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Size and scale effects as constraints in insect sound communication

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For optimal transfer of power to the surrounding medium, a sound source should have a radius of 1/6 to 1/4 of the sound wavelength. Sound-waves propagate from the source as compressions and rarefactions of the fluid medium, which decay by spreading and viscous losses. Higher frequencies are more easily refracted and reflected by objects in the environment, causing degradation of signal structure. In open air or water, the sound spreads spherically and decays by the inverse square law. If the sound is restricted to two dimensions rather than three, it decays as the inverse of range, whereas waves within a rod decay largely due to viscous losses; such calls are usually rather simple pulses and rely on the initial time of arrival because of multiple pathlengths or different propagation velocities in the environment.

Because of the relationship between calling success and reproductive success, singing insects are under selective pressure to optimize the range, and to maintain the specificity, of their calls. Smaller insects have less muscle power; because of their small sound sources, higher frequencies will be radiated more efficiently than lower frequencies, but in order to produce brief loud pulses from a long-duration muscle contraction they may use both a frequency multiplier mechanism and a mechanical power amplifier. Airborne insect sounds in the range from 1–5 kHz tend to have sustained pure tone components and a specific pattern of pulses which propagate accurately. Where the song frequency is higher, the pulses tend to become briefer, with a rapid initial build-up that gives a reliable time of onset through obstructed transmission pathways. These scale effects may be related both to the sound-producing mechanism and the auditory system of the receiver.

Tiny insects have the special acoustic problem of communicating with only a small amount of available power. Some, such as fruit flies, communicate at low frequencies, at close range, by generating air currents; these currents may also be used to waft specific pheromones. Other small insects, such as Hemiptera, beetles, etc., communicate using substrate vibration. This enables long-range communication, but signal structure degrades with distance from the source; vibration signals tend to be confined to certain types of linear substrate, such as vegetation.

Keywords: insect acoustics; acoustic scale effects; muscle power transduction; acoustics of environment; environmental sound degradation; sound signal range

1. INTRODUCTION

Insects cover a range of sizes from fractions of a milligram in body weight at a body length of about 1 mm, to a weight of over 10 g at a length of over 50 mm. Insect sound communication occurs throughout this size range, either as airborne sounds or as substrate-borne vibrations. The signals may propagate through air, water or in the substrate, but the major part of this discussion considers airborne sounds; these sounds may be deafeningly loud or almost inaudible. Their frequencies may occur within our range of hearing, or both above and below it; the signals may appear as musical pure tones or as broad-band brief transients.

Since the sound signals can give information about species, sex, fitness and source position, calling insects may be under selective pressure to maintain the specificity of the call. Since the signals often serve as attractants, it may be important to maximize the effective range of the signal. Both these aspects of insect sound communication have been reviewed extensively (e.g. Dumortier 1963*b*; Bennet-Clark 1971, 1989, 1995; Michelsen & Nocke 1975), and there is experimental evidence that loud songs with the species-specific pulse pattern and frequency are biologically more effective than quieter songs with different patterns and frequencies (e.g. Ulgaraj & Walker 1975).

Sound-waves propagate as compressions and rarefactions of the fluid medium, such as air or water. Sound decays by spreading and viscous losses. In the real world, this fluid medium is rarely free from obstructions; indeed, many insects sing from within vegetation, so the songs propagate through a cluttered environment.

Insect sound communication can be regarded as a series of interactions between the physical environment and the insect's anatomy or physiology. These interactions, which will be explored here, are summarized in figure 1.

2. PHYSICAL ACOUSTICS OF SOUND PRODUCTION AND PROPAGATION

As a medium for sound propagation, air has a specific acoustic resistance (ρc, the product of fluid density, ρ, and

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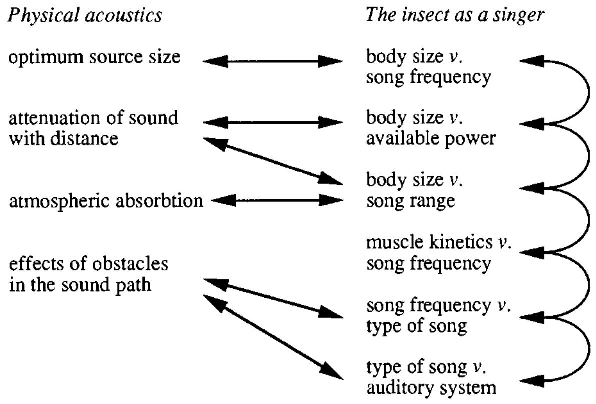

Figure 1. Diagram of the physical and biological factors that might interact as determinants of the type of song an insect produces.

velocity of sound in air, *c*). For good matching of the sound source to the fluid medium, the specific acoustic resistance of the source should match that of the load, which is the fluid medium; this is the condition of maximum efficiency of transduction of vibration of the sound source into sound power (Olson 1957; Bennet-Clark 1995).

The specific acoustic resistance of a source depends on its configuration and its size (Olson 1957). Various animal sound sources can be modelled as relatively simple, well-known types of sound source: a frog's vocal sac can be treated as a sector of a pulsating sphere; the sound-radiating eardrums of cicadas, or the mouth of the singing burrow of mole crickets (e.g. *Gryllotalpa* spp.), can be regarded as a monopole or a vibrating piston radiating sound from only one of its surfaces (figure 2*a*); the wings of tree crickets (e.g. *Oecanthus* spp.), or fruit flies (e.g. *Drosophila* spp.), can be regarded as dipole sources, or a free-edged vibrating piston which is equivalent to a pair of sound sources of opposite sign situated close to one another, with resultant sound leakage from one surface to the other (figure 2*b*) (Bennet-Clark 1971).

The specific radiation resistance, and therefore its efficiency as a sound source, depends on the ratio between its diameter (or another linear dimension) and the sound wavelength. The minimum source size for good source-to-medium matching has a radius of about 1/6 of the sound wavelength, λ, if it is a monopole source, or about 1/4 of λ if it is a dipole source (figure 2); below these sizes the specific radiation resistance decreases more or less rapidly depending on whether it is a dipole or a monopole source (the effective diameter of the tiny wings of *Drosophila* form a dipole source about 1/1000 of the sound wavelength, and the calculated specific acoustic resistance is about 10^{-8} times that of air (Bennet-Clark 1971)). The way in which this physical property relates an insect's body or sound source size to the frequency of the song is considered in § 4 below.

Sound attenuates with distance from the source due both to spreading and atmospheric absorption. At ranges greater than about 2/3 wavelength from a source, in the free field where sound spreads in three dimensions, the source intensity (the power per unit area in $\mathrm{W\,m^{-2}}$) decays by the inverse-square law. As sound intensity is the product of the sound pressure and the particle velocity in the wave (Olson 1957; Bennet-Clark 1971), both of these components vary inversely with distance from the source; thus a twofold change in pressure is taken to be a change of 6 dB. Within a sheet of solid material, or in a shallow pool of water, the propagation of sound-waves is restricted to approximately two dimensions. In such cases only circular spreading may occur. Within a rod, such as a plant stem or a fluid-filled tube, there is no spreading and little attenuation occurs beyond that due to frictional or viscous losses in the medium (table 1).

Viscous or frictional losses in the medium occur as the particles vibrate to and fro during the passage of the sound-wave. Because the rate of vibration increases as the frequency rises, the higher the sound frequency, the greater the effect (figure 3). The rate of attenuation varies approximately as the square of the frequency (Beranek 1949); this frequency-dependent extra attenuation accounts for the contrast between the high frequency crackling sound made by thunder straight overhead and the low-frequency rumble thunder makes at long-range. Because the viscous losses depend solely on the properties of the medium, the rate of attenuation per unit distance at a particular frequency is a constant. The actual values of the extra attenuation in air vary with factors such as the air pressure, temperature, and humidity (see figure 3).

This extra attenuation restricts the effective range of high frequency sounds, such as bat sonar, and provides one of several selective pressures for lower frequency sound production in large insects that act to maximize the range of their signals. The effect of this attenuation for different types of song is shown in figure 3, which also shows the frequency range of the sounds in various animal groups. In this context, it is significant that both the loudest insect known, the cicada *Cyclochila australasiae* (Young 1990), and the mole cricket *Gryllotalpa vineae*, which is audible at ranges of hundreds of metres (Bennet-Clark 1970), produce songs at 4.3 kHz and 3.4 kHz, respectively.

3. EFFECTS OF OBSTACLES IN THE SOUND PATH

When a sound-wave hits the interface between two media of different specific acoustic resistance (ρc), some of the sound may be transmitted. The proportion of the power transmitted (P_t) from medium 1 to medium 2 is given by Olson (1957):

$$P_\mathrm{t} = \frac{4\rho c_1 \times \rho c_2}{(\rho c_2 + \rho c_2)^2}. \tag{1}$$

The specific acoustic resistance of water is about 3500 times that of air, and that of wood is about 5000 times that of air. Thus, from equation (1), less than 0.1% of the incident sound power is transmitted at an air–water or air–wood interface; 99.9% is reflected as an echo.

Extending this to the real-life situation of the presence of leaves, branches, and the substrate encounters complications. Very thin membranes may be set into vibration by the sound and also transmit more sound than thick sheets of the same material; this effect is frequency-dependent, with the proportion transmitted being inversely proportional to the sound frequency. Thus, leaves may act as sound reflectors or absorbers at high frequencies, but effectively allow the transmission of low-frequency sounds.

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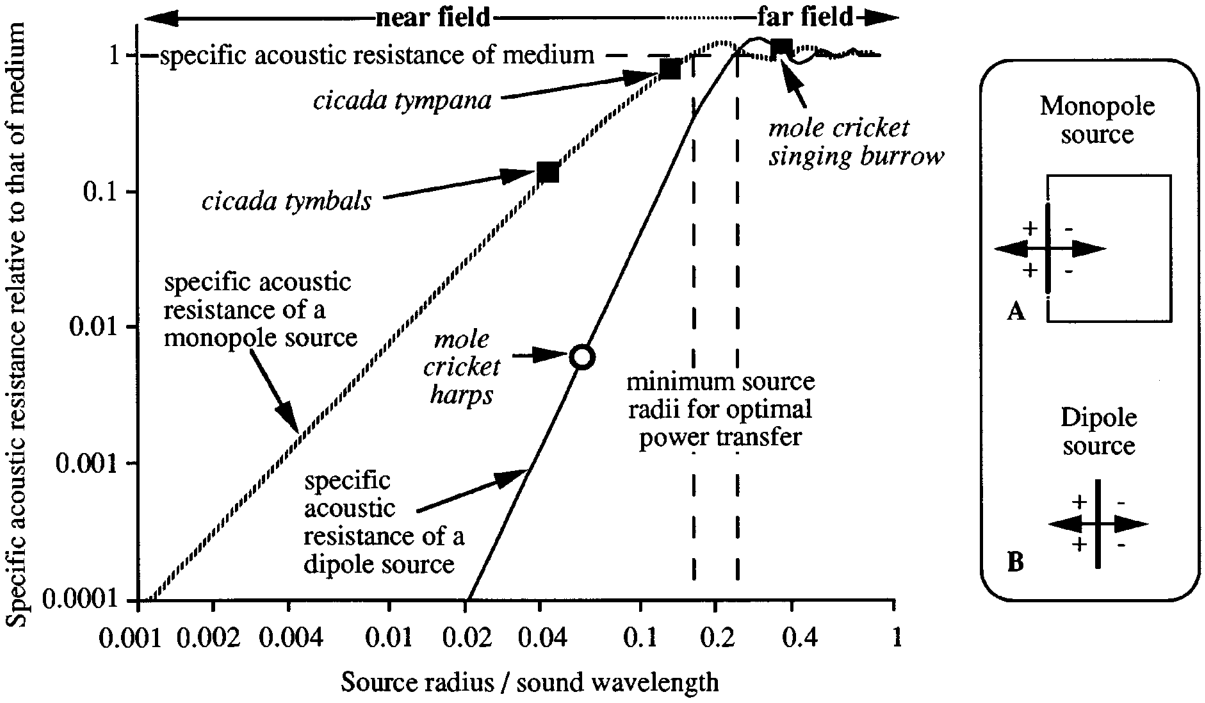


Figure 2. Graph of the specific acoustic resistance of sound sources of different sizes relative to the specific acoustic resistance of the fluid medium, to show minimal source dimensions for optimal sound power transfer from a vibrating source to the medium. For air the specific acoustic resistance, ρc, is 410 kg m^2 s^{-1}. The far field and near field are discussed in § 9. The inset shows the configuration of the two types of source, the relative specific acoustic resistance of which is shown in the graphs: A, a monopole source radiates only from the exposed surface; B, a dipole source can be regarded as two sources, separated by the dimensions of the source, that radiates sound from both sides but in opposite phase, causing destructive interference.

Table 1. *Attenuation due to sound spreading at source-to-receiver distances of over 2/3 λ*

(In addition to losses due to spreading, viscous or frictional losses will occur within the medium—see the text and figure 3. At ranges far below 1/3λ, the pressure and particle velocity components of the wave are 90° out of phase. In this 'near field' region, spherical spreading of the sound wave causes the attenuation of pressure and particle velocity with distance to occur at different rates to those given above—see figure 4.)

mode of propagation	attenuation of sound intensity (W m^{-2})^a	attenuation of sound pressure (N m^{-2})^b	attenuation in dB per doubling of distance
spherical spreading (in free field)	intensity $\propto$ (1/distance) squared (*plus viscous losses*)	pressure $\propto$ 1/distance (*plus viscous losses*)	> 6 dB
circular spreading (in a disc of medium)	intensity $\propto$ 1/distance (*plus viscous losses*)	pressure $\propto$ $\sqrt{(1/\text{distance})}$ (*plus viscous losses*)	> 3 dB
linear propagation (along a tube or rod)	only viscous losses	only viscous losses	> 0 dB

^{a}Intensity = sound pressure × particle velocity.
^{b}Intensity $\propto$ sound pressure squared.

The size of the obstacle is also important because the amount of sound reflected is the product of its specific acoustic resistance and its area (e.g. Sales & Pye 1974). Since the specific acoustic resistance of the object depends on its size relative to the sound wavelength (figure 2), an object such as a leaf, if it is smaller than 0.1λ radius, will reflect only about 0.01 times as much sound as a leaf of radius 1 λ. This scale-effect can be seen with bats, which can just detect fruit flies that are about 1/8 λ radius, or long wires that are 0.008λ radius (calculated from data in Sales & Pye (1974)), but only at close range when the echoes become louder. Bats can, of course, detect larger objects more readily and at a greater range.

As with other waves, when a sound-wave is reflected from a surface, the angle at which the sound is reflected equals the angle between the surface and the incident sound-wave. Hence, an object normal to the sound-wave may reflect the wave back towards the source, and objects that are nearly parallel to the wave will cause reflections that continue in the direction of propagation. This effect is used in anechoic rooms (Olson 1957), where sound-absorbent wedges longer than λ/4 cover the sound-reflective walls. Similarly, grass can act as a very effective absorber of sound-waves parallel to the blades; although the blades individually may reflect sound, the density and non-homogeneity of the growth, as well as the turf at ground level, make the overall plant

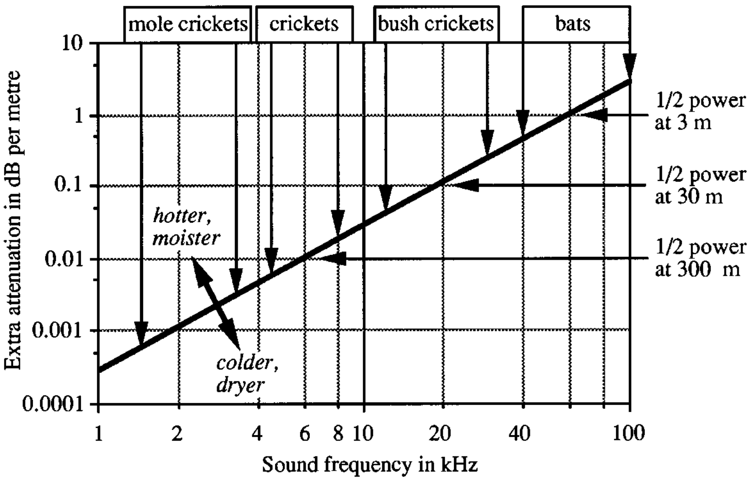
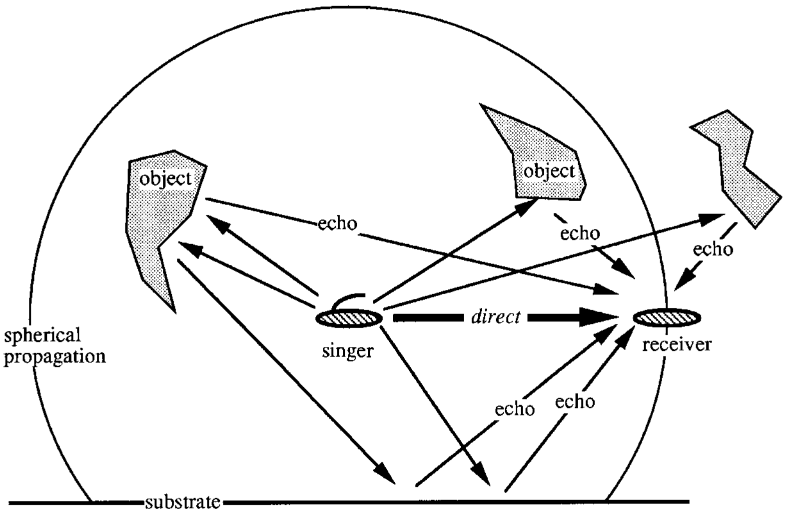


Figure 3. Graph showing the approximate rate of extra attenuation of sound in air, against sound frequency. The extra attenuation with distance is largely due to viscous losses in the fluid medium and is affected by air temperature and humidity (see the arrows); this attenuation is in addition to the losses due to spreading (see table 1). Boxes at the top of the figure show the range of frequencies of various animal sounds. For more exact data, see Beranek (1949).



All reflected pathways are longer so their sound arrives after the direct sound: reflected sound interferes with later components of the direct sound wave.

Figure 4. Diagram showing possible sources of multiple pathlengths in sound reaching a receiver from a singing insect. The direct singer-to-receiver pathway is the shortest; echoes travel indirectly over longer paths so they arrive after the onset of the direct signal, interfering with and degrading later components of the original signal.

growth fairly non-reflective. As with anechoic rooms, this effect is frequency-dependent.

In the insect's environment, various types of object are likely to cause multiple pathlength effects that will disrupt the coherence of the signal by interfering with the direct-path signal (figure 4). Because of its infinite size, this effect will always occur at the substrate (but the substrate may be covered by partially non-reflective plant growth). Other reflectors such as trees, leaves, leaflets and even rain, mist or fog (Pye 1971), will interfere with or significantly attenuate sound-waves, particularly if they are set into vibration by the sound and thus absorb power (Rayleigh 1896; Pye 1971). Different natural objects, depending on their size, will affect sound of a particular frequency and wavelength to a greater or lesser extent. The probable effect is shown in figure 5*a*. Some consequences of multiple pathlength effects on the types of songs that are appropriate for different environments are considered in § 7 below.

In this context, it should be noted that within natural habitats such as forests, there appears to be an optimal window between 1 and 4 kHz for maximum range of signal transmission (many large cicadas and mole crickets seem to operate within this window). In this frequency band, signal absorption and degradation appear to be minimal (Wiley & Richards 1978). It is likely that a modulated pure tone signal within this frequency band will be propagated relatively faithfully, allowing the use of a receiver that is tuned to the dominant frequency of the signal and better signal-to-noise ratio at the receiver. As the frequency rises, the effect of echoes during transmission is to lengthen the period of onset of a sharp transient, and to introduce rapid amplitude modulations (Wiley & Richards 1978).

The types of songs that are produced at different frequencies can be related to the habitat of the sound producer (figure 5*b*). In general, lower frequency songs appear to be pure tones that are found in more open habitats, while songs with major high frequency components are found in denser vegetation. This is discussed further in § 7.

4. SCALING INSECT SOUND SOURCES

From figure 2, it can be predicted that smaller insects will produce higher frequency songs. This can be re-expressed in terms of the minimum sound source size for optimal source-to-air coupling versus sound frequency (figure 6). When the probable sound source dimensions of a range of insects are entered, it can be seen that most

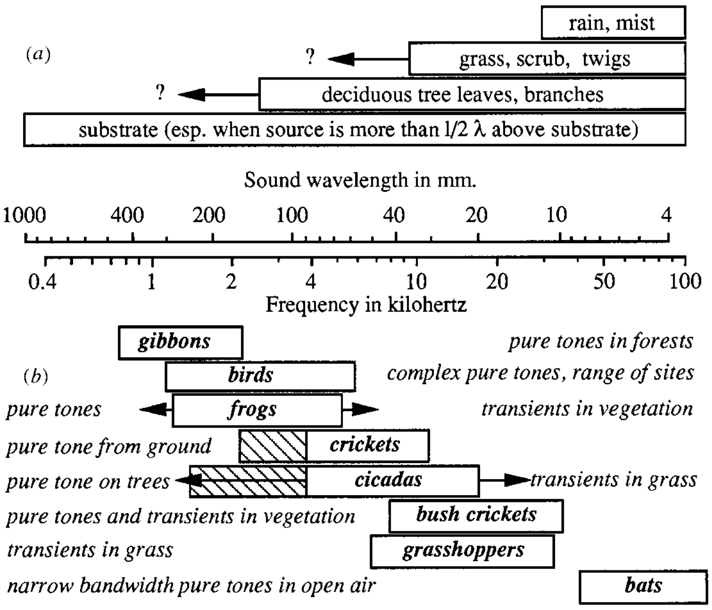


Figure 5. (*a*) The type of natural object that might cause echoes and other environmental degradation of sound signals against the sound wavelength and frequency. (*b*) This shows against the same wavelength/frequency scale as in (*a*), the frequency range of the sound signals produced by various animals groups with, in italics, the type of signal and the typical habitat.

crickets have dipole sound sources that are smaller than optimal (calculated from data, in Chopard 1951; Dumortier 1963*a*; Leroy 1966; Bennet-Clark 1970, 1971; Sales & Pye 1974; Young 1990), but that some of the loudest insects known, mole crickets and cicadas, have monopole sound sources that are close to optimal in size (data from Bennet-Clark 1970; Young 1990). The highest frequency insect songs that are known, the 120 kHz calls of the lesser wax moth *Achroia*, are produced by a tymbal that is about 0.6 mm in diameter (from data in Spangler 1984) by a moth that is only 8 mm long.

Not much is known about how, within an insect taxon, song frequency scales with body size, but over a wide range of tettigoniid species with song frequencies between 4 kHz and 50 kHz, the song frequency is inversely proportional to the square of the length of the mirror frame, the primary resonator in the sound-producing structure (Morris & Pipher 1967; Bailey 1970; Sales & Pye 1974). In this case, the calculation is complicated by the fact that this primary sound source is a small vibrating structure that is part of only one of the two forewings of the insect. Moreover, in many tettigoniids, the wings are relatively large, and during singing, form a baffle-like surround to the small primary resonator.

The situation is far clearer in many cicadas, where the sound is radiated via the large acoustically transparent eardrums or tympana which span the width of the ventral side of the abdomen. Here the effective dimensions of this sound source are close to optimal for the song frequency. Over a range of body lengths from 15–45 mm, similar sound-producing mechanisms are found, and song frequency scales closely as 1/body length (Bennet-Clark & Young 1994). (This is shown on figure 6.) Other cicadas, such as the bladder cicada *Cystosoma*, which sings at 850 Hz (Simmons & Young 1978; Young 1980), and uses a different sound-producing mechanism, depart from this scaling rule (figure 6).

Overall, it appears that many insects produce songs at frequencies that are lower than the optimal for the size of the sound-producing structures. A few insects use tricks such as acoustic horns (Bennet-Clark 1970), or baffles (Prozesky-Schulze *et al*. 1975; Forrest 1982), which increase the effective size of the sound source and the loudness of the sound. However, the majority of insects appear to sacrifice efficiency of source-to-medium power transfer for sound production at lower frequency with less environmental interference.

5. SCALING MUSCLE POWER AND SOUND RANGE

The power available from muscle is approximately proportional to its mass for a wide range of muscles operating at frequencies above 10 Hz (Weis-Fogh & Alexander 1977), as occurs in many singing insects (table 2). Assuming dimensional similarity, the available power for singing will therefore scale as body mass or as body length cubed.

By the inverse-square law, sound range in air scales as sound power$^{0.5}$ (table 1) but, since the available muscle power scales as body length^{3}, so the song range scales as body length$^{1.5}$, and the capture area ($\propto$ range^{2}) for a given sound intensity therefore scales with body mass rather than with body length. A 45 mm long cicada, such as *Cyclochila*, produces about 60 dB (relative to 10^{-12} W m^{-2}) at a range of 100 m (calculated from data in Young (1990)) where it is clearly audible; small cicadas such as *Tympanistalna* or *Cicadetta* spp. (both about 15 mm long) are only easily detected or located from ranges of less than about 20 m (H. C. Bennet-Clark, personal observation). In the most extreme case, *Drosophila* which is only 2 mm long and sings at an effective frequency of about 300 Hz has a song range of only a few millimetres (Bennet-Clark 1971) (but see § 8).

There is also selection for the evolution of large sound-producing muscles. In the evolution of the sound-production mechanism, insects have often exploited and specialized existing large locomotor muscles, for example the mesothoracic wing muscles of many Orthoptera (suborder Ensifera). In cicadas, the abdominal tymbal muscles are as large as the major flight muscles (Pringle 1954). These and other examples emphasize the selective importance of loud signals on many insect groups.

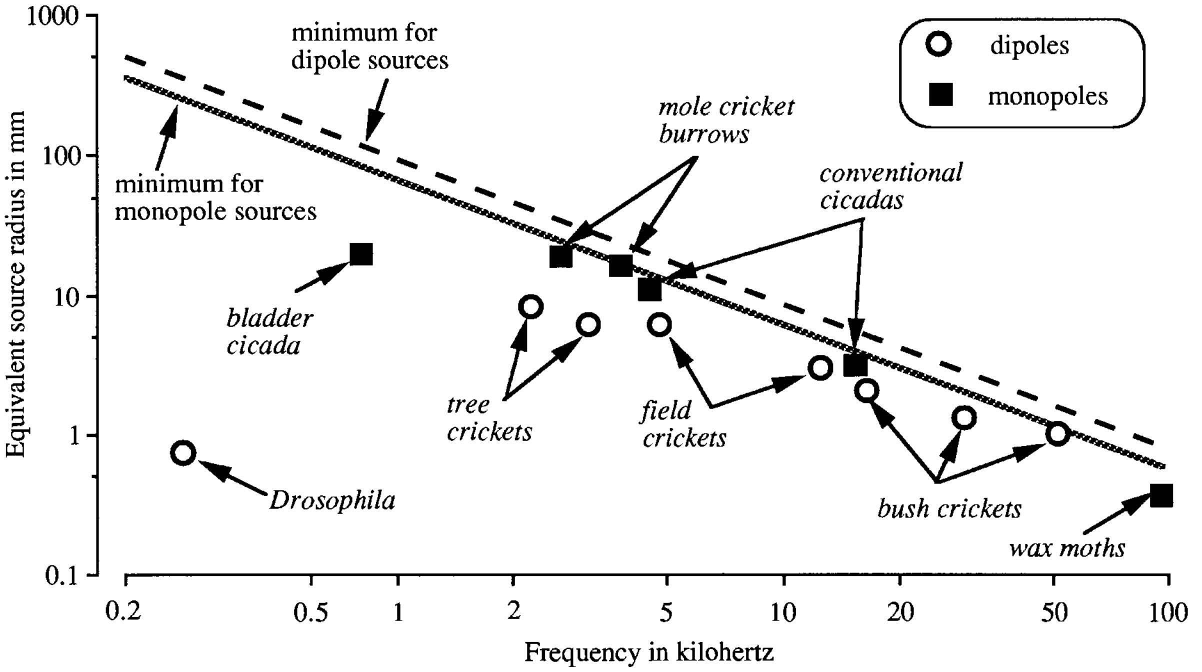


Figure 6. Minimum source radius for optimal source-to-medium sound power transfer, calculated from data in figure 2, against the sound frequency. Actual source sizes for various singing insects are shown as solid squares (monopole sources) or hollow circles (dipole sources). Note that for the majority of dipole source singers, the source size seems to be far smaller than optimal.

This leads to two conclusions: (i) there may be strong selection on singing insects for large body size, to maximize the effective song range; and (ii) from § 4, smaller insects will tend to have higher song frequencies than large insects.

6. TRANSDUCING MUSCLE CONTRACTIONS INTO SOUND

Contracting muscle, as a source of mechanical power, provides discrete packets of energy with each cycle of contraction. Over a wide range of rates of contraction, from 16 Hz to the highest known frequencies for which measurements are available, around 240 Hz, the peak power output of insect muscle is approximately constant at around 150 W kg^{-1} (Weis-Fogh & Alexander 1977). The energy available in each cycle varies inversely with the operating frequency, from 9.4 J kg^{-1} cycle^{-1} at 16 Hz to 0.63 J kg^{-1} cycle^{-1} at 240 Hz.

Most insects produce sound in discrete pulses, produced either as a single pulse or train of pulses which is driven by a single muscle contraction. Examples are the long pulses produced by a single wing-closing stroke of a cricket (e.g. Elliott & Koch 1985), and the song pulse produced by a single contraction of the tymbal muscles of many cicadas (Pringle 1954; Young & Josephson 1983; Young & Bennet-Clark 1995).

Raising the pulse rate in a song lowers the muscle energy available for that song pulse; alternatively, if the muscle contraction that drives sound production is long, more total energy may be available than is available from a brief contraction.

The conversion of muscle power to sound power in many insects usually involves a frequency-multiplier mechanism that causes a single, relatively slow muscle contraction to produce many cycles of mechanical vibration at a higher frequency (Michelsen 1983; Bennet-Clark 1995). Mechanisms of this type are widespread and include the file-and-plectrum mechanism of crickets, the tymbals of cicadas, etc. In field crickets and mole crickets, each wing-closing muscle contraction is relatively slow, and causes a plectrum to pass over a series of file teeth which catch-and-release to produce a long coherent sound pulse (for reviews, see Dumortier 1963*b*; Bennet-Clark 1989). In tettigoniids, the wing-closing movement may be fast or slow, and the successive impacts of the plectrum on the file teeth may produce either a coherent sound pulse, as in *Homorocoryphus nitidulus* (Bailey 1970), or a train of transients, each transient being produced by a single tooth impact, as in *Ephippiger ephippiger* (Pasquinelly & Busnel 1955; also reviewed in Dumortier 1963*b*).

In cicadas, a wide range of different songs are produced, but two extreme cases are noteworthy. *Cyclochila australasiae* and *Tympanistalna gastrica* both have tymbals with four ribs that are used in sound production. *Cyclochila* is large, *Tympanistalna* is small, and the dominant song frequency of the larger species is about one-third of that of the smaller species, as is expected from scaling considerations (Bennet-Clark & Young 1994) (table 2).

The scaling of sound output with body size has been examined in cicadas (Sanborn & Phillips 1995). They found that sound pressure levels scaled approximately as $(\text{body mass})^{1.2}$, but the scatter of their data was too large to exclude the possibility that the sound power produced by cicadas scales linearly with body mass, as the simplest theory predicts.

However, there may be additional complicating factors. These are considered below.

When the energy available per cycle has gone through the stage of frequency multiplication to be converted to the song frequency, it will be affected by the frequency multiplication mechanism. Consider first the case of field crickets,

Table 2. *Sound production in insects of different sizes, to show some relations between muscle contraction kinetics, the type of sound-producing mechanism, and the type of sound that is produced*

insect group and species	body length	multiplier mechanism	muscle drive frequency	duration of movement	major song frequency	effect of multiplier	song type	source of data
Gryllus campestris (Orthoptera: Gryllidae)	25 mm	file on elytron (*ca.* 150 teeth)	*ca.* 30 Hz	18 ms	4.5 kHz	80 cycles in pulse	loud pure tone	Leroy (1966)
Nemobius f. fasciatus (Orthoptera: Gryllidae)	10 mm	file on elytron (*ca.* 190 teeth)	*ca.* 12 Hz[a]	22 ms[a]	7.5 kHz[a]	160 cycles in pulse	quiet pure tone	Pierce (1948)
Ephippiger ephippiger (Orthoptera: Tettigoniidae)	35 mm	file on elytron (*ca.* 50–55 teeth)	7 Hz[c]	100 ms[b]	8–15 kHz	45 transients[b]	loud hiss or ‘zips’	Dumortier (1963)
Gryllotalpa vineae (Orthoptera: Gryllotalpidae)	45 mm	file on elytron (*ca.* 45 teeth)	*ca.* 65 Hz	6–8 ms	3.5 kHz	28 cycles in pulse	very loud pure tone	Bennet-Clark (1970)
Cyclochila australasiae (Hemiptera: Cicadidae)	43 mm	four-rib tymbal in abdomen	240 Hz	3 ms[d]	4.3 kHz	8–12 cycles in pulse	very loud pure tone	Young (1990)
Tympanistana gastrica (Hemiptera: Cicadidae)	15 mm	four-rib tymbal in abdomen	200 Hz	0.5 ms[e]	12 kHz	one transient of six cycles maximum	quiet ‘ticks’	Fonseca (1994)

[a] One long coherent pulse per contraction.
[b] Each transient <1 ms, six cycles maximum.
[c] Each contraction produces a train of transients at one pulse per file tooth at each tooth impact.
[d] Each contraction causes the ribs to buckle every second or third cycle to produce a coherent pure tone pulse
[e] Each contraction causes three coupled ribs to buckle as a unit producing a single transient.

in which the song is produced as a long coherent pulse that builds up slowly, is sustained by the coherent catch-and-release of file teeth by the scraper or plectrum, and then decays as the wing movement ceases (e.g. Dumortier 1963*b*). This type of song pulse builds up slowly into a long tone burst, which then decays after the excitation from the file teeth has ended (see figure 7*a*); the energy is usually confined to a comparatively narrow frequency band.

This type of song may be greatly affected by scale, as the following comparison shows. The crickets *Gryllus* and *Nemobius* produce song pulses of rather similar duration (table 2). *Nemobius* is a small cricket, about 0.4 times the length of *Gryllus*, so if simple scaling applies, it has only $(0.4)^3=0.064$ times as much muscle power available. The frequency of the song of *Gryllus* is nearly half that of the song of *Nemobius*, so the energy that *Nemobius* can put into each cycle of the sound, per unit weight of muscle, will be halved and, consequently, the mean power of the song will be reduced by a further 3 dB as a simple consequence of producing a long sound pulse at high frequency. Simple multiplication of these two factors suggests that the song of *Nemobius* should be about 0.03 times as loud as that of *Gryllus* or about 30 dB quieter. The song of most *Nemobius* spp. is indeed very quiet.

However, production of loud high frequency songs is achieved by certain bush crickets, such as *Ephippiger*. This is a robust insect that produces a high frequency song at between 8 and 15 kHz (table 2). The file that excites the sound-producing mechanism has large teeth and, as each tooth is struck by the contralateral wing's scraper or plectrum, the impact produces a single sound pulse, which has a rapid build-up and then decays (Pasquinelly & Busnel 1955). (This type of pulse is modelled in figure 7*b*.) The sound, therefore, is produced as a series of transients with a sharp, loud attack, but because of their brevity, with a broad frequency spectrum. This song may be compared with that of the mole cricket *Gryllotalpa vineae*, which uses the file and scraper to sustain a low-frequency (table 2), pure tone song (Bennet-Clark 1970); here, because the energy of each muscle contraction produces a relatively low-frequency pulse, these insects make very loud sounds in which the energy is confined to a narrow frequency band.

One trick for increasing the instantaneous power in a motor task is to use an energy store which can store the energy relatively slowly and release it rapidly, with power amplification being approximately equal to the ratio of storage time to release time. Mechanisms of this type are used in jumping insects to produce the rapid high-power movements required for take-off of a small animal (Bennet-Clark & Lucey 1967; Bennet-Clark 1975). Analogous mechanisms appear to operate in the tymbal clicks of cicadas (Young & Bennet-Clark 1995) and wax moths (Spangler 1984, 1985).

The domed tymbal of a cicada such as *Cyclochila* bears a series of arc-shaped ribs (Pringle 1954; Young & Bennet-Clark 1995) which are separated and supported by the elastic protein resilin (Weis-Fogh 1960). As the large sound-producing muscle contracts, it initially stresses the ribs of the domed structure, which then makes a large-amplitude inwards elastic buckling-movement over a period of about 60 µs (derived from data in Young & Bennet-Clark (1995)), creating a large sound pressure pulse inside the insect's abdomen. Although the kinetics of the preceding muscle contraction are not known, it is probable that a muscle contraction lasting about 2 ms is required

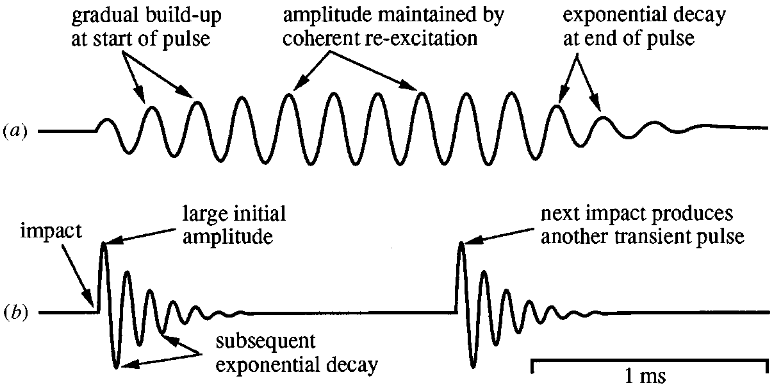


Figure 7. Diagram showing the waveforms of two types of sound pulse that are commonly found in insect songs. (*a*) Shows the type of long pulse that is produced by successive coherent excitation of a resonant system; this type of pulse is produced by gryllid crickets and such large cicadas as *Cyclochila*. (*b*) Shows a pair of brief transients, such as might be produced by an impact giving a single excitation of a damped resonant system; pulses of this type are produced by grasshoppers, many bush crickets, and small cicadas such as *Tympanistalna*.

to stress the elastic cuticle of the tymbal to the point at which the first rib buckles. The initial contraction therefore lasts about 30 times as long as the release of energy that occurs as the first tymbal rib buckles, with a corresponding 30 times power amplification. Thereafter, the second and third tymbal ribs buckle in–out with the same rapid 60 μs time-course at intervals of either 470 or 700 μs, providing successive high-power impulses to sustain the song's pulse. The initial rib-buckling release of energy appears to act as an impulse to initiate the sympathetic resonance of the abdominal air sac, from which the sound is radiated via the tympana (Young 1990) at the start of the sound pulse, and the later rib movements sustain this resonance to extend the duration of the sound pulse (Bennet-Clark & Young 1992; Young & Bennet-Clark 1995); the resulting sound-pulse envelope is similar to that illustrated in figure 7*a*. The tymbal appears to act as a short-term energy store that provides substantial power amplification, particularly at the start of the pulse.

The sound produced by the small cicada *Tympanistalna* differs from that of *Cyclochila*. The sound pulse is brief, with maximum amplitude in the first cycle (from oscillograms in Fonseca (1994)) followed by an exponential decay; each pulse resembles the song pulses produced by the plectrum-to-file tooth impacts in *Ephippiger* (modelled in figure 7*b*). Although the basic tymbal anatomy of *Tympanistalna* is similar to that in *Cyclochila*, with four tymbal ribs, there is a dorsal bar that connects ribs 2 and 3 to the tymbal plate which is absent in *Cyclochila*. From the shape of the song-pulse envelope, it appears that in *Tympanistalna* there is only one large impulse as the tymbal buckles and no later sustaining impulses of the type found in *Cyclochila*, so it is likely that all three tymbal ribs buckle inwards simultaneously to give a single large impulse in this species. This type of song pulse is seen in a number of other small cicada species (e.g. Popov 1992; Fonseca 1994), which share a similar type of tymbal anatomy. In these, the tymbal appears to act as an energy store, releasing the energy of the muscle contraction in a single explosive impulse as all three ribs buckle in unison.

The song of the small cicada *Tympanistalna* has its maximum energy in a relatively broad frequency band from 10–13 kHz (Fonseca & Popov 1994), compared with a narrow band centred on 4.3 kHz in the larger *Cyclochila*. Important differences are seen when these two species are compared: the dominant frequency differs by a factor of 3, from 4.3 kHz to 10–13 kHz; the song pulse at 4.3 kHz is a sustained pure tone with a slow build-up and decay (of the type shown in figure 7*a*), whereas that of *Tympanistalna* at 10–13 kHz is a brief transient which is loudest at the start (of the type shown in figure 7*b*).

Similar power amplification may occur in *Ephippiger*, but by a different mechanism. The file teeth are widely separated, so, as the plectrum is released by one tooth, the wings close together silently until the plectrum impacts with the next file tooth. During this silent closing, the wings acquire considerable kinetic energy which is dissipated on impact, producing a transient sound pulse. From the published records (Pasquinelly & Busnel 1955), the sound-to-silence ratio of the song of *Ephippiger* is about 1:5, suggesting that a fivefold power amplification may occur. The songs of most bush crickets are of this general type. However, a few, such as *Homorocoryphus*, produce comparatively pure tone songs at frequencies of 15 kHz or higher (e.g. Bailey 1970).

In crickets such as *Gryllus* that produce long pure tone song pulses, each cycle of the song is produced by the catch and release of a single file tooth by the plectrum escapement mechanism (Elliott & Koch 1985). It is unlikely that mechanical energy storage or power amplification of the types described above occur in these insects, regardless of their body size.

However, as a general rule, larger insects produce purer tone songs at lower frequencies than small insects. The correlation between the song frequency, the type of song pulse, and the habitat was noted in § 3 (figure 5). The significance of these differences is considered in § 7 below.

7. TRANSMITTING ACOUSTIC INFORMATION THROUGH THE ENVIRONMENT

A series of obstructions in the environment is likely to influence sounds of different wavelengths in rather different ways (figures 4 and 5). The relative positions of the source, the receiver, and the obstructions are likely to vary the effect of the obstructions on the propagation of sound between two individuals (e.g. Wiley & Richards 1978; Römer & Lewald 1992).

For low frequency sounds, the signal will be propagated relatively easily, both with little attenuation (figure 3) and with little environmental interference, because there are likely to be only a few large echo-producing objects in the signal path (figure 5). As a consequence, a slowly modulated pure tone signal (figure 7*a*) may be transmitted faithfully.

As the signal frequency rises, the environment will cause degradation of the signal, which will worsen as the range or frequency increase. The signal component that will propagate most faithfully will be its onset because it may follow the direct-line shortest propagation path between the source and the receiver (figure 4). In this situation, a transient signal with a large initial amplitude (figure 7*b*) will provide good temporal information of its time of onset, providing directional cues as well as allowing information about song structure to be maintained. There is evidence from the transmission of model signals that it is only this information that can be propagated through vegetation (Stephen & Hartley 1990).

8. SOUND SIGNALS AND HEARING

For effective communication, the auditory system should meet the following requirements. It should be able to (i) detect the sound signal: this implies that there are receptors that are tuned to the frequency of the sound, that the receptors' sensitivity is adequate, and that the sound stimulus is capable of eliciting a response; (ii) detect the direction of the sound: this implies that there is a paired auditory system that is capable of giving a directional response, and that the signal should provide appropriate cues that the auditory system is capable of analysing; and (iii) recognize species-specific elements of the sound signal: this implies that the central neural processing of the receptor response is appropriate. This requirement is beyond the scope of this review.

The first two requirements relate qualitative or quantitative features of the sound signal to the auditory system: in other words, the type of auditory system will be related to the type of sound signal and vice versa.

If the song is sharply tuned, the ear can also be tuned to the same frequency as the signal, whereas the broad bandwidth required for detection and analysis of a transient signal requires an ear that is sensitive throughout the signal's bandwidth.

The narrow band songs of crickets are associated with sharp tuning of the tympanic membrane and tracheal system close to the song frequency of the insect (Paton *et al.* 1977). Even though individual receptors may show frequency response spectra that cover many octaves (Hutchings & Lewis 1983; Oldfield *et al.* 1986), there are several receptors in the tonotopic array that are tuned close to the 5 kHz of the species' song, with two types of threshold and intensity–response curves (Oldfield *et al.* 1986), which suggests that auditory analysis will be best at the frequency of the insect song.

The brief transients that make up the song pulses of such insects as grasshoppers or bush crickets (Dumortier 1963*b*), or small cicadas (Fonseca 1994), cover broad frequency spectra. The ears of both grasshoppers (acridiids) and bush crickets (tettigoniids) contain elaborate receptor arrays (Schwabe 1906), in which different receptors are tuned over a frequency band covering several octaves, within which individual receptors are tuned to particular frequencies with Q values of about 3 (Michelsen 1971; Oldfield 1982). These arrays, covering a wide band, are likely to be able to make the type of time and frequency discrimination that is required for the analysis of songs consisting of a complex sequence of transients. Note, however, that the ears of gryllids also have arrays of tuned receptors that cover a broad band of frequencies (Hutchings & Lewis 1983).

Directional hearing has been studied in a range of insects. The major acoustic problem is that the bodies of most insects are too small to allow large differences in either time-of-arrival or intensity to occur on the two sides of the body (or at the two auditory organs).

Directional auditory mechanisms have been described in crickets, grasshoppers and tachinid flies (Michelsen 1983; Michelsen & Rohrseitz 1995; Robert *et al.* 1996) which all seem to rely on a similar principle: interaural coupling associated with the introduction of an interaural time delay. In both crickets and grasshoppers, the mechanism is partly acoustical, through the tympana and air sacs, and partly mechanical, through the interaural membranes (Michelsen 1983; Michelsen & Rohrseitz 1995). In the tachinid fly *Ormia*, the interaural coupling is via a viscoelastic lever (Robert *et al.* 1996). In all these systems, the interaural coupling increases the small differences in time of arrival at the two ears to give a phase difference of the tympanal vibration of around 90°, as well as giving a significant difference in the amplitude of tympanal vibration on the ipsi- and contralateral sides (table 3). In *Ormia*, a time-of-arrival difference of below 2μs in the sound reaching the two tympana outside the ear is increased to a time difference between the vibration of the two tympana of 50 μs. Measured differences in the responses of the ears to ipsi- and contralateral sound are between 5 and 13 dB (table 3).

At the levels of the receptor and auditory interneurones, various mechanisms act to enhance further the small differences that occur. The dependence of latency of response upon signal intensity is well known from a variety of taxa (e.g. Mörchen *et al.* (1978) for grasshoppers; Liberstat & Hoy (1991) for bush crickets). In such cases, a change in signal level of 10–20 dB can bring about a shift in response latency of 6–10 ms, or a rate of $0.5\ \mathrm{ms\ dB^{-1}}$. This effect can bring about a dramatic increase in the asymmetry of the interaural response. The effect is further enhanced by rapid contralateral inhibition of the response to stimuli of equal intensity (Rheinlaender & Mörchen 1979). Similar effects are reported with other sensory systems and all serve to increase the temporal discrimination—and hence increase the directionality—of signals that only have small differences in intensity or time-of-arrival.

Thus, several mechanisms along the auditory chain are exploited to give good directionality despite the limitations of small size and initially small interaural differences.

9. THE ACOUSTIC PROBLEMS OF TINY INSECTS, AND SOME SOLUTIONS

Among the smallest insects that are known to use acoustic communication are the drosophilid fruit flies. Their effective song range is a few millimetres and an estimate of the sound pressure at such ranges is only 35 dB (Bennet-Clark 1971). From the arguments presented in § 5, the available muscle power is perhaps 1/1000 of that available to a cricket, which, if the song were to be produced at high efficiency, would give a range of 1/30 of that of a cricket (which would give a quite respectable range of maybe 10–50 cm). For comparable efficiency to sound production in a

Table 3. *Interaural distance, time-of-arrival and phase difference of the sound arriviing at the outsides of two ears, compared with the delay due to inter-aural transmission*

(The measured difference in the amplitude of vibration of the tympanum to ipsi- and contralateral sound is also given.)

species	*Schistocerca gregaria* locust	*Chorthippus biguttulus* grasshopper	*Ormia ochracea* tachinid fly
(*a*) external interaural distance	6 mm	2 mm	500 µm
(*b*) external interaural time difference	17 µs	6 µs	< 2 µs
(*c*) external interaural phase difference	24° at 4 kHz	17° at 8 kHz	2.7° at 5 kHz
(*d*) external sound pressure difference	2.5 dB at 5 kHz	—	≪ 2 dB
(*e*) time delay due to interaural transmission	*ca.* 60 µs	*ca.* 40 µs	*ca.* 50 µs
(*f*) difference in amplitude of tympanum vibration with ipsi- versus contralateral sound	> 10 dB at 5 kHz	> 5 dB at 8 kHz	> 13 dB at 5 kHz
(*g*) souce of data	Michelson & Rohrseitz (1995)	Michelson & Rohrseitz (1995)	Robert *et al.* (1996)

gryllid, the song would have to be produced at 50 kHz, but typical *Drosophila* songs have frequencies of 200–450 Hz (Ewing & Bennet-Clark 1968). These songs are produced by beating the wings, which are only about $1/200\lambda$ in radius, which offer a poor impedance match to the medium (figure 6), so the song is, to our pressure-sensitive ears, very quiet.

The effective range of *Drosophila* song is about $1/50\lambda$. At such short ranges, sound spreads as a spherical-wave (this acoustic regime is termed the near field). At ranges of many wavelengths, the sound propagates as a plane-wave (this is termed the far field). Propagating sound-waves have two components: the sound pressure and the particle velocity. In a plane wave, both these components vary with the inverse-square of distance but, in the near field, the relative magnitude of the particle velocity increases (Olson 1957). The magnitude of this 'near field' effect is less for a monopole source than for a dipole source (table 4) because, in the latter, there is also destructive interference between the sound components produced by the two sides of the source.

The wing of a *Drosophila* can be regarded as a tiny doublet source and the sound receptor, the antenna, as a particle velocity detector (Bennet-Clark 1971). Calculation suggested that, at the ranges at which *Drosophila* courtship occurs, the particle velocity of the sound of the wing-beat is equivalent to that of a plane-wave sound of 70–90 dB; that their communication occurs at this high level is borne out by behavioural tests with calibrated sound stimuli (Crossley *et al.* 1995).

This song uses a sensory modality, the detection of sound particle velocity, that is unfamiliar to us but which is appropriate to the body size and sound producing mechanism of *Drosophila*. Because the song range is extremely short, other means must be employed to bring the singing and receiving insects into acoustic proximity; in *Drosophila* the long-range attractant is the odour of the food upon which they congregate, after which medium range contact is made visually, which allows the singer to approach to within acoustic range and then use species-specific signalling (e.g. Ewing & Bennet-Clark 1968; Bennet-Clark *et al.* 1980).

The problems of signal detection and analysis that are discussed in § 8 for long-range signals do not apply here. Particle velocity is vectorial. It therefore has an intrinsic directionality within the signal and thence at the displacement-sensitive receptor. However, songs of this type cannot be regarded as calls but as close-range courtship signals.

Other small insects get past the scaling problems of available power (§ 5) and the range-limiting problems of the inverse-square law (table 1) by using vibration signals in the substrate (see Gogala (1985) for a review).

Signal transmission within the substrate has several advantages: the rate of attenuation of the signal is low (table 1); and the signal tends to be confined within the substrate (equation (1), § 3), so, for a given amount of available power, long-range communication is possible. The head-tapping of the death watch beetle, *Xestobium rufovillosum*, which is only about 8 mm long, has a range of many metres. The disadvantages are that (i) contiguity of the substrate is required; (ii) the receiving insect must be standing on or positioned so that it can detect the vibration; and (iii), possibly most importantly, that vibrations of different frequencies travel at different speeds, so signal structure tends to become increasingly degraded with increasing distance from the source. As a consequence, many substrate-borne signals take the form of impulses or broad-band buzzes, which give directional information by the time of onset or differences in the time of arrival of the different frequencies.

10. CONCLUSIONS

Although scaling has been applied to topics such as locomotion (Pedley 1977), skeletal design or metabolic rate (Schmidt-Nielsen 1984), the problems of size and scale effects in insect sound production have received little attention. Part of the difficulty I have encountered when trying to find some general rules is the complexity of the interactions along the sound transmission pathway.

Sound transmission can be viewed as a chain from the sender starting with (1) neural patterns→(2) muscle power→(3) mechanical vibration of the sound source→(4) acoustic loading of the source→(5) sound radiation into the fluid medium. This leads in the medium to (6) signal propagation through the environment and, at the receiver, to (7) acoustic-to-mechanical vibration transduction→(8) adequate stimulus of sensory cells→(9) neural response→(10) signal analysis.

Table 4. *Attenuation of the components of the sound-wave with distance from the source for monopole and dipole sources*

(For diagrams of these two types of source, see figure 2. Data from Olson (1957).)

source type	monopole	dipole
(*a*) *far field conditions*	range $\gg 1/3\lambda$	range $\gg 1/3\lambda$
sound pressure attenuation with distance from source	$\propto 1/\text{range}$ (6 dB/doubling)	$\propto 1/\text{range}$ (6 dB/doubling)
particle velocity attenuation with distance from source	$\propto 1/\text{range}$ (6 dB/doubling)	$\propto 1/\text{range}$ (6 dB doubling)
(*b*) *near field conditions*	range $\ll 1/3\ \lambda$	range $\ll 1/3\ \lambda$
sound pressure attenuation with distance from source	$\propto 1/\text{range}$ (6 dB/doubling)	$\propto 1/\text{range}^2$ (12 dB/doubling)
particle velocity attenuation with distance from source	$\propto 1/\text{range}^2$ (12 dB/doubling)	$\propto 1/\text{range}^3$ (18 dB/doubling)

Awkwardly, most of these links are so variable and so hard to define that it is difficult to apply formal scaling methods to them. However, it appears that the song frequency of large insects is usually lower than that of small ones. It also appears that the problems of transduction of muscle power to mechanical vibration at the song frequency result in a variety of mechanisms for energy conservation and mechanical power amplification, which may result in different types of song pulse at different frequencies. Moreover, because a number of the links may have constraints acting in the same direction, it is hard to separate the additive effects that may occur at different stages in the pathway.

The type of song is also related to the environment of the singing insect. Many of the larger insects appear to make use of low frequencies, by which their songs propagate faithfully over long ranges; the requirements for fidelity and range appear often to override the physical constraint that the size of the sound-producing structure may be too small for high-efficiency sound-production. At these low frequencies, simple amplitude modulation may be employed but, as with radio signals, this is only valid where the transmission path does not cause interference or degradation of the signal (Langford-Smith 1953). As with high frequency radio waves, where environmental degradation of the signal also occurs, pulse-time and pulse-width modulation may usefully be employed in high frequency insect songs transmitted through obstructed environments to ensure accurate transfer of information. Given that rather similar problems occur in radio wave transmission and insect song transmission, it is not surprising that closely parallel solutions have been adopted.

Taking the parallel a stage further to hearing, the type of auditory system is related to the song and the transmission path. But there may be a significant difference between radio receivers and insect auditory receivers insofar as the auditory receptors respond to a signal by producing a series of nerve impulses which may go through a series of stages of analysis and decoding (e.g. Schildberger *et al.* 1989) but always remaining as a pattern of pulses, whereas radio receivers tend to demodulate the signal and to reconstruct the modulation. Another significant difference, however, is that relative to the carrier frequency, the frequency of modulation or bandwidth of radio signals tends to be low so the signal bandwidth is narrow; in insect songs, the modulation may be very rapid or the pulses very brief, so the signal bandwidth is often large. In this situation, much of the initial signal analysis may be done peripherally at the level of the receptors, leaving recognition to a central integrator and pattern decoder.

There are exceptions to most of the correlations made in this review. That is the nature of biological systems. But there do appear to be certain unavoidable physical and physiological constraints which are likely to act in particular directions to determine the types of song and auditory system that are appropriate to insects of different sizes and insects living in different environments.

This review arose out of a talk I gave at the 10th International Meeting on Insect Sound and Vibration, held at Woods Hole in September 1996. I am grateful to many participants at that meeting for their encouraging comments that led me to write this material up as a review. I am also grateful to Ron Hoy for honouring me by asking me to give the talk. Many thanks to Win Bailey who has made many useful and encouraging comments on the manuscript. Particular thanks to Alisdair Daws: he has made many constructive criticisms of the manuscript, which has benefited greatly from his extensive knowledge of this field.

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