syllables or successive parts of syllables, species such as brown thrashers (*Toxostoma rufum*) may use the two sides to produce two concurrent notes that are not harmonically related. This, combined with a specialization of the right side of the syrinx for rapid modulations, allows this group to produce some very complicated sounds.

Many songbird males include trills in their songs. These are very rapid and long duration bursts of successive notes. At lower trill rates, the singers can take **mini-breaths** between syllables to maintain sufficient air to continue the trill over long periods; at higher rates, no inhalation is possible and the birds simply pulse the labial valve on one side of the syrinx until they run out of air [171, 172]. As a result, there is often an inverse relationship between trill duration and the trill rate, with larger birds having to switch to pulsatile trills at a lower trill rate than smaller birds [374]. A similar trade-off occurs between the frequency range over which a trill syllable can be swept and the trill rate [18]. Many songbirds thus appear to have pushed vibration production to a point where any further increase in one property (e.g., trill rate) degrades another concurrent property (e.g., trill duration or frequency range of each syllable). These

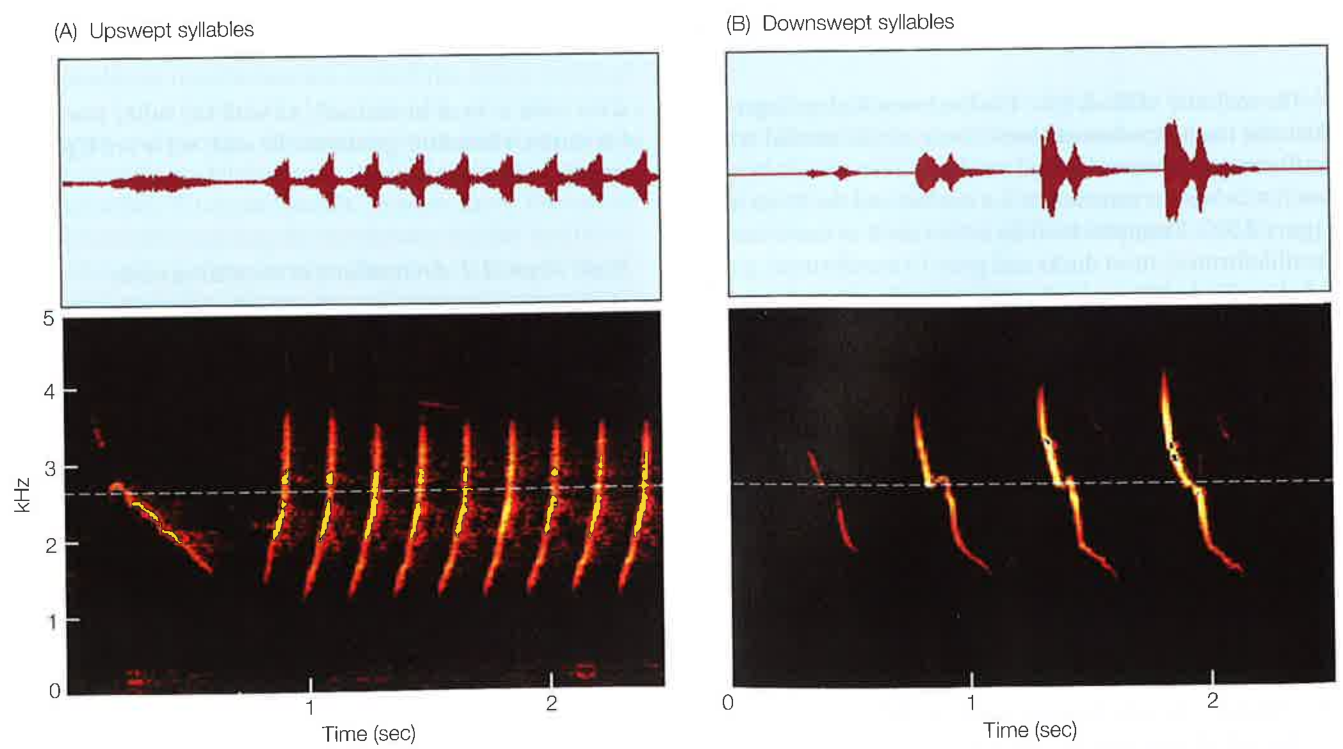


FIGURE 2.33 Two examples of frequency-modulated syllables in cardinal song (*Cardinalis cardinalis*) In each example, the horizontal dashed white line in the spectrogram shows the break point (at about 2.7 kHz) at which one side of the syrinx takes over from the other to produce a nearly continuous single syllable. (A) Male song showing upswept syllables. Very faint break can be seen in spectrogram at 2.7 kHz as the left side of the syrinx takes over from the right side, but no break is visible in the waveform. (B) Female song showing downswept syllables. Note the visible break in both spectrogram and waveform when the right side of syrinx takes over from the left side.

trade-offs will be of relevance later when we discuss the role of song in avian mate choice.

The final mechanism involving fluid flow over solid parts is called **aerodynamic vibration** [119]. In contrast to the vocalizations just discussed, the solid parts remain immobile as fluid passes over them and do not themselves vibrate. Instead, the flow of fluid through an aperture or against a hard obstacle will generate local turbulence in the medium. Turbulence takes the form of eddies or vortices that spiral away from the aperture or obstacle; their size determines the frequencies of any far-field sounds produced [119, 392]. There are three general types of aerodynamic sounds. Streaming of fluid through an aperture in a solid barrier will generate a wide range of vortex sizes; the resulting sounds will have many different frequencies present and be noisy and atonal like a hiss. This is an inefficient process, and the resulting sounds are likely to be useful at close range only. It is how humans generate many of their consonants. A second method involves aiming a steady stream of fluid against a small or sharp obstacle. This is more likely to produce vortices of similar size than is an aperture, and thus produces somewhat tonal sounds that can be heard at a distance. An example is the musical wail generated by wind against the outside corners of a building. Finally, positioning an aperture or obstacle to an airstream near a cavity can result in selective amplification (resonance; see next sections) of a limited number of vortex frequencies, resulting in a relatively pure-tone whistle. It is the most efficient of the three aerodynamic mechanisms and can generate sounds heard at significant distances. Humans whistle using the oral cavity in this manner.

A number of insects force air (or in grasshoppers, foam) out of their respiratory spiracles to produce hissing sounds [92, 271, 357]. In a similar manner, various reptiles force air through a partially closed and immobile glottis or through their mouths or nostrils to produce hisses [130, 410, 412–414]. Similar oral or nasal hisses are produced by some birds and mammals. More whistle-like mechanisms have been described in the death's-head hawkmoth (*Acherontia atropos*), which draws air into and out of its pharynx creating a squeaky sound in each direction [92, 330], and the king cobra (*Ophiophagus hannah*), which "growls" using tracheal air spaces to amplify vortices generated as air passes through its glottis [410]. While it was initially suggested that some bird vocalizations might be whistles [54, 136, 137, 275], this proposition has since gained no experimental support [155, 374].

Web Topic 2.8 ***Linear versus nonlinear systems***
Although animal sound vibrators typically change frequency and amplitude linearly as the forces on them are changed, most will adopt less predictable nonlinear behavior at extreme force values. Some animals such as parrots, zebra finches, and canids use nonlinear vibration behavior to increase their vocal diversity.

Modification and coupling of sound signals

Clearly, there are several ways that arthropod and vertebrate animals can generate vibrations. It is not so easy, however, to convert these initial vibrations into useful sound signals. There are two problems. First, many of the initial vibrations are of such low amplitude that by the time they are coupled to the propagating medium, they are no longer detectable at the required distances. Second, many mechanisms for coupling vibrations from animals into a propagating medium can be hopelessly inefficient. The obvious solution is to amplify the vibrations before coupling, and then use those mechanisms that provide the most efficient coupling. As so often happens in physics and biology, the best amplifiers are not necessarily compatible with the best coupling mechanisms, and sound production is necessarily compromised. Below, we examine each of these options in principle, and conclude this chapter with some of the compromises that animals have adopted in practice.

MODIFICATION OF SOUND SIGNALS: RESONANCE AND FILTERING The vast majority of vibrations generated by animals have periodic but nonsinusoidal waveforms, and thus will consist of many different frequencies. Noisy sounds (e.g., hisses) also contain many different frequency components. When a vibrational pattern is introduced into an object such as a wing, swim bladder, or pharyngeal cavity, some of the component frequencies will have wavelengths that fit within the dimensions of the object, and some will not. If the acoustic impedance of the object is similar to that of the adjacent medium, this fit does not matter, as all frequencies will simply propagate across the boundary and into the medium. If there *is* a significant impedance difference between the object and the medium, then much of the sound energy inside the object will be reflected back at its boundary and the object will store successive energy inputs cumulatively. The result is a series of superimposed waves for each frequency component in the vibration: some will have just entered the object from the vibrational source, some will have already traversed the object and bounced back the other way, and still others will have been reflected multiple times between opposite sides of the object. Given the right ratio between the wavelength of a frequency component and the dimensions of the object, both incoming and reflected waves will be in phase; successive waves will combine their sound pressures additively; and over time, the amplitude of the original vibrations will be amplified. This is known as **resonance** and those frequencies that fit and are amplified are called **normal modes** of the object. At the same time, those components that do not have the appropriate wavelength-to-object ratio, (e.g., do not fit), will produce reflected waves that are out-of-phase with incoming waves, and the resulting destructive interference will reduce the amplitudes of these components. This is known as **filtering**. See the examples of resonant systems at Web Topic 2.2.

Whether a given frequency component is amplified by resonance or reduced by filtering depends on the object's size, shape, speed of sound, and acoustic impedance relative

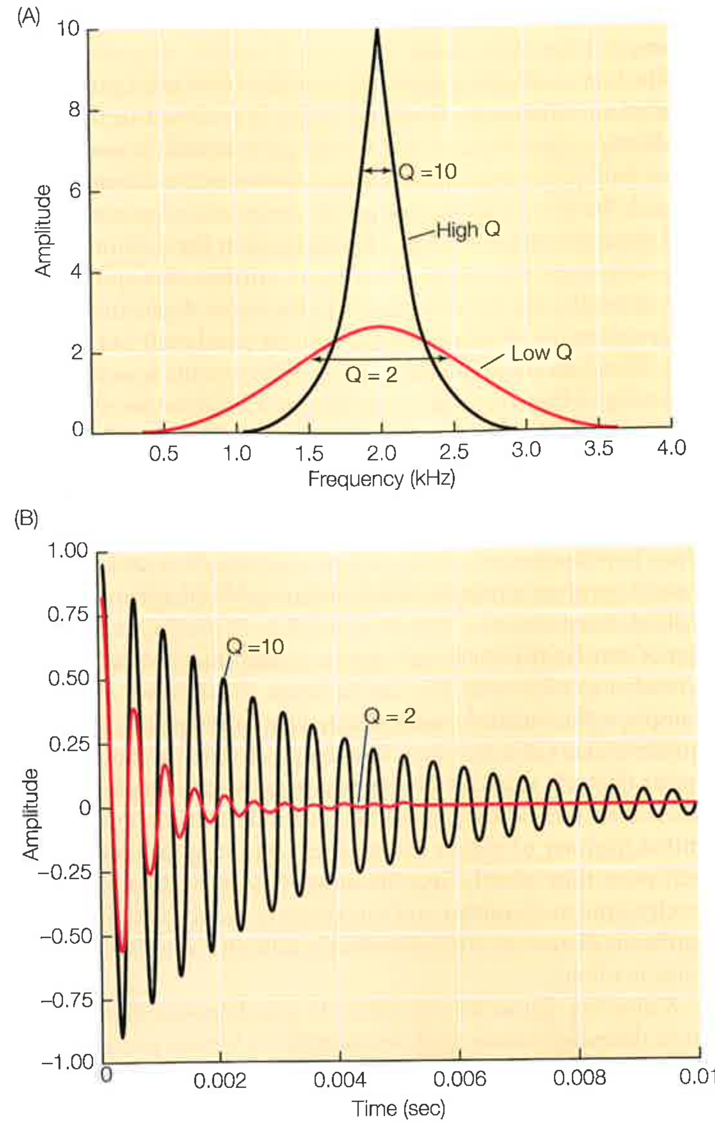


FIGURE 2.34 Frequency and time responses of resonators (A) Two resonators with a resonance at 2000 Hz but differing in their Q (quality) factor. The high-Q resonator is a better amplifier than the low-Q resonator at their shared resonant frequency. Q values can be estimated from such a graph by finding those frequencies on either side of the resonant frequency for which the pressure amplitude is 70.7% (–3 dB) of the peak value. (These will also be the frequencies at which the power is *half* of the peak value). The –3 dB bandwidth is the difference between these two frequencies and is marked with arrows on the graphs. Q is then the ratio of the resonant frequency to this bandwidth. (B) Damping properties of the same two resonators at their resonant frequency. Graphs show the amplitude of successively radiated cycles once the source of sound vibrations ends. The high-Q resonator is poorly damped, and continues to radiate for many cycles after stimulation ceases. The highly damped low-Q resonator, on the other hand, quickly loses all prior sound energy and becomes silent. Damping and Q are inversely related.

to the nearby medium. Small objects cannot accommodate large wavelengths; thus any resonant amplification will be limited to higher frequencies. However, if a given fundamental frequency of the introduced vibration fits within an object, most of the higher harmonics in a periodic nonsinusoidal vibration will also fit and can be amplified. The natural modes are then likely to be integer multiples of some fundamental value. If the fundamental frequency of the introduced vibrations is less than the lowest natural mode of the object, the latter will filter out the fundamental, amplify subsets of adjacent harmonics (called **formants**), and filter out intervening subsets. Nonsymmetrical objects may be able to accommodate several unrelated frequencies and thus can have normal modes that are not necessarily harmonics of the same fundamental frequency. The speed of sound in the object is important because this determines the wavelength of each frequency component in the introduced vibrations. Where the object is a solid, (e.g., a cricket wing), the relevant speed of sound is that of the relevant tissues. Many animals use gas-filled cavities either in their bodies or in a substrate for resonance. The relevant value in such **cavity resonators** is the speed of sound of gas in the cavity.

If the acoustic impedance of the object is sufficiently similar to that of the medium, introduced sound energy is quickly lost through the boundary. A sudden short pulse of vibrations will cause only a few cycles of successive wave overlap before the signal has completely moved into the medium. We say that such a system is **highly damped.** Because only a few recent waves will overlap in this object even with sustained stimulation, there is less opportunity to produce significant resonance or filtering, and thus the frequency selectivity of the object will be low (**Figure 2.34**). We say that the object supports a **wide bandwidth** (of frequencies). Objects with wide bandwidths and high damping are said to have a **low Q** (quality of resonance). In contrast, an object with an acoustic impedance very different from the medium will be very slow to transfer sound energy to the medium. Many successive waves will build up inside it, allowing for very strong resonance and filtering. Such an object generally will have a very narrow bandwidth around each normal mode frequency. A prior signal may continue to reflect back and forth inside the object long after the input source has halted. This is called **ringing** and reflects very low damping. An object that loses sound energy slowly and has a narrow bandwidth and low damping is said to have a **high Q**.

While a high-Q resonator can significantly amplify a narrow bandwidth of frequencies if these are present in the introduced vibrations, it will smear and distort any rapid amplitude and frequency modulations of those vibrations. Similarly, a low-Q resonator can track and replicate rapid modulations accurately, but it will result in much lower levels of amplification. There is thus a trade-off between amplification and accurate temporal tracking when using secondary objects to amplify signals. In general, animals communicating over long distances, such as cicadas, are more likely to use high-Q resonators to maximize signal range. The cost is that they will lose any rapid temporal patterns in the signal. At shorter distances, animals need less amplification, and one expects—and finds—sound signals with greater temporal complexity.

COUPLING TO THE MEDIUM: LIMITS ON EFFICIENCY At some point, an animal's vibrations must be radiated into the propagating medium (air, water, a solid substrate, or some boundary between two media). If the medium is a fluid (e.g., air or water) the surface of a vibrating radiator forces a layer of medium away from itself during part of each cycle, and causes medium to flow toward it during the rest of the cycle. If the medium is a solid, the pressure forces of the radiator generate corresponding pressure waves in the solid with little if any movement of medium molecules. The efficiency of this vibrational transfer is critically dependent on the size of the radiating organ, the way in which the organ moves, and the organ's acoustic impedance relative to that of the medium.

For fluid media, a larger radiator is better than a small one, because larger radiating surfaces will move more fluid per cycle. Another way to see this advantage is to consider two spheres differing in diameter by a factor of ten and both pulsating in air or water at the same rate. Suppose each sphere expands and contracts the same small distance per pulsation. The amount of medium moved *per unit area of sphere surface* will be very similar for the two spheres, and thus the initial energy provided per unit area will be similar. However, by the time the sound generated by the small sphere travels a distance from its center equal to the radius of the large sphere, its pressure will have decreased significantly due to spreading loss. It follows that at any further location equidistant from the two spheres, the larger sphere's sound pressures will always be greater. As a result, larger radiators produce more intense sounds for all frequencies.

Efficiency can also be affected by *how* the radiator moves, especially at low frequencies. A **monopole** radiator, like the spheres in the example above, simply expands and contracts equally in all directions. It thus changes its size to couple its vibrations to the medium. A **dipole** radiator, in contrast, is coupled to the medium by moving back and forth along an axis. The simple disk that we discussed at the beginning of this chapter is a good example of a dipole radiator. Finally, a **quadrupole** radiator maintains its location and size but changes its shape. A fish swim bladder that is compressed at one end and balloons out on the other is a good example of a quadrupole radiator. While there are additional radiators used by animals, nearly all of these behave like one or some combination of these three basic types. For example, the open mouth of a vocalizing bird or mammal radiates sound in a manner similar to a monopole placed close to a solid reflecting surface [119].

The coupling of vibrations to a medium becomes increasingly inefficient as the wavelengths of the sounds being radiated grow larger than the diameter of the radiator. This is true regardless of which type of motion is used. However, whenever the radiators are smaller than the wavelength, monopoles are much more efficient than dipoles, which in turn are more efficient than quadrupoles [119, 167]. In part, the increased inefficiency of dipoles and quadrupoles, when compared to monopoles, arises from acoustic **short-circuiting.** Because these radiators create rarefactions and condensations in different locations but at the same time, sufficiently slow oscillations (e.g., low frequencies) allow the condensation enough time to propagate to the rarefaction and cancel it out [255]. Once the radiator is at least one-third the size of the wavelength or larger, short-circuiting is minimal, efficiency becomes dependent only on the absolute size of the radiator (as noted earlier), and the type of motion is largely irrelevant.

Web Topic 2.9 ***Radiation efficiency and sound radiator size***
Monopoles, dipoles, and quadrupoles all show reduced efficiency when the wavelengths being produced are larger than the sound source. Here we explain in more detail why this happens.

These effects essentially limit sounds useful for long-distance communication to those with wavelengths no greater than 1–2 times the sender's body size. For animals smaller than 30 cm, this requires vibration frequencies of 0.5 kHz or more in air, and 2–3 kHz in water. The fastest muscles known in vertebrates are those used to generate repetitive vibrations in toadfish swim bladders; their maximal contraction rate is several hundred Hz [325]. Insect flight muscles just reach the minimal value of 1 kHz for 15 cm animals, but can barely generate the 5 kHz rate required for a 3 cm katydid [388]. Some cicadas achieve vibration rates twice that of their maximal muscle contractions by buckling their two tymbals out-of-phase with separate muscles [124]. Sea robins achieve doubling by alternating contractions of the muscles on each side of their swim bladder [74]. However, the more widespread solution to this problem is a **frequency multiplier:** a device that produces many vibratory cycles for every muscle stroke. Stridulation and vocalization are two vibration-generating mechanisms that act as frequency multipliers: each stroke of a katydid's wings causes many successive teeth in its file to pass over the corresponding plectrum, and each expelled breath by a vertebrate produces many successive vibrations of its glottis, labia, or tympaniform membranes. Without devices for frequency multiplication, most small animals would be unable to send sound signals or be limited to very short-range acoustic communication.

In addition to creating differences in low-frequency efficiency, different radiator motions also produce different distributions of sound pressure in the medium. The spatial pattern of pressure around a sound source is called its **sound field.** For example, a spherical monopole far from any boundaries produces the same pressure at all points equidistant from its center. A dipole, however, suffers negative interference between radiating condensations and rarefactions at points midway between its ends and perpendicular to its vibrational axis. Points closer to one or the other end of the vibrational axis show only minor interference and thus higher pressures. A graph connecting all locations at a given pressure around a dipole will show two large **lobes**, one radiating from each end of the vibrational axis. These lobes become narrower at higher frequencies. A quadrupole typically shows a sound field graph with four lobes (see Web Topic 2.2 for animated examples). Note that proximity between a radiator and a reflecting surface can change the sound-field shape. A monopole near to a reflecting surface will generate lobes similar to those of a dipole in open space; a dipole close to a surface will reduce acoustic short-circuiting and act more like a monopole. The significance of sound fields for communicating animals is that sounds from monopole radiators can be detected at equal distances in all directions, whereas the range of detection of a dipole can be highly dependent on the relative angle of sender and receiver.

The final factor affecting radiation efficiency is the relative acoustic impedance of the radiator and the propagating medium. Ideally, the impedance of the radiator would be identical to that of the medium to ensure complete transfer of the vibrations across the boundary. Aquatic organisms consist largely of water, and sounds are easily radiated into the medium. A hippopotamus lying at the water's surface is an interesting case: when it vocalizes to produce airborne signals, its submerged tissues also vibrate, coupling the same sounds to the surrounding water, where submerged conspecifics can detect them [19, 20]. More commonly, a terrestrial radiator has an acoustic impedance that is quite different from the medium. The acoustic impedance is much higher within a tracheal tube than in the outside air, causing sound vibrations to be reflected back into the trachea when they reach the mouth opening. The solution to this problem is to provide an **impedance matching device** at the boundary to ease the transition.

One impedance-matching device used by many terrestrial vertebrates is an inflated air sac. The thin membrane of the sac and the contained air create a combination that has an acoustic impedance intermediate between ambient air and solid living tissues. If sufficiently inflated, it can also produce a much larger radiating surface than any other part of the animal. Examples include the throat sacs of most frogs and toads, and the esophageal sacs of doves and pigeons.

Another common impedance-matching device is a **horn** like the bell on a trumpet: its narrow end matches the high acoustic impedance of the attached tube, and as the bell flares, it provides a gradual match to the acoustic impedance of open air. Horns can greatly improve the efficiency of radiation. The cost is that, like most acoustic tools, they can only radiate sound efficiently over a limited frequency range that depends on their shape and size. In addition, the resulting sound fields are usually very directional, with one or more lobes [119]. Despite these constraints, many birds and mammals use an opened mouth or beak as a horn, and some species even elaborate the opening to produce a flared bell like a trumpet (**Figure 2.35**).

Horns made of living tissue will not work underwater because sound will pass through the horn walls without any channeling. Toothed whales (Odontocete Cetacea) have evolved an aquatic equivalent, however (**Figure 2.36**). The **melon** on the whale's forehead consists of multiple layers of special oils and fats that form a graded sequence of acoustic impedances. Sounds generated by phonic lips are reflected off of the bony skull and then focused and radiated forward through the melon [11, 61, 131, 190, 210, 260–262, 273, 419].

FIGURE 2.35 Horns on bats for sound emission (A) Flared bell around the mouth of a male hammer-headed bat (*Hypsignathus monstrosus*). These bats produce loud calls to attract females for mating. (B) African leaf-nosed bat (*Hipposideros cyclops*). This bat emits its echolocation calls through its nostrils, which are surrounded by a horseshoe-shaped horn. (C) Neotropical leaf-nosed bat (*Mimon crenulatum*). This bat also emits its echolocation calls through its nostrils, but in contrast with the prior species, hosts a vertically elongated horn that can be moved in concert with pulse emission.

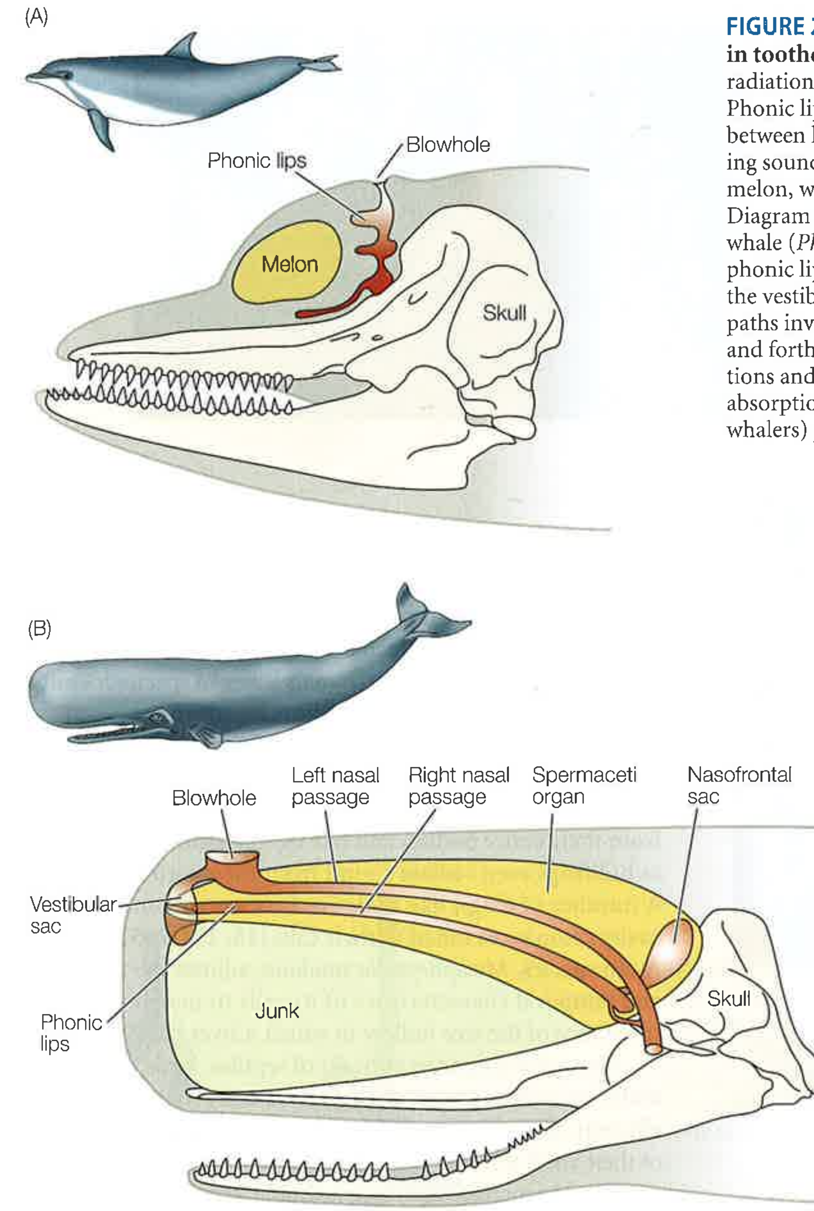


FIGURE 2.36 Resonance and impedance matching devices in toothed (Odontocete) cetaceans (A) Diagram of acoustic radiation structures in the spinner dolphin (*Stenella longirostris*). Phonic lips are a presumed source of vibrations and are interposed between lungs and blowhole. The skull is a partial reflector aiming sounds forward, where they are focused and radiated by the melon, which consists of a layered mixture of oils and fats. (B) Diagram of acoustic radiation structures in adult male sperm whale (*Physeter macrocephalus*). Vibrations are thought to arise in phonic lips located at the junction of the right nasal passages and the vestibular air sac. They may then follow several concurrent paths involving direct radiation into the water, reflections back and forth between the vestibular and nasofrontal air sacs, reflections and modification inside the oil-filled spermaceti organ, and absorption and radiation from the fatty material (called junk by whalers) just below the spermaceti organ.

Balancing amplification and efficiency

Some animals do not require special modification or coupling devices for their vibrations. The beating wings of displaying fruit flies are dipoles, and the wavelengths of the sounds produced are several thousand times as large as the insects themselves. They are thus very inefficient as sources of far-field sounds. However, because female receivers are within a body length of a displaying male, the strong near-field flows are sufficient stimuli at that close distance. Certain arthropods [15, 23, 58, 62, 64, 65, 67, 69–71, 96, 97, 148, 185, 194, 254, 308, 320, 390] and elephants [165, 279–282] transfer vibrations through their appendages into solid substrates. Because the vibrating animal legs (and insect proboscises) are also solid, impedances between the animals and the medium are not sufficiently different to require elaborate modification and coupling devices. However, some filtering and resonance in the appendages themselves probably affect which frequencies are most apparent in the substrates.

Crickets and katydids produce stridulations by rubbing their forewings together. The file and plectrum are both small and thus inefficient sound radiators. However, they transfer the vibrations to adjacent areas of the forewings, (called the *harp* in crickets and the *mirror* in katydids), that act as resonant radiators [31, 34]. Cricket harps have low damping and radiate a highly amplified narrow band of frequencies. Katydid mirrors are more highly damped but produce a wider bandwidth of sound. In both groups, the sound-radiating wings act as dipoles, which makes them susceptible to acoustic short-circuiting at low frequencies. Because low frequencies propagate further, this poses a problem for long-distance signalers. Tree crickets (Oecanthinae) deal with this problem by calling near the edge of a leaf or putting their bodies in a hole or notch in a leaf (**Figure 2.37A,B**); by increasing the distance between concurrent condensations and rarefactions, they can radiate low-frequency sounds at reasonable amplitudes [125, 126]. The short-tailed cricket (*Anurogryllus muticus*) excavates a horn-shaped depression in the ground and positions itself in the cavity so that reflections of its stridulations from the cavity walls minimize short-circuiting and turn the cavity into a directional monopole [30, 125]. Mole crickets also create a horn in the ground surface, but then connect it through a narrow tunnel to a bulbous cavity below (**Figure 2.37C**). The combination of horn and cavity results in a complex

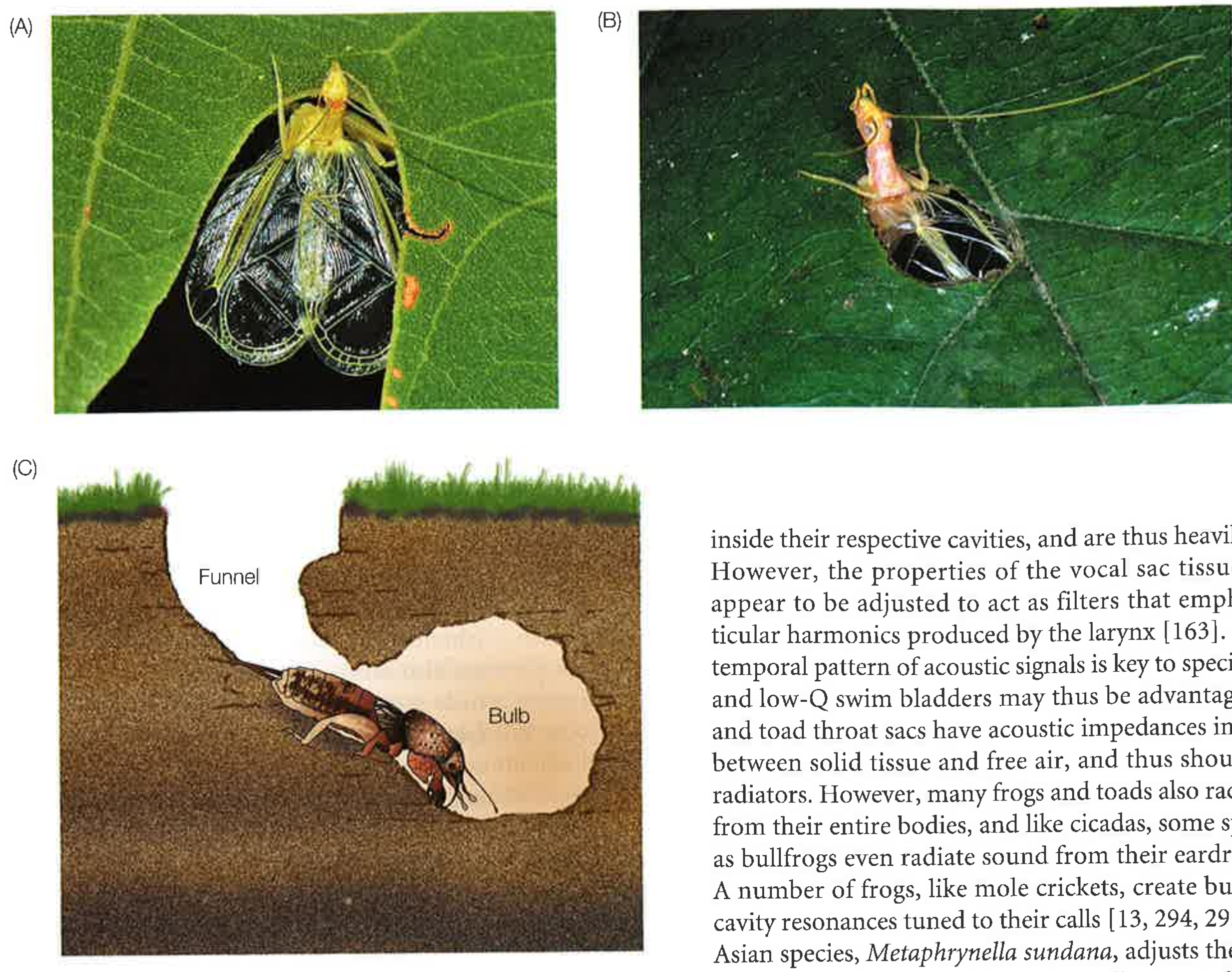
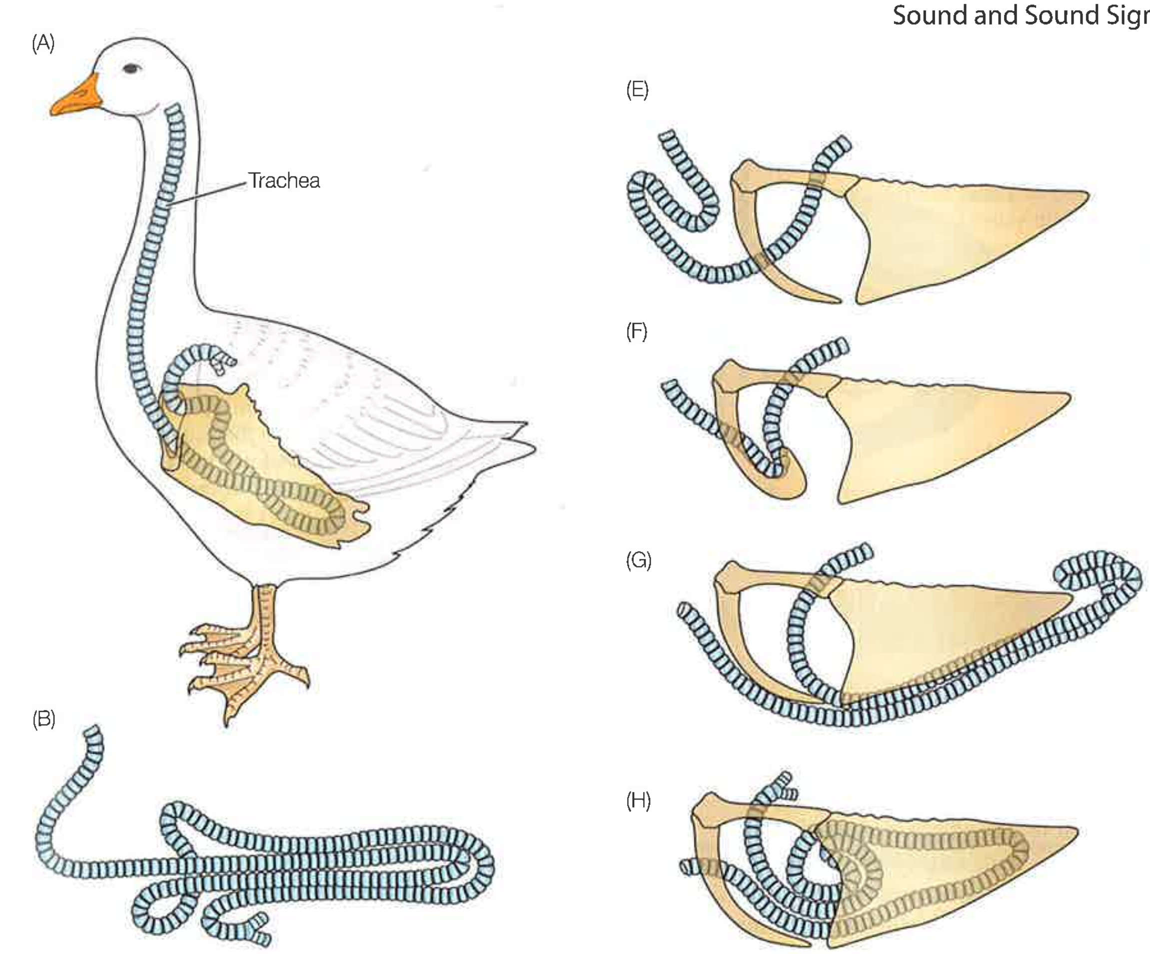


FIGURE 2.37 Insect strategies to maximize radiated sound pressures *Oecanthus fultoni* (A) and *Neoxabea bipunctata* (B), both tree crickets, reduce acoustic short-circuiting by placing their bodies in notches or holes that they have chewed in leaves. By the time a pressure condensation has propagated away from one side of the body and around both sides of the leaf, it is too attenuated to interfere significantly with a rarefaction. (C) Mole cricket (*Scapteriscus acletus*) stridulating at a critical location in its burrow that provides both a resonant amplification of its vibrations in the nearby bulb and enhanced radiation efficiency due to the funnel dug into the opening. (C after [29].)

resonance structure that is carefully tuned to the insect's fundamental stridulation frequency [27, 29, 31, 34].

Most cicadas have a large air-filled sac in the center of their abdomen that acts as a tuned cavity resonator for the vibrations produced by the two nearby tymbals [33–35, 305, 332, 333, 354, 389]. The amplified sound is radiated through two large eardrums located on either side of the body. In contrast, the gas-filled swim bladders of fish [106, 220] and inflated throat sacs of frogs and toads [145, 198, 307, 310] do not appear to function as cavity resonators. The walls of both types of structures do not differ sufficiently in acoustic impedance from the medium to retain successive waves inside their respective cavities, and are thus heavily damped. However, the properties of the vocal sac tissues in frogs appear to be adjusted to act as filters that emphasize particular harmonics produced by the larynx [163]. In fish, the temporal pattern of acoustic signals is key to species identity, and low-Q swim bladders may thus be advantageous. Frog and toad throat sacs have acoustic impedances intermediate between solid tissue and free air, and thus should be good radiators. However, many frogs and toads also radiate sound from their entire bodies, and like cicadas, some species such as bullfrogs even radiate sound from their eardrums [307]. A number of frogs, like mole crickets, create burrows with cavity resonances tuned to their calls [13, 294, 295], and one Asian species, *Metaphrynella sundana*, adjusts the frequency and temporal characteristics of its calls to match the cavity resonance of the tree hollow in which it lives [224, 225].

The opened mouths or beaks of reptiles, birds, and mammals function as monopole radiators and are thus relatively efficient. However, most species exploit resonant properties of their vocal tracts to modify the patterns in the initial vibrations and to increase coupling further. Even when the beak or mouth is used as an impedance-matching horn, the acoustic impedance inside the vocal tract is sufficiently higher than outside that some sound energy is reflected at the opening back into the tract. The reflected sound waves then interfere with subsequent waves moving toward the mouth to produce resonance. Since the vocal tract is roughly tubular, its normal modes depend primarily on the length of the tract and whether the ends are open or closed. If the tube is open on both ends, the lowest normal mode will have a wavelength approximately equal to twice the length of the tube; if it is closed on one end, the first mode's wavelength will be four times the length of the tube. Thus closing one end decreases the frequency of the lowest normal mode by a factor of two. Since most birds and mammals produce vibrations with a fundamental frequency lower than the lowest normal mode of their vocal tract, the upper vocal tract acts as a resonator and filter to emphasize some vibrational frequencies over others. Attaching additional cavities to the vocal tract can both alter and accentuate the normal modes of the vocal



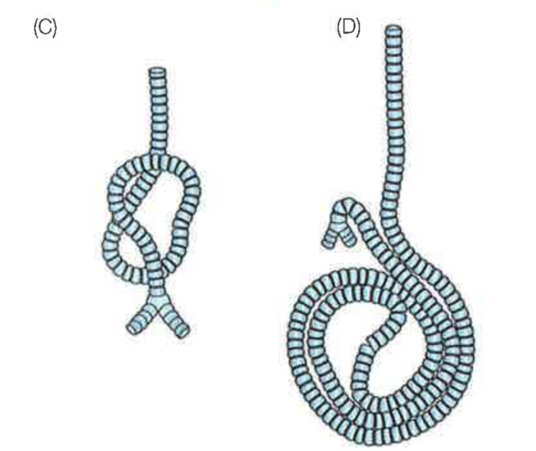


FIGURE 2.38 Elongated tracheae in birds (A) Trumpeter swan (*Cygnus buccinator*) showing coiling of elongated trachea inside hollowed breastbone. (B) Magpie goose (*Anseranas semipalmata*). Elaborate tracheal coils are located just under skin of breast. (C) Spoonbill (*Platalea leucorodia*). The tracheal coils lie above the breastbone (sternum). (D) Manucode bird-of-paradise (*Manucodia keraudrenii*). Highly convoluted trachea is also arrayed just under skin of breast. (E) Capercaillie grouse (*Tetrao urogallus*). Single loop lies just under skin of breast. (F) Crested guinea fowl (*Guttera edouardi*) with single loop stored in special hollow of clavicle bones. (G) Helmeted curassow (*Crax pauxi*). Elongated coil lies along breastbone just under skin. (H) Whooping crane (*Grus americana*). Sternum is hollowed out to accommodate extensive tracheal coils. (B after [113]; A, C–H after [251].)

tract. As a general rule, males are more likely than females to have such additional cavities or to have larger ones; however, there are exceptions, such as painted snipe (*Rostratula* spp.), in which females have the more elaborated vocal tracts [251].

The basic avian vocal tract consists of the beak, pharyngeal cavity, trachea, and syrinx when the vibrating valve(s) are closed. When the vibrating valve(s) are open, the upstream respiratory components, including the bronchi, lungs, and air sacs, are similar in acoustic impedance and must be included in the calculation of the length of the vibrating column of air. Thus a typical bird may have two sets of normal modes: one in which the vibrating valves are open, and another in which they are closed. As long as damping in the vocal tract is low relative to the vibration rate of the valves, both sets of normal modes can contribute to the formants in the radiated sound [119].

Birds have multiples ways to adjust the normal modes of their vocal tracts (Figure 2.38). A permanent mechanism is to elongate the trachea beyond a direct connection between syrinx and mouth. This will lower the frequencies of all normal modes. Elongated tracheae are found in curassows and their allies, grouse, and guinea fowl (Galliformes); swans and magpie geese (Anseriformes); limpkins and cranes (Gruiformes); painted snipe (Charadriiformes); spoonbills and wood ibises (Ciconiiformes); and manucode birds-of paradise (Passeriformes) [26, 63, 110, 113, 128, 140, 251]. Oilbirds have

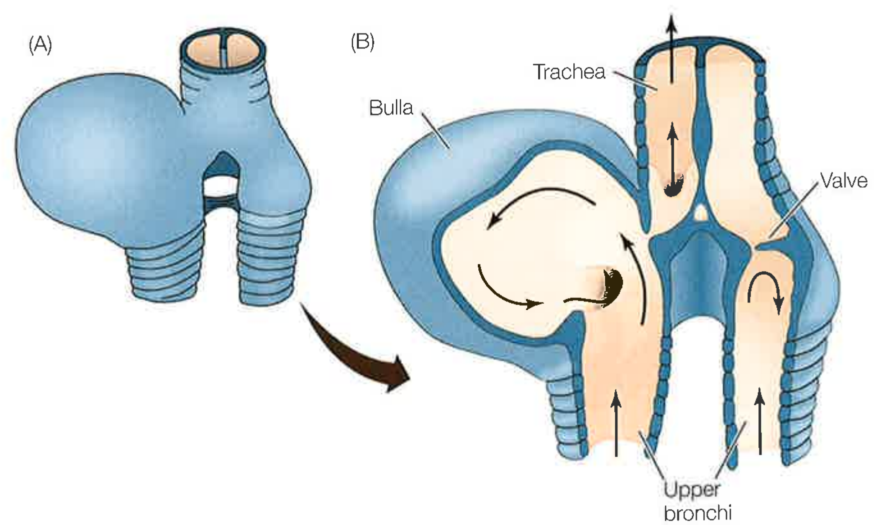


FIGURE 2.39 Syringeal bullae in ducks Males of many species of ducks have a cartilaginous bulla on the left side of their syrinx or just above the syrinx on their trachea. The shape and complexity differs among species, and the bulla is often a useful character for taxonomy. (A) Dorsal view of tracheal bulla, trachea, and upper bronchi of male mallard duck (*Anas platyrhynchos*). (B) Cut-away view of mallard syrinx showing presumed airflow during vocalization. A valve in the right bronchus can block airflow on that side while airflow on the left is routed through the bulla before rejoining the trachea (arrows). (After [207].)

asymmetrical bronchial syringes with the valves on the two bronchi situated at different distances from the junction with the trachea. This results in different normal modes for the two sides of the vocal tract [367]. An additional permanent mechanism is the attachment of a fixed resonant cavity at a location along the vocal tube. This is largely found in male ducks (Anseriformes), which have one or more bony **bullae** (Figure 2.39) attached just above or to the side of the syrinx [26, 202, 207].

A more customizable approach is to open or close the oral end of the vocal tract with the beak or tongue: closing lowers the frequencies of all the normal modes in the tract; opening increases these modes [187]. The greatest effect will be on higher modes and thus on the higher harmonics in the syringeal vibrations [120]. Many birds vary their beak and tongue positions in synchrony with the amplitude and frequency modulations of their syringeal vibrations [25, 156, 157, 191, 300–302, 398]. Cardinals (*Cardinalis cardinalis*) coordinate beak gape with a muscular expansion and contraction of the pharyngeal cavity and upper esophagus to remove all but the fundamental component in their syringeal vibrations before radiating the songs [122, 318]. Because many syllables of these songs are rapidly frequency modulated, the volume of the cavity must be altered just as quickly to track the changing fundamental frequency of the vibrations. See the animation at Web Topic 2.6.

Other birds use air-filled chambers to modify, amplify, and even radiate their vocalizations (Figure 2.40). Doves keep their beaks closed during vocalization; airflow toward the head picks up vibrations in the syrinx, and then passes through the glottis into an inflatable esophageal chamber. The wall of this chamber, enveloping the trachea and puffing up the breast of the bird, acts both as a filter/resonator and as the main radiator of the dove's vocalizations [24, 121]. Many species of grouse (Tetraonidae, Galliformes) inflate esophageal sacs and use them for modifying and radiating vocalization as well as for eversion of colored skin patches on the sides of the head or body [188]. Other birds that use inflatable sacs for vocalization resonance and radiation include emus (Struthioniformes), bustards (Gruiformes), musk ducks (Anseriformes), the kakapo parrot (Psittaciformes), the American bittern (Ciconiiformes), and button quail (Charadriiformes) [83, 207, 250, 251].

In mammals, the acoustic impedance of the respiratory tract upstream from the glottis is sufficiently greater than that downstream that even when the valves are open, the upstream tubes have little effect on resonance and filtering [119]. This excludes the trachea as a possible resonant cavity, and limits most terrestrial mammals to the short space between the glottis and the mouth or nostrils for any resonance, filtering, or coupling devices. Despite these constraints, many mammalian species rely heavily on these processes during sound emission.

The open mouths of many mammals, as well as special nose-leaf structures around the nostrils in some echolocating bats, can easily function as impedance-matching horns [119, 168, 170]. Certain body positions may accentuate this effect and modify normal modes [174]. Pharyngeal and nasal cavities are often used as resonance- and impedance-matching devices [110–112, 114, 313-315, 317]. To make these cavities large enough to accommodate lower frequencies, some mammals depress their larynx away from the mouth, either permanently or when vocalizing, to increase the cavity dimensions. Examples include dogs, roaring cats (lions, tigers, jaguars, and leopards), pigs, goats, and tamarin monkeys [110, 114, 115, 173, 249, 397]. In humans, particularly adult males, the larynx is positioned away from the mouth to facilitate the resonant filtering of vowel sounds [234]. Pharyngeal and nasal cavities in many echolocating bats filter out all but certain harmonics in their echolocation calls [169, 170, 364, 365]. For those species emitting the sounds through the nostrils, nasal sacs may also function as impedance-matching devices [168, 169]. Males of the non-echolocating hammer-headed bat (*Hypsignathus monstrosus*) have exaggerated nasal

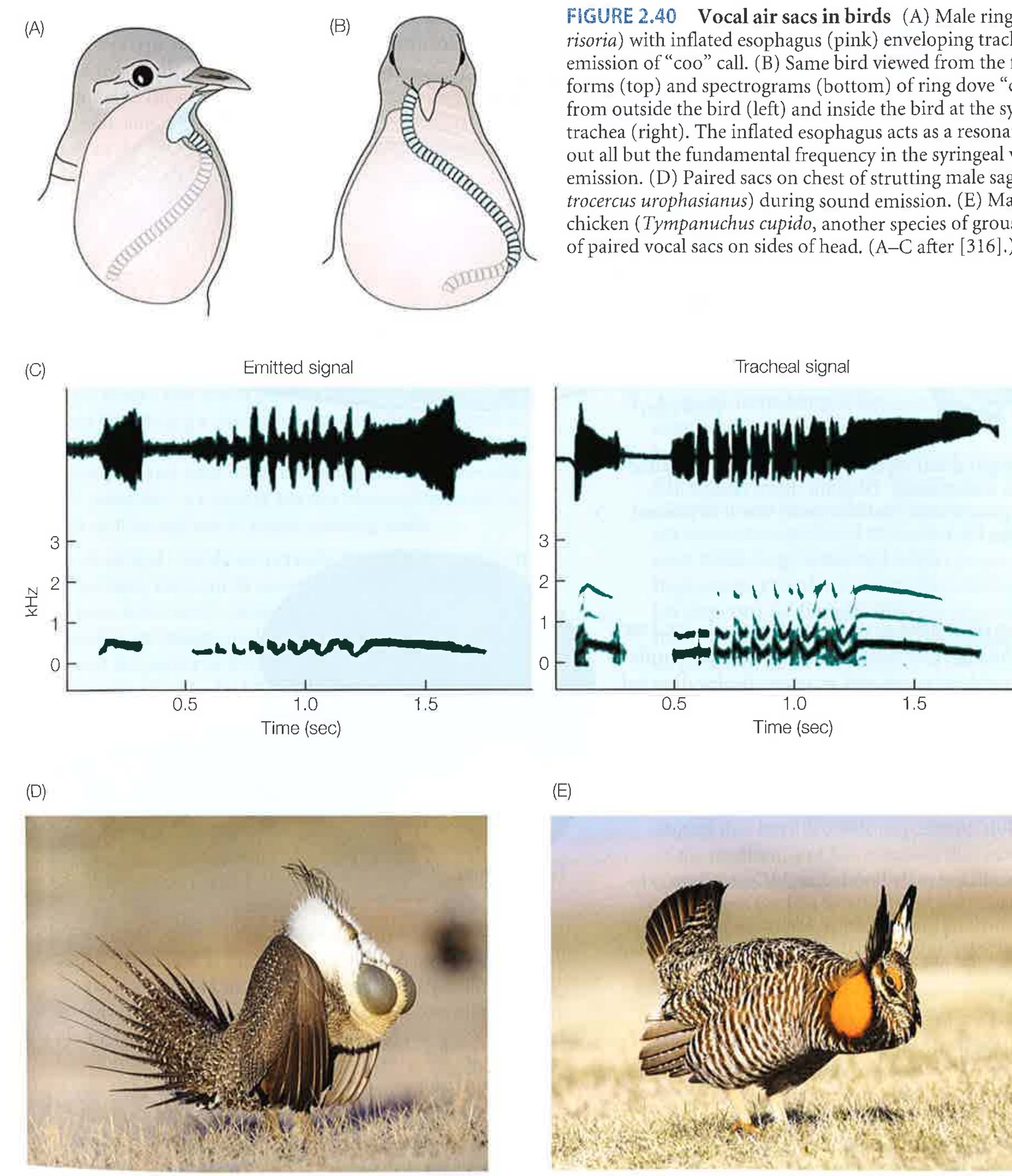


FIGURE 2.40 Vocal air sacs in birds (A) Male ring dove (*Streptopelia risoria*) with inflated esophagus (pink) enveloping trachea (blue) during emission of "coo" call. (B) Same bird viewed from the front. (C) Waveforms (top) and spectrograms (bottom) of ring dove "coo" recorded from outside the bird (left) and inside the bird at the syringeal end of the trachea (right). The inflated esophagus acts as a resonance device to filter out all but the fundamental frequency in the syringeal vibrations before emission. (D) Paired sacs on chest of strutting male sage grouse (*Centrocercus urophasianus*) during sound emission. (E) Male greater prairie chicken (*Tympanuchus cupido*, another species of grouse), showing one of paired vocal sacs on sides of head. (A–C after [316].)

cavities that appear to function as resonators and filters of their sharp honking calls (Figure 2.41). These bats also have an enlarged and cartilaginous larynx that fills nearly two-thirds of their body cavity [342].

Other mammals have air-filled sacs located just downstream from the glottis or in adjacent tissues and cartilages [206, 270, 341]. Reindeer and muskoxen have a single inflatable sac in their throat used to amplify their calls [127, 270]. Other taxa such as bears and epomophorine bats have paired pharyngeal pouches that function in a similar way [396, 417]. Resonant and impedance-matching air sacs are widespread in primates [110, 111, 141, 142, 206, 270, 350]. Males of forest species such as the African De Brazza's monkey (*Cercopithecus neglectus*) and the neotropical howler monkeys (*Alouatta* spp.) have particularly well-developed vocal sacs and produce calls that can be detected at great distances [141, 343]. Perhaps the most spectacular mammalian air sacs occur on the male hooded seal (*Cystophora cristata*), which can inflate a dark

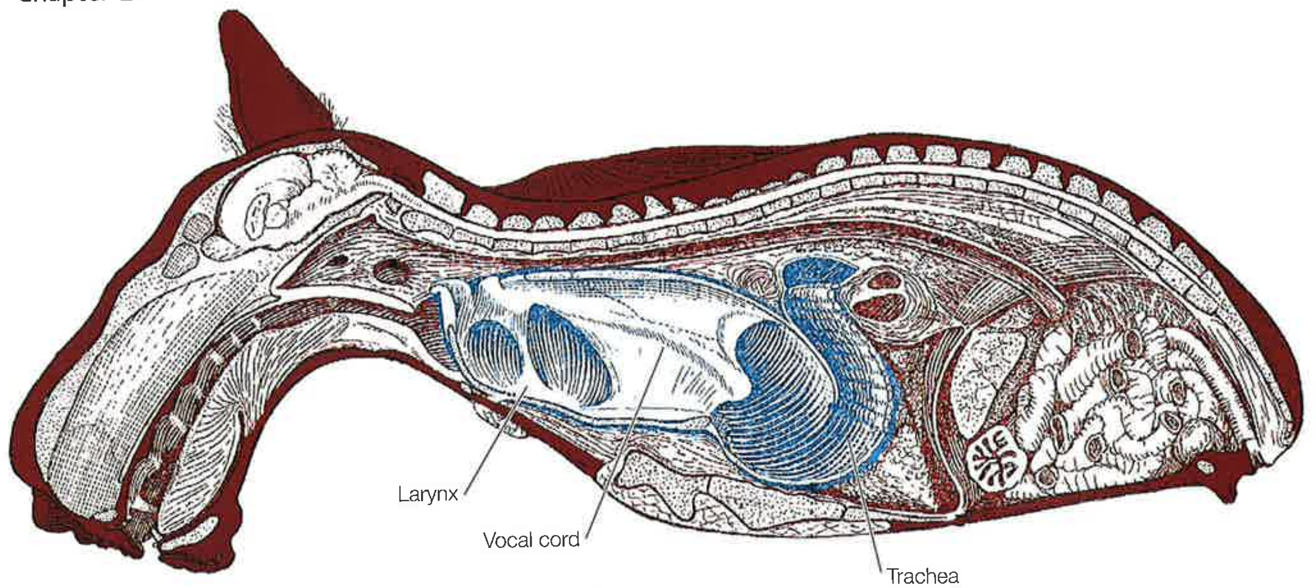


FIGURE 2.41 **Longitudinal section of male hammer-headed bat (*Hypsignathus monstrosus*)** Diagram shows relative locations of internal organs (brown) and enormous size of larynx and trachea (blue). (From [3].)

nasal sac on the top of its head as well as a bright red septal sac that is extruded through one nostril (**Figure 2.42**). Sac inflation is part of a combined visual and acoustic display directed toward competing males during the breeding season. Interestingly, males perform the display in the same way whether in the air or underwater [17, 36, 229, 384]. How the sacs might modify sound radiation in each medium remains unknown.

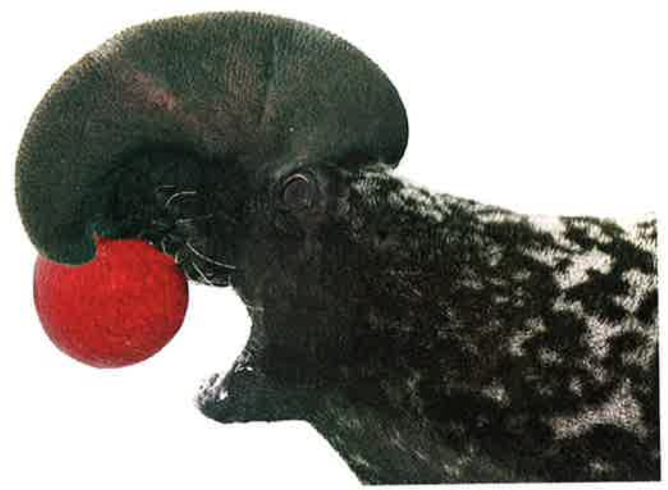


FIGURE 2.42 **Vocalizing male hooded seal (*Cystophora cristata*)** Male with black nasal hood inflated and red nasal septum inflated so that it protrudes out of nostrils. Males can inflate either sac or both when performing combined visual and acoustic display to opponent males.

SUMMARY

1. Sound propagation requires a material **medium** containing atoms or molecules. The atoms or molecules may be in the form of a **fluid** (such as a gas or liquid), a **solid**, or an interface between two of these phases of matter. **Pressure** is a measure of the degree to which the motions of atoms and molecules affect the motions of other nearby atoms and molecules.
2. **Sound** is the propagation of a perturbation in local pressure away from an initial location. It thus consists of alternating regions of higher-than-average pressure (molecular **condensations**) and lower-than-average pressure (molecular **rarefactions**).
3. Inside fluids, the molecules that pass on a pressure disturbance tend to move back and forth along the same axis on which the sound is propagating. The pattern of successive condensations and rarefactions moving away from the source of the disturbance is called a **longitudinal wave**. The molecules of a vibrating string propagate sounds along the string's length, but they do so by vibrating on a line perpendicular to the direction in which the sound is propagating. This is called a **transverse wave**. The molecules on the surface of a body of water that is propagating ripples move elliptically and thus have both longitudinal and transverse components in their motion. Solids can also propagate sounds, but the molecules can move only tiny distances, if at all. Solids can support longitudinal and transverse waves, as well as a variety of elliptical and more complex patterns such as **Rayleigh**, **Love**, and **bending waves**.
4. A **periodic wave** repeats the pattern of pressure variation over time. The **period** of the wave is the amount of time (seconds) required to produce one complete cycle. The simplest type of periodic wave shows a **sinusoidal pattern** in pressure over time. The **frequency** of such a wave is equal to the number of times the pattern is repeated per second, and is measured in **Hertz** (abbreviated **Hz**). The part of the cycle that occurs at some reference time is called the **phase** of the wave. Finally, a wave's deviations of pressure from ambient levels provide a measure of its **amplitude**. Amplitudes are usually measured on a logarithmic scale relative to some reference value. The units are called **decibels** (abbreviated **dB**).
5. Two waves of the same sinusoidal frequency passing through the same location are **in phase** if they have maxima and minima at the same time and **out of phase** otherwise. Waves that are in phase will show positive **interference** by creating a composite wave of similar frequency but enhanced amplitude; waves that are out of phase interfere negatively and tend to cancel each other out. Two sinusoidal waves that are similar but not identical in frequency will drift in and out of phase, creating **beats**.
6. Most animal sounds are periodic but not sinusoidal. In most cases, they can be decomposed into the sum of a set of pure sine waves (called a **harmonic series**) with frequencies that are integer multiples (called **harmonics**) of the lowest frequency in the set (called the **fundamental**). The decomposition (called **Fourier analysis**) can also be performed on aperiodic signals, but the sine wave components then tend to be more numerous, and their frequencies are not integer multiples of a single fundamental. Where the periodicity varies within animal sounds, one can usually break the sound into roughly periodic segments and perform a Fourier analysis on each segment. A plot of the Fourier decomposition of successive segments in an animal sound is called a **spectrogram**.
7. Inside fluids, all frequency components of a complex sound propagate at the same speed. In air, the speed of sound is about 344 m/sec (with variation depending on temperature and humidity). The speed of sound in water is about 4.4 times as fast as that in air, and the speed of sound in solids is about 15 times as fast as that in air. On the surface of a body of water and in certain solids, different frequency components may propagate at different speeds.
8. The spatial distance between the beginning and end of one cycle of a propagating sinusoidal wave is called its **wavelength** and is measured in meters. Wavelengths are inversely related to the wave frequency and directly related to the speed of sound in the medium. Wavelengths for a given frequency are thus longer in water than in air. Wavelengths may also be decreased, (and the effective frequency increased), if a sender and receiver are moving toward each other; wavelengths will increase if they are moving apart. This is called a **Doppler shift**.
9. Close to a sound source, medium molecules flow back and forth in unison. This is called the **near field** around the source. At distances of about 1/3 of the wavelength of the sound (or 2/3 the diameter of the source), medium molecules pass on the pressure disturbance without taking part in a cohesive tidal flow back and forth. The propagating medium at this and further distances from the source constitutes the **far field** of the sound.
10. Sound amplitudes decrease with distance from the source. Inside fluids such as water or air, the pressure of a sound radiating away from the source decreases with the reciprocal of the distance from the source. This is called **spreading loss**. Spreading losses are less severe for ripples on the water's surface or inside the solid stems of plants. In addition to spreading losses, propagating high frequencies cause molecules to collide more often, and thus lose pressure to **heat losses** faster than propagating low frequencies. Spreading losses are the same in air and water, but heat losses are much higher in air.
11. **Acoustic impedance** is the resistance of a medium to a change in its molecular behavior. Away from interfaces between media, acoustic impedance depends on the density and speed of sound of that medium. Media with low acoustic impedances (e.g., air) propagate sound with weak pressures but significant molecular velocities; high-impedance media (e.g., water and solids) propagate sounds with high pressures and low molecular velocities. At an interface between two media with different acoustic impedances, most of the sound traveling in one medium will be **reflected** back into the same medium at the boundary. If the impedances are not too different, then some sound energy will pass into the second medium, but its direction of travel will likely be bent (**refraction**).
12. In addition to spreading and heat losses, a propagating sound can be attenuated by reflective **scattering** from objects that have acoustic impedances different from that of the medium, and by refraction that bends sound waves out of the path connecting sender and receiver.
13. Most animals produce sound signals in three steps: generation of vibrations, vibration modification, and coupling of the modified vibrations to the medium. Generation of vibrations can be achieved in many ways. Hard-bodied animals can use **percussion** (striking a body part against a substrate or another body part); **stridulation** (rubbing a file over a plectrum); **buckling** (of flat plates); or **tremulation** (vibrating the whole body on the surface of water or solid substrates). Animals in fluid media can also use **pulsation**, **fanning**, **fluid compression**, or **streaming** as vibrational sources. Finally, animals can force respiratory system air through openings to create **aerodynamic vibrations** in the form of hisses or single-frequency whistles, or through a valve like a **glottis** to create periodic but nonsinusoidal vibrations. Frogs, reptiles, and mammals have their vocalization valves in a **larynx** at the top of their trachea, whereas birds may have one valve at the bottom of the trachea (parrots and chickens), or a separate valve on each bronchus (songbirds, oilbirds, and woodpeckers). Wherever the bird valve is located, the associated tracheal-bronchial junction is called the **syrinx**. Birds with a valve on each bronchus can produce two different sounds at once, or more commonly, assign high frequencies to one valve and low frequencies to the other.

14. **Modification** usually involves linking the vibrational source to a flat surface or cavity with an acoustic impedance sufficiently different from the medium that successive vibrations overlap and can interfere. This facilitates positive interference and amplification (**resonance**), and negative interference (**filtering**) depending on the sound frequencies. **High-Q** modifiers provide strong amplification of a few select frequencies (**normal modes**), but have **low damping** that muddles rapid temporal patterning in the sound. **Low-Q** modifiers track temporal patterns accurately, but are much less selective for frequency and provide only minimal amplification.
15. Effective **coupling** of vibrations to the propagating medium depends in part on the size of the radiating surface, and in part on how it moves: **monopoles** expand and contract in all directions at once, **dipoles** oscillate along a single axis, and **quadrupoles** change shape by moving along two axes at the same time. Unlike monopoles, dipoles and quadrupoles produce directional **sound fields**. All three mechanisms are inefficient when the wavelengths of the radiated sounds are larger than the radiator, and the latter two are even more inefficient due to acoustic **short-circuiting**. These effects limit small animals communicating over moderate or greater distances to high frequencies. To create sufficiently high frequencies given limits on muscle contraction rates, small animals often resort to **frequency multipliers**. Examples include stridulation and vocalization mechanisms. Terrestrial animals can also improve radiation efficiency with acoustic horns or inflated sacs, which have acoustic impedances intermediate between that inside their bodies and that of the outside air.
16. Different species have evolved different compromises between elaborated sound structure and amplitude. Adaptations such as elongated tracheae in cranes and currasows, or cartilaginous vessels in ducks and howler monkeys, allow great amplitude at the cost of severely constraining what kinds of sounds can be produced and radiated. Species such as frogs, tree crickets, and mole crickets excavate or select calling sites that dramatically increase the resonance or radiation efficiency of the sounds they produce. Finally, species such as cardinals and humans actively vary the dimensions of their internal resonant cavities dynamically to amplify different frequency combinations during the production of a given sound.

Further Reading

Readers interested in more detailed treatments of biological acoustics should consult Fletcher [119] and Michelsen [255]. Additional explanations of monopole, dipole, and quadrupole radiator efficiencies can be found in Harris [167] and Kalmijn [204]. Most other reviews or general treatments of the topics in this chapter are taxon-specific. Suggested resources include: Bailey [14], Bennet-Clark [30-34], Gerhardt and Huber [145], Greenfield [161], and Virant-Doberlet and Čokl [390] for insects; Barth [22, 23] for spiders; Ladich [219] and Ladich and Fine [220] for fish; Gerhardt [143] and Gerhardt and Huber [145] for amphibians; Young [415], Kirchner [208] and Gans [130] for reptiles; Goller and Larsen [155, 227] and Suthers [360, 372, 374] for birds; Fitch and Hauser[111], Fitch et al. [116], and Frey et al. [127] for terrestrial mammals; and Tyack [384] for marine mammals.

COMPANION WEBSITE
sites.sinauer.com/animalcommunication2e

Go to the companion website for Chapter Outlines, Chapter Summaries, and References for all works cited in the textbook. In addition, the following resources are available for this chapter:

Web Topic 2.1 ***Measuring sound pressure***
Microphones are used to measure the variations in pressure caused by a propagating sound. Specialized types of microphones exist for sound propagation in air, water, and solid substrates. These microphones work by converting pressure variation into electrical signals that can then be measured, stored, and characterized.

Web Topic 2.2 ***Visualizing sound waves***
The best way to understand the differences between different types of sound waves is to view an animation that shows how the molecules move as the sound propagates. We list a number of websites where you can watch visualizations of most of the basic acoustic processes described in this chapter.

Web Topic 2.3 ***Quantifying and comparing sound amplitudes***
A variety of methods are available for measuring and comparing sound amplitudes. Here we define some of these methods, show how they are computed, and discuss when each might be most useful.

Web Topic 2.4 ***Fourier analysis of animal sounds***
Here we provide an introduction to the logic behind Fourier decomposition of animal sounds, including links to several excellent software packages for creating spectrograms and introductions on how to use these packages. We also provide links to sites where one can use such methods to compare archived animal sounds.

Web Topic 2.5 ***Reflection and refraction***
The fraction of sound energy reflected or refracted at a boundary is a complicated function of incident angle, relative acoustic impedances, and relative sound speeds. Here we present the equations for several different cases, and provide some real physical examples.

Web Topic 2.6 ***Sample animal sounds***
Visit this website to hear examples of the kinds of animal vibrations discussed in this and following sections of the chapter. You will also be able to see the waveform and spectrogram of each example.

Web Topic 2.7 ***Animations of vocalizing birds***
Dr. Roderick Suthers and his team at Indiana University have pioneered our understanding about how the avian syrinx works. His lab has conveniently produced several animated clips demonstrating key steps in song production by northern cardinals and brown-headed cowbirds.

Web Topic 2.8 ***Linear versus nonlinear systems***
Although animal sound vibrators typically change frequency and amplitude linearly as the forces on them are changed, most will adopt less predictable nonlinear behavior at extreme force values. Some animals such as parrots, zebra finches, and canids use nonlinear vibration behavior to increase their vocal diversity.

Web Topic 2.9 ***Radiation efficiency and sound radiator size***
Monopoles, dipoles, and quadrupoles all show reduced efficiency when the wavelengths being produced are larger than the sound source. Here we explain in more detail why this happens.