SOUND RECEPTION IN DIFFERENT ENVIRONMENTS

AXEL MICHELSEN

Institute of Biology, Odense University

DK-5230 Odense M, Denmark

INTRODUCTION

The aim of this book is to discuss "sensory ecology", that is the adaptation of sense organs to the properties of the environments. For hearing organs, it is at present only possible to describe such a correlation for hearing in air and water. Some physical parameters are different in these two homogeneous media (see below), and the hearing organs are adapted to the medium in which they are being used (references to the literature on hearing in fish, seals and whales can be found in Schuijf and Hawkins, 1976; Møhl and Ronald, 1975; and Payne and Webb, 1971). The vast majority of hearing animals, however, live in terrestrial environments, and very little is known about the acoustical properties of these environments.

One aim of this chapter is to review our present knowledge of outdoor acoustics, especially the acoustical properties of terrestrial ecosystems. I have tried to point out a number of problems, which should be further investigated, and some of the pitfalls for such investigations. Sensory ecology is an area of research where the investigator is likely to drown himself in data, if he does not manage to keep in mind the order of magnitude of the various phenomena. On the other hand, all the important parameters must be measured simultaneously, if he wishes to analyse, for example, the acoustic properties of vegetation. So far, the majority of the field studies have been performed by acousticians (or biologists), who appear not to be very familiar with the complexity of the problem. In many cases the investigators have

M. A. Ali (ed.), *Sensory Ecology*

ignored important parameters in the environment.The result of such studies are, of course, less useful. (After this chapter was written, I had the opportunity to see the manuscript of a similar review by Wiley and Richards (1978), which is highly recommended. It contains much new material (e.g. on temporal fluctuations in sound pressure), as well as many biological examples, especially from birds. In the present paper the examples have been drawn mainly from insects).

Throughout the chapter a number of examples of acoustic communication in animals are given. I have tried to relate the strategy adapted by each group to known acoustic parameters of the environment. But this correlation is between the environments and the types of *acoustic signals* used by animals living in these environments. Our present knowledge does not allow us to relate the properties of the *hearing organs* to the acoustic properties of the environments. The reason is that we are in most cases ignorant about the nature of the information needed by the listening animal.

The kind of information, which may be of interest to the listening animal, is the identity of the sound producing animal (who is he?), its location (where is he?), and the nature of the message (what is he saying?). In some situations, all this information is important; for example, animals looking for a mate need most of the information mentioned. Other listening animals are only interested in a part of the information. The prey of bats, for example, do not care much about which kind of bat is coming near, but they are very interested to know, how far away, and in which direction the bat is.

This means that there may be more than one reason for the different complexity of the hearing organs in various animals. Animals may need complicated ears and an elaborate system of acoustic neurons in the central nervous system, because they need to extract as much information as possible from the sound signals. In contrast, if the animal happens to live in a very complex acoustical environment, a rather complicated auditory system may be needed to obtain just a small amount of information. Therefore, a meaningful correlation between environments and sensory capacities, is not possible unless the role of sound in the behaviour of the animal is known.

Unfortunately, there is no easy solution to this problem. Some animals have simple calls; others have very complicated calls. We need behavioural studies for determining how much signal redundancy is needed in complex environments, where much filtering takes place as the call propagates to the listening animals. We have very little information on this problem.

SOUND PROPAGATION IN COMPLEX ENVIRONMENTS

There are several reasons why so little is known about the acoustical conditions of relevance to animals in terrestrial environments. One is that most field studies have been performed by acousticians interested in the propagation of noise from traffic or other noisy human activities. The frequency range of most annoying noises is mainly below a few kHz. Most studies have therefore been limited to frequencies below 4 kHz, but biologists are often interested in animal communication at much higher frequencies. Furthermore, humans hearing noises (or rather humans annoyed by noises) normally keep their heads 1.5-2 m from the ground, and therefore most studies have been concerned with the sound propagating to a receiver situated at least 1 m from the ground. So, if one is interested to know, for example, how a grasshopper manages to locate another grasshopper in the vegetation, the majority of the field studies are not of much help.

Another reason for our ignorance is the lack of theoretical understanding of the process of sound propagation in natural environments. A number of theories can be found in the acoustic literature, but very few studies have combined theory and field measurements. Most of these problems have to be studied by biologists or by acousticians working with biologists. The relevant questions about the acoustics of the environment should be asked by scientists who are concerned with the sound parameters carrying the specific information of relevance to the animals.

Sound propagation in complex environments embraces a number of processes of very different natures. It is very important for the investigator to realize, which process is dominant in the particular situation (Lyon,1973). These processes can be divided into 5 groups: geometric spreading, reflection, absorption, refraction and diffraction (scattering).

Geometric spreading. The pressure of sound waves travelling from a sound source will decrease with distance. This is a simple consequence of the geometry of the air space occupied by the sound energy. Some sound sources (such as pulsating spheres) radiate sound energy evenly in all directions. The geometric spreading from such a *monopole* source will cause a 6 dB (2 times) decrease in sound pressure per doubling of the distance from the origin of the sound wave (Fig. 1,A).

Other sound sources do not behave in this simple manner. A loudspeaker without the backing enclosure is a *dipole* source. Close to the dipole (in the acoustic *near-field*), the sound pressure decreases 12 dB (four times) with distance doubled (abbreviated dd); far away (in the *far-field*) the decrease is

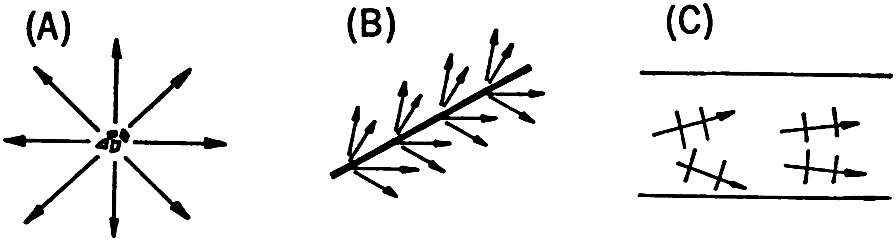

FIG. 1. Geometric divergence of sound waves and resulting attenuation. A. Spherical spreading, attenuation 6 dB/dd (dd = distance doubled). B. Cylindrical spreading, 3 dB/dd. C. Sound in channel, 0 dB/dd. (From Lyon, 1973).

6 dB/dd (as in the monopole source). Furthermore, unlike the sound radiation from a monopole source, the radiation from a dipole source is directional. Singing insects often behave as mixed monopole-dipole sources (Michelsen and Nocke, 1974)

Still other kinds of sound sources exist, which have a different behaviour (see Crocker and Price, 1975). In some bioacoustic problems (e.g. the spreading of low frequency sounds in the oceans, Payne and Webb, 1971) one is dealing with a cylindrical spreading of sound, where the decrease is only 3 dB/dd. Finally, if the sound waves are being reflected without loss in a channel, the attenuation may approach 0 dB/dd (Fig. 1(C)).

It is important to remember that the decrease for other parameters of the sound wave (the oscillation velocity of the molecules, the pressure gradient) is more rapid close to a sound source than is the decrease in sound pressure. This is important for animals with receptors sensitive to such parameters, for example in the near-field communication in fruit flies (Bennet-Clark, 1971).

Reflection. Sound waves are redirected at the surface of another medium if the surface is several wavelengths long and if the acoustic impedance of the two media are different. (The *acoustic impedance* is the density of the medium multiplied by the velocity of sound in the medium). Important examples in a biological context are the reflection from an air-water or water-air interface (where less than 1/1000 of the sound energy is transmitted to the other medium) and reflection from the ground. The magnitude and phase angle of the reflected wave depends upon the ratio of the impedances, Z_1 and Z_2 in Fig. 2, and upon the "grazing" angle ψ (Fig. 2).

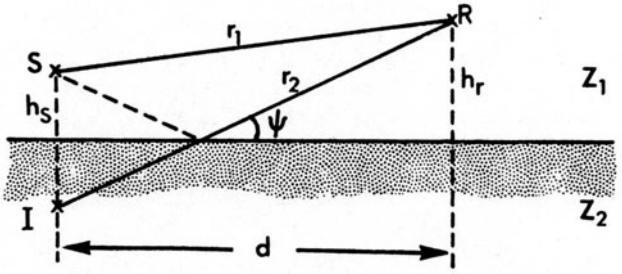

FIG. 2. Reflection from the ground. Location of source (S), and receiver (R) at heights h_s and h_r above flat ground. Z_1 and Z_2 are the impedances of the air and of the ground surface, respectively. The reflected sound wave, which at point R appears to have come a distance r_2 from the sound source I, is interfering with the direct wave (r_1). (From Embleton et al.,1976).

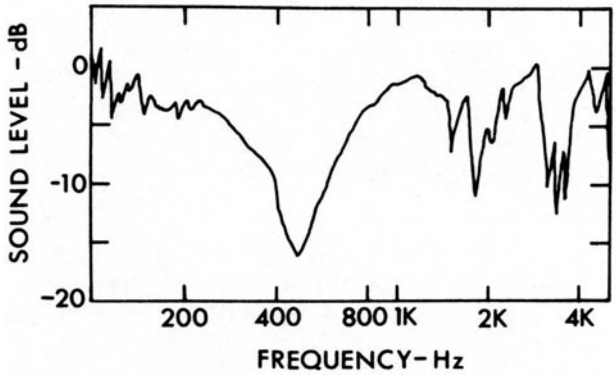

FIG. 3. Reflection from the ground. Frequency filtering of pure tones propagating about 15 m and about 1.2 m above grass. Reference sound level is that due to geometric spreading (6 dB/dd) alone. (From Embleton et al., 1976).

The magnitude of the ground reflection (and ground absorption) is one of the very uncertain parameters, when guesses about the range and filtering of an animal call are made. Two mechanisms are important in causing a filtering of the frequency content of the call: the ground may interfere with the propagation of a sound wave close to the ground (see below), and the reflected wave, r_2

in Fig. 2, may interfere with the direct wave, r_1 in Fig. 2. The latter mechanism may lead to an enhancement (r_1 and r_2 in phase at the receiver), or a destruction (r_1 and r_2 out of phase). The frequency filtering caused by this interference depends very much upon the exact positions of the sender and receiver in space. The magnitude of the filterings may be substantial, when the source and/or receiver are a few metres from the ground. Fig. 3 shows an example of this.

A substantial part of the energy of sound signals in the sea is reflected from the bottom. Also, as previously noted, sound waves are almost entirely reflected by the water-air interface. These reflections, and the small absorption of sound in water (see below), are probably the main reasons why some whales use very short ultrasonic clicks and not longer sound signals for echolocation. But even with short pulses, the reflection from the surface and bottom may cause trouble for the orientation of echolocating animals. This is especially evident in whales, which happen to enter narrow fiords. (By the way, deep and narrow fiords are also ideal hiding places for submarines, which may be impossible to locate by means of sonar or directional listening devices).

Absorption. The absorption of a sound wave includes the dissipation of sound energy to heat, and the transmission of sound into other media. It is, however, often difficult to distinguish between absorption and other causes of attenuation. Good absorbers of sound energy (in air) are porous materials like mineral wool. The air itself also absorbs sound energy. The effect is commonly expressed as a change in sound pressure level over a fixed distance (dB/m).

One can use Fig. 4 for evaluating the effect of absorption on the total decrease in sound pressure from the sound source to the receiver. The sound source is assumed to have an initial level of 0 dB at a distance of 0.1 m from the source, and the sound waves are assumed to spread spherically (attenuation due to geometric spreading: 6 dB/dd). In using the figure, one should subtract the threshold of the receiver from the sound pressure produced by the sound source. If this value is 80 dB, and the attenuation in the path of propagation is 1 dB/m, one finds that the maximum distance, at which the listening animal can hear the sound source, is about 30 m.

Note that "*threshold*" in this context means the smallest sound pressure, which can be heard (and/or "understood") by the listening animal. So, one must allow for the background noise level. For example, the "threshold" may be dependent upon the wind. When the vegetation rustles in the wind, a broadband noise is produced. The sound level of this rustling sound has been measured to about

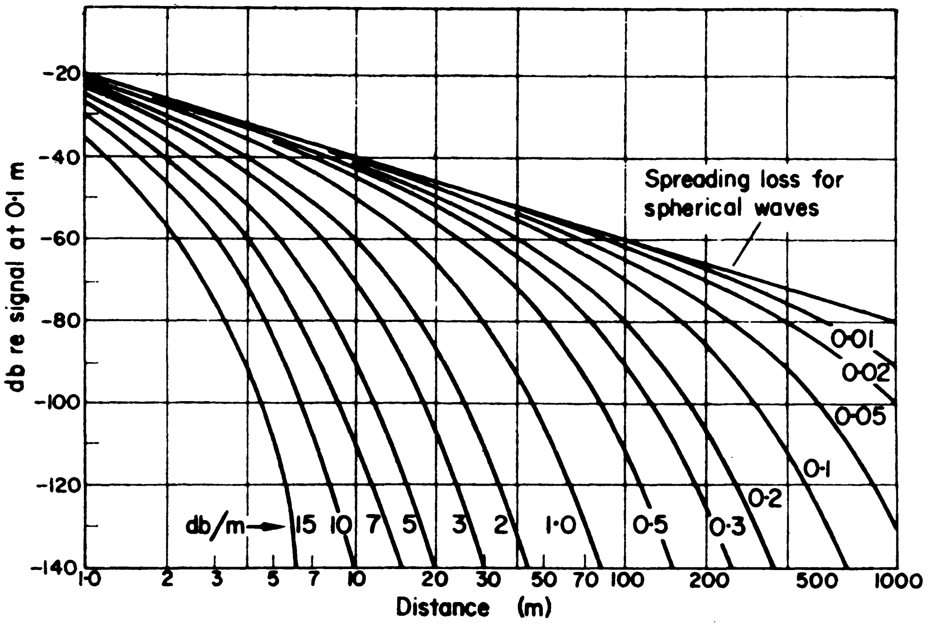

FIG. 4. The relative intensity of a sound wave at various distances from the source. Geometric spreading is assumed to be spherical (6 dB/dd). The sound intensity is arbitrarily assigned an intensity of 0 dB at a distance of 10 cm from the source. Each curve represents a given value of atmospheric attenuation (dB/m); the upper line showing the spreading loss with no atmospheric attenuation added. (From Griffin, 1971).

35 dB(A) at 1 m/s wind speed and to about 60-70 dB(A) at 8 m/s wind speed (Yamada et al., 1977). The presence of such noise is likely to have a masking effect on some animal calls and thus acts to increase the "threshold".

Dissipation in air is caused by several processes: shear viscosity, heat conduction in the air, mass diffusion, thermal diffusion and molecular vibrational relaxation. The attenuation of sound caused by these processes is a fairly complicated function of temperature, relative humidity and sound frequency. The literature and theories have been reviewed recently by Piercy et al. (1977). Rather different estimates of the dissipation can be found in various textbooks, since the contributions from molecular vibration relaxation were not fully understood in some classical papers. The upper curve in Fig. 5 indicates the dissipation in dB/100 m for a pressure of 1 atm, a temperature of 20°C and a relative humidity of 70%.

The effect of *humidity* is not well understood at the molecular level. A fair amount of experimental data is available at various humidities at 20°C, but more data are needed at other temperatures and especially at low humidities. In dry air the dissipation attains a maximum at low frequencies. The position of this maximum is shifted towards higher frequencies when the humidity is increased. (see Piercy et al., 1977).

From the data in Figs. 4 and 5, it is obvious that the use of high frequencies impose a considerable limitation on the range of

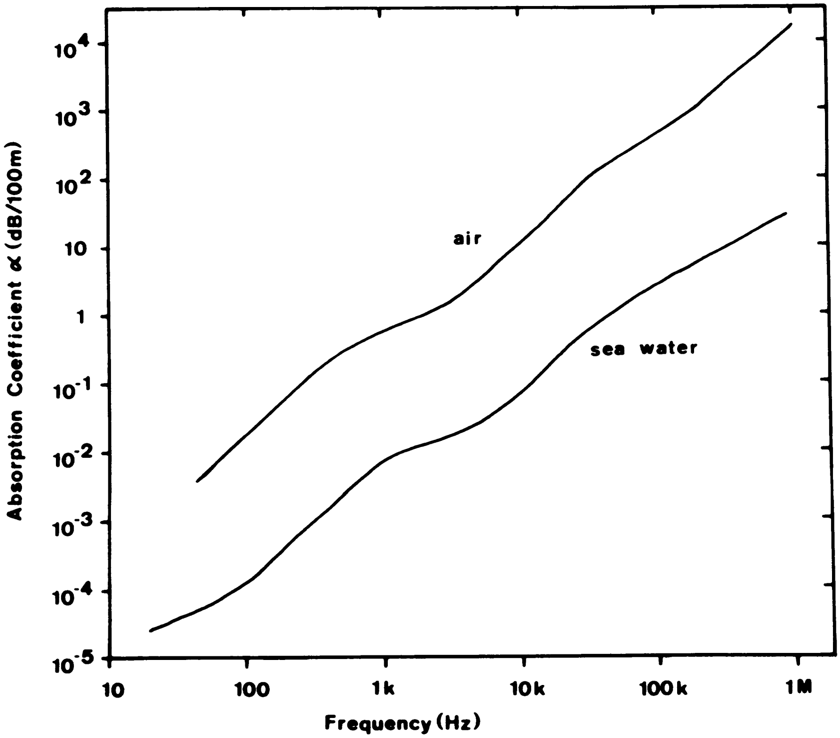

FIG. 5. Dissipation of sound in air (upper curve) and sea water (lower curve) at a pressure of 1 atm. The dissipation in air is for 20°C and a relative humidity of 70% and is redrawn from Piercy et al. (1977). The dissipation in sea water is for 4°C and a salinity of 3.5%. The curve is based on data from Fisher and Simmons (1977) and Payne and Webb (1971).

communication in air. For example, at 100 kHz and at 70% relative humidity the atmospheric attenuation is about 4 dB/m. From Fig. 4, and assuming an 80 dB difference between source pressure and receiver threshold, one finds a maximum distance for communication of about 10 metres. In ecological terms this means a high population density.

I shall not go into the mysteries of bat echolocation in tropical forests where the air is very hot and humid (see Suthers, this volume). The attenuation is enormous under such conditions, and the range of echolocation may be as small as one or two metres (Griffin, 1971). In our part of the world similar unfavourable conditions occur only in foggy weather, and our bats seem to avoid flying in fog (Pye, 1971).

The *dissipation of sound energy in water* (lower curve in Fig. 5) is much less than that in air. At very low frequencies, the absorption is so small that communication over hundreds of kilometres becomes (at least a theoretical) possibility (Payne and Webb, 1971). The absorption in water also increases with increasing frequency, but dissipation never becomes a significant factor within the frequency range used by animals. On the contrary, the absorption is so small that echolocation may be very difficult.

Refraction. The deflection of sound waves known as refraction is caused by an abrupt or gradual change in the velocity of the sound wave. The velocity of sound depends upon the temperature and the density of the medium. The velocity of sound relative to an observer also depends upon the velocity of the medium, the wind. (Water currents are too slow to have any significant effect).

The *velocity of sound in air* depends mainly upon temperature. The velocity is about (331.4 + 0.607C)m/sec, where C is the temperature in degrees Celsius. An increase in temperature of one degree thus causes an increase in sound velocity of about 0.2%. The sound velocity also increases with increasing humidity, except in very dry air (Harris, 1971). At 20^{o}C the sound velocity at 100% relative humidity (R.H.) is about 0.3% larger than at 30% R.H.

Close to the ground or to the surface of objects one often finds *gradients of temperature*, wind and humidity. These parameters vary not only with height above ground, but they may change considerably when the terrain or vegetation change along the path of sound propagation. On sunny days the temperature decreases with distance from the ground (Fig. 6,a) as does the velocity of sound. The sound waves will therefore bend upwards, leaving a *shadow zone* beyond a certain distance from the source (Fig. 7,A). The border of this shadow zone is not sharp. No direct sound can penetrate into the shadow zone, though sound may be scattered into the zone.

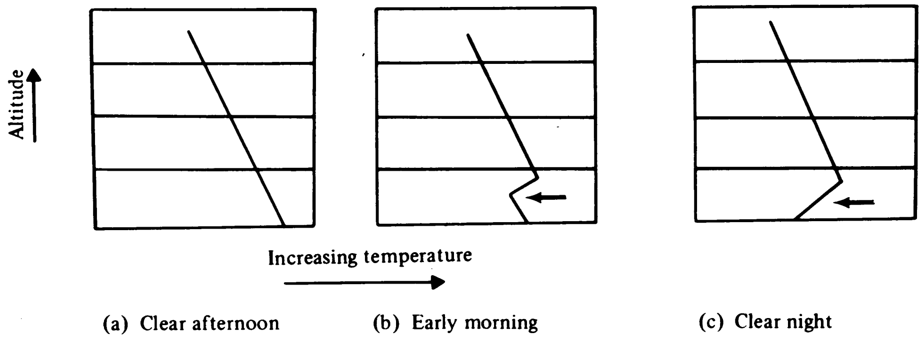

FIG. 6. Typical examples of temperature variation with altitude. Arrows indicate that "channeling" of sound is possible. (From Crocker and Price, 1975). (Changed).

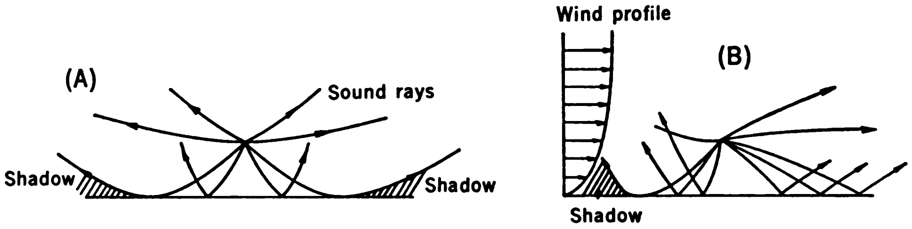

FIG. 7. Refraction of sound by wind and temperature gradients. A. Temperature lapse, no wind. B. Temperature lapse, with wind. (From Lyon, 1973).

If a *wind* is blowing, the wind speed will increase with the distance from the ground, and its effect on sound velocity will add to that caused by temperature. In the upwind direction, the refraction due to temperature and wind cooperate to create an even more pronounced shadow zone (Fig. 7,B). On sunny and windy days the shadow effect for sound propagating upwind may amount to 25 dB (Wiener and Keast, 1959). In contrast, in the downwind direction the effects of temperature and wind will cancel each other, and the result will depend upon the relative strengths of the two parameters.

The situation at other times of the day may be quite different. On a clear night the temperature often increases with distance from the ground, reaching a maximum at a certain altitude (Fig. 6,c). Under these circumstances the sound waves are "caught" in a channel close to the ground, and sounds may be heard at much larger distances from the sound source than during the day. In the early morning, the development of temperature gradients with distance from the ground may be even more complex. Channelling of sound with only little loss is now possible at some distance from the ground (marked with an arrow in Fig. 6,b).

In *water*, the velocity of sound increases with increasing temperature, hydrostatic pressure and salinity. The variation in sound velocity with depth below the surface depends upon the local conditions. In tropical and temperate oceans, the decrease in temperature with increasing depth causes the sound velocity to decrease to a minimum about one to two km from the surface. At larger depths, the velocity again increases due to the hydrostatic pressure. The minimum of sound velocity at a certain depth creates the so-called SOFAR-channel, in which sound communication is particularly favourable (Williams, 1972). In arctic oceans the temperature does not change so much with depth, and the velocity of sound is determined mainly by the hydrostatic pressure (Fig. 8).

Fluctuations of sound pressure. In the previous sections we have seen that geometric spreading, molecular dissipation and refraction caused by wind and temperature gradients all contribute

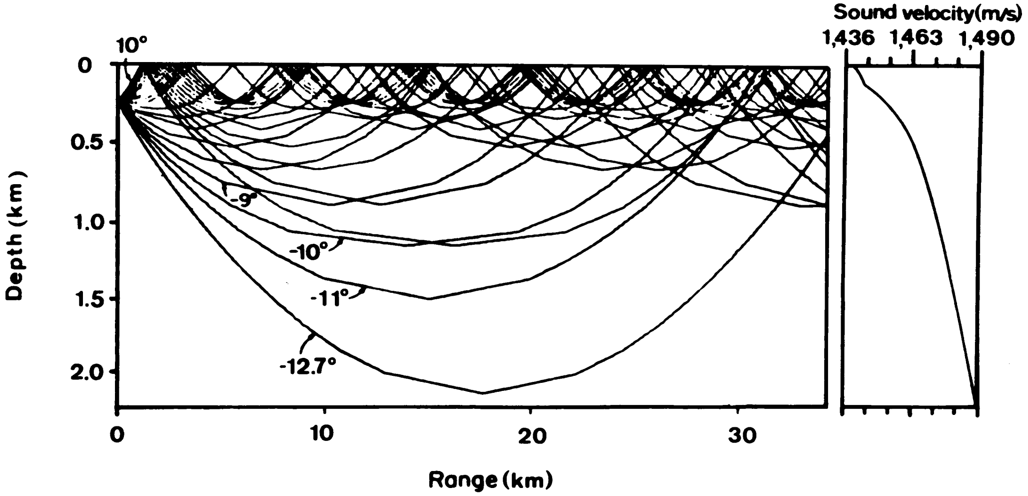

FIG. 8. Propagation of sound waves in Arctic oceans. The velocity profile is shown at the right. The sound source is located about 200 m below the surface. Sound rays are shown at 1° intervals. Rays leaving the source at steep enough angles to reflect from the bottom are omitted. (From Urick, redrawn from Payne and Webb, 1971).

to a smoothly increasing attenuation of sound pressure with distance. The total attenuation depends very much upon the local conditions. It is therefore difficult for an animal to judge the distance to a sound source (another animal) just by measuring the sound pressure. We have also seen that the addition of direct and reflected sound waves may cause local maxima and minima in sound pressure at various distances from the sound source. It is therefore not possible for an animal to locate a sound source just by walking towards higher sound pressure levels.

We noticed before that gradients of wind speed, temperature and humidity are likely to exist close to the ground or to the surface of objects. The mean values of these micrometeorological parameters follow diurnal and seasonal patterns. Furthermore, temperature gradients are only stable, if the cool air is below the warmer air. On sunny days, however, the opposite is true. Due to convection currents, travelling turbulent eddies are formed. They scatter and attenuate the sound waves and cause the sound pressure and phase of the transmitted sound to fluctuate at the receiver. The frequency range of the amplitude fluctuations is about 0.5 to 20 Hz, and their magnitude may be quite large. Wiener and Keast (1959) found peak-to-peak fluctuations of the sound pressure level between 5 and 20 dB during the daytime. At night, the fluctuations are smaller (about 5 dB), but even these fluctuations are very large compared with the change of sound pressure, which an animal experiences when walking towards a distant sound source.

Scattering. The term reflection was used above for describing the redirection of a sound wave impinging upon a "large" surface. If the object is much smaller than the wavelength of sound, it will hardly affect the sound wave. (Physically, the situation is similar to the interaction between light and a virus particle in a light microscope). If the size of the object is of the same order of magnitude as the wave length, the sound (or light) will be redirected. Small objects will scatter the sound in all directions, while large objects will redirect the sound wave almost as a mirror. The redirection of sound from objects of intermediate size may be very complicated, and will depend in part on the shape of the object. The process of redirection will be referred to as scattering in this paper, though it is frequently called diffraction in the literature. The terminology is not quite fixed.

The interference of the scattered sound wave with the sound wave striking the object causes a change in sound pressure around the object. At the surface of a hard object facing the sound source the scattered wave is in phase with the incoming wave, so their pressures will be additive. If the object is large enough compared to the wavelength of sound, the total sound pressure at this region of the surface becomes twice that of the plane wave (6 dB more).

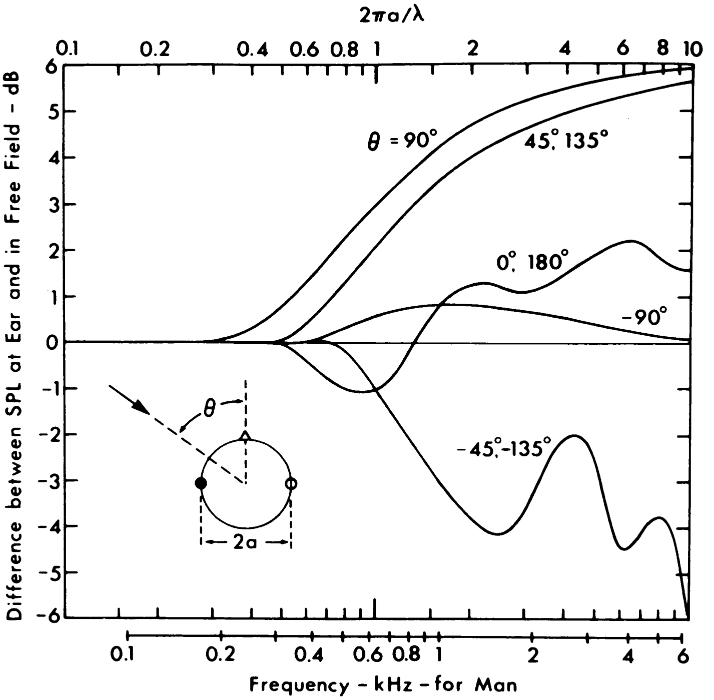

FIG. 9. Calculated transformation of sound pressure level from a free field to a simple ear (point receiver) on the surface of a hard spherical head of radius *a* as a function of $2\pi a/\lambda$ (where λ = wavelength of sound) for various values of azimuth θ of the incident plane waves. The frequency scale at the bottom is for a sphere of radius a = 8.75 cm. (From Shaw, 1974).

At other parts of the surface or at some distance away from the obstacle, the two sound waves are sometimes in phase and sometimes out of phase. So, the total sound pressure at a point in space may be larger, equal to, or smaller than that in the incoming sound wave. As the sound frequency is varied, a receiver placed at a fixed distance from an object will measure a number of minima and maxima of sound pressure. The fluctuation of the sound pressure with frequency can be calculated for hard objects of simple shape, but such calculations are not realistic for most of the obstacles found outdoors.

The differences in sound pressure caused by scattering around the body (head) is one of the main mechanisms responsible for directionality of hearing (Fig. 9). Scattering also seems to be very important in the attenuation of sound passing obstacles like vegetation (see below). A special case is the scattering of sound from inhomogenities in the medium (like the turbulent eddies mentioned in the previous section).

THE EFFECT OF VEGETATION

The effectiveness of plants for attenuating sound (noise) has been much debated. Several parameters contribute to the total attenuation observed outdoors, and it is very difficult to sort out the contribution of each parameter. In several experimental studies, the attenuation has been observed for sound travelling through a belt of vegetation and compared with the attenuation occuring over an equal distance without vegetation. The ground absorption is, however, not likely to be the same in the two situations. Further, the presence of the vegetation affects the microclimate (temperature, humidity, turbulence of the air, wind) and this again affects the attenuation of sound waves. Most investigators have ignored these parameters in their studies, and only few investigators control the directionality of their sound source (which is important in determining the amount of reflection from the ground). It is therefore not surprising that one can find very different values for the attenuation in a certain kind of vegetation in the literature.

The confusion over the attenuation caused by vegetation becomes even larger, when one compares the physical concepts used by various investigators. One may assume that the attenuation in the vegetation is due mainly to *multiple scattering* by tree trunks, branches and leaves. If this is true, then both theory and experiments demonstrate that the 'excess attenuation' (to be added to the attenuation caused by geometric spreading) should be about 6 *dB per distance doubled* (dd) (Meister and Ruhrberg, 1959; Meister, 1960). In the case of spherical spreading from a monopole source (attenuation 6 dB/dd) the total attenuation should be about 12 dB/dd. In contrast, if the attenuation in the vegetation is due mainly to *absorption*, one would expect the attenuation to be the geometric spreading plus a certain number of *dB per meter*. Most investigators assume that multiple scattering is a major contributor to the excess attenuation in vegetation, but still they express the measured excess attenuation as a certain number of dB per meter. Furthermore, some investigators derive their attenuation values from data collected at only two distances from the sound source. Such experiments do, of course, not allow the investigator to distinguish between attenuation caused by multiple scattering and absorption.

An excess attenuation caused mainly by multiple scattering is found at high frequencies (above 4 kHz) in dense crowns of conifers (Meister and Ruhrberg, 1959). This kind of attenuation is also

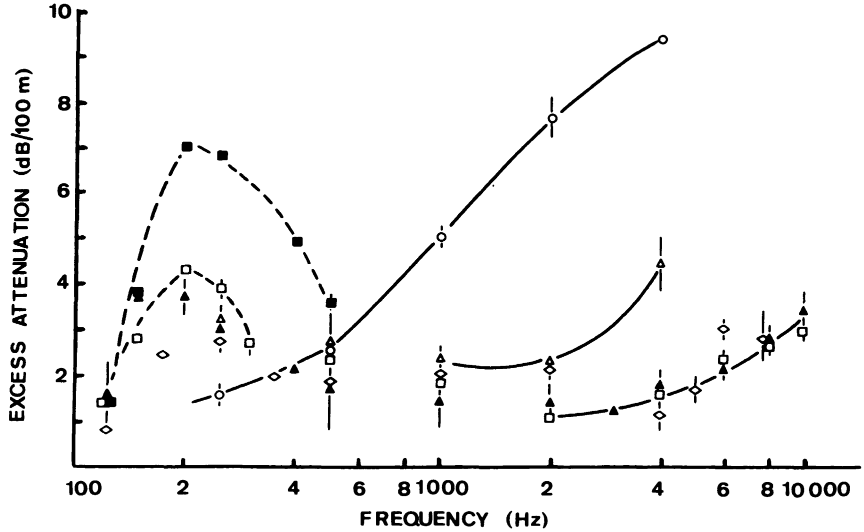

FIG 10. Excess attenuation in decibels/100 m for maize (o), hemlock (◇), pine measured at 30.5 m (■), pine measured at 61 m (□), brush in summer (Δ) and brush in autumn (▲). The source height was 1 m for the maize and 1.5 m for the hemlock, pine and brush. (Redrawn from Aylor, 1971,a).

observed in dense bushes. In contrast, close to the ground, and especially in high grass, these authors found excess attenuations mainly caused by absorption. Still other kinds of vegetation were found to have excess attenuation of a mixed origin.

Some investigators (e.g. Aylor, 1971b) have considered foliage to be a major factor in the attenuation of sound at rather low frequencies (0.5 - 1 kHz). Other authors find, however, that foliage has very little effect at frequencies below 2 kHz (Beck, 1965; Carlson et al., 1977). Beck (1965) investigated the sound attenuation properties of a large number of bushes and trees. He found that a maximum attenuation in the frequency range 2 - 11 kHz was produced by plants with big, hard leaves pointing perpendicular to the direction of the sound.

The total attenuation by bushes and trees reported in the literature varies considerably. Fig. 10 shows the results reported by Aylor (1971a). Most estimates of attenuation are in the range 10 - 30 dB/100m. Most investigators agree that the attenuation increases with frequency. The evidence for a possible minimum of attenuation around 1 - 2 kHz is discussed below.

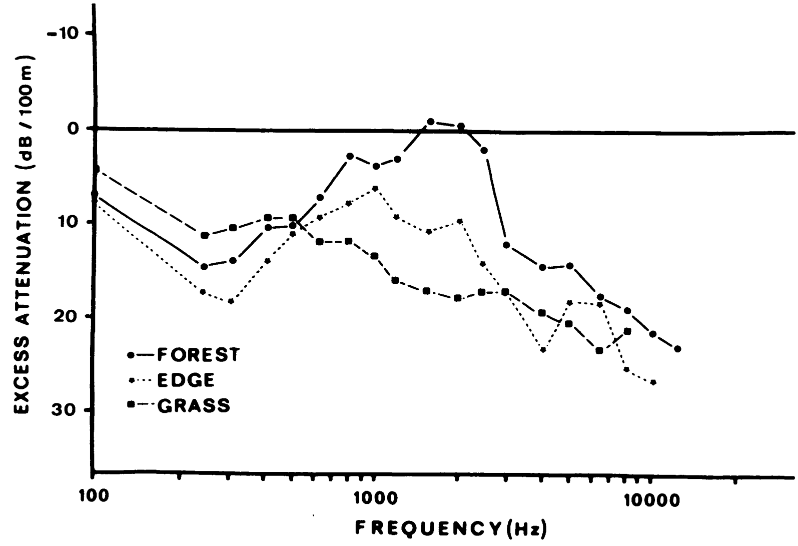

FIG. 11. Excess attenuation levels for pure tone sound propagation about 0.3 m above ground in forest, edge, and grassland habitats. (From Morton, 1975,changed).

BIRD SONG IN DIFFERENT HABITATS

A few attempts have been made to relate the characteristics of animal calls with the acoustical properties of different environments. Morton (1975) investigated the propagation of sound in tropical forest and grassland (Fig. 11) and measured the main frequencies in the songs of the birds living in these habitats (Fig. 12). In the forest he found the transmission to be a maximum around 1.5-2.5 kHz (Fig. 11), if the loudspeaker and microphone were placed about 0.3 to 1.5 m from the ground. At these frequencies the excess attenuation (that is the decrease in sound pressure after correction for spherical geometric spreading) was close to 0 dB. The maximum of transmission around 1.5-2.5 kHz in the forest was, however, not present at about 3 m from the ground, nor was a maximum apparent in the grassland. The edge of the forest appeared to have intermediate properties (Fig. 11). The frequencies emphasized in the song of birds living close to the ground in forests (Fig. 12, "low forest") also showed a maximum around 2 kHz and were significantly different from those of grassland and edge birds (Fig. 12). From these results Morton concluded that the "low forest" birds were well suited for communicating over long distances, while the birds in the other habitats were less capable of long distance communication. The birds in the "low forest" were found to have predominantly pure tonelike calls, whereas the grassland- and edge birds had both pure tone and modulated tone elements.

One unsolved problem is, why the grassland birds are not equally adapted to long distance communication in their environment. In the grassland the excess attenuation increases with fre-

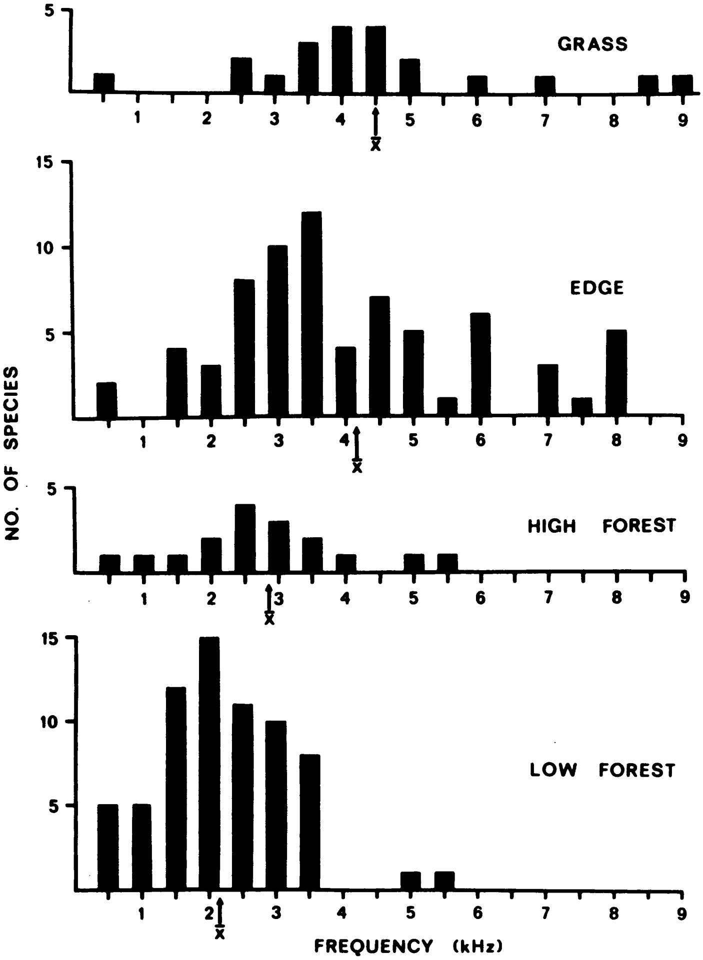

FIG. 12. Histograms showing the frequencies emphasized in the song of bird species living in different habitats. X̄ indicates the mean frequency for each group. From Morton, 1975.

quency (Fig. 11), so one would expect the birds to use very low frequencies. However, this is not the case (Fig. 12). Morton suggests that temporal patterns carried by broad frequency bands provide a more efficient means of communication in open habitats than do pure tone signals, since such signals should be better adapted for preserving the specific information in the presence of shadow-zones and air turbulence. This is a very interesting idea, which may also be applied to grasshopper and bushcricket songs (see below). The validity of this hypothesis should be investigated further.

A central point in Morton's argument is that the selection operating during the evolution of animal calls has favoured communication over as great a distance as possible. This may be true for species which need to have low population densities. But, as pointed out by Marler (1955), several other features of the calls may be important (e.g. the calls should be conspicuous to conspecific animals, but inconspicuous to predators or prey, and the calls should also differ distinctively from the song of other, sympatric, species).

If we now turn to the properties of the auditory system in birds, one might perhaps expect the ear to be most sensitive at the main frequency of the conspecific song. This is, however, not always so (Konishi, 1970). It is hardly surprising that such a connexion does not exist. The sense of hearing is used for many purposes in birds, and the properties of the ear are not determined by just one factor. Probably, the same will appear to be true for the properties of the song of birds. In contrast, in many frogs and insects the main function of the auditory system may be the detection of conspecific calls. So, in these animals one may expect a closer correlation between the acoustical properties of the call and those of the auditory system.

Morton's results are very interesting, but rather different results can be found in the literature. Some studies support the idea of a "sound window" around 1-2 kHz close to the ground (Aylor, 1971a; Carlson et al., 1977), but other studies do not (Eyrings, 1946; Wiener and Keast, 1959). Furthermore, the measurements performed by Embleton (1963) show this maximum only at short distances from the sound source (0-20 m), and not at greater distances. Finally, the "sound window" has been found not only in forests, but also in open habitats (Marten and Marler, 1977; Marten et al., 1977).

The crusial question is, whether this disagreement is due to real differences between the habitats investigated, or to the differences between the apparatus and experimental design in the investigations. In a properly performed investigation the sound power produced by the loudspeakers and their directionality should be known from measurements performed in the laboratory. The attenuation of sound with distance should be measured with at least three microphones placed at different distances from the sound source. Further, the temperature and wind gradients should be measured. So far, no study has been performed, in which all the major sources of error have been controlled.

The directionality of the loudspeaker affects the amount of reflection of sound wave (from the ground or as multiple scattering). Some investigators try to estimate the power output of the loudspeaker by means of a microphone placed several metres away. This is, of course, not possible. For example, in one study (Marten and Marler, 1977) a microphone was placed 2.5 m from the loudspeaker and another microphone about 100 m away. The difference in the reading of the two microphones was then used to calculate the "excess attenuation per 100 m" (by subtracting the attenuation due to geometric spreading). The published attenuation curves clearly demonstrate the presence of fluctuations in sound pressure at the 2.5 m microphone similar to those illustrated in Fig. 3. Furthermore, only two microphones were used, and therefore it is not possible to know, whether the attenuation was due to absorption (dB/m), to multiple scattering (dB/dd) or to something in between (see the section on vegetation above).

THE CRICKET AND THE GROUND IMPEDANCE

The males of field crickets sing their "calling song" while on the ground. The song is heard by other crickets, which are also on the ground. Nocke (1971,1972) measured the sound pressure level produced by a singing male *Gryllus campestris* L. to be around 102 dB at 5 cm distance. The average threshold of hearing at the same frequency (4 kHz) was 44 dB. From these values he calculated a theoretical range of communication of 42 metres, assuming the attenuation to be due only to (spherical) geometric spreading (attenuation 6 dB/distance doubled). We have already seen that the range may be much less, if temperature or wind gradients are present. The acoustical properties of the ground itself may, however, cause further attenuation. In the following we shall examine the propagation of sound waves close to the ground. It will be demonstrated that the actual range is considerably smaller than that calculated by Nocke, even when temperature and wind gradients are absent.

Most of the existing evidence shows that propagation of sound over the ground is adequately described by treating the ground as a locally reacting surface, thus neglecting wave propagation in the ground itself (Piercy et al., 1977). In the habitats of field crickets, the grassy ground surface is behaving as a locally reacting porous medium. In terms of impedance this means a mixed stiffness-resistant element (Embleton et al., 1976).

In the description of reflection (above) we noticed that the magnitude and phase angle of the reflected wave depend upon the impedances of the two media (Z_1 and Z_2) and upon the grazing angle (ψ). For a plane wave the relationship is (Piercy et al., 1977):

$$R_p = \frac{\sin \psi - Z_1/Z_2}{\sin \psi + Z_1/Z_2}$$

where R_p is the amplitude reflection coefficient. Z_1, Z_2 and ψ are shown in Fig. 2. Z_1/Z_2 can be ignored, if the ground is hard, and if the grazing angle is rather large ($Z_2 >> Z_1$ and $\sin \psi >> Z_1/Z_2$). The phase change on reflection will then be almost zero. For grounds similar to the habitats of crickets and at 4 kHz (the frequency of the calling song), however, both the resistive and stiffness (real and imaginary) components of Z_2 are only a few times larger than Z_1 (see Fig. 8 in Embleton et al., 1976). This means that at small grazing angles (the sound wave travelling almost parallel to the ground) R_p will be negative, and the reflected wave will be almost out of phase with the incoming wave. So, for crickets on the ground the waves r_1 and r_2 (Fig. 2) will tend to cancel each other, even though their path lengths are about equal.

In practice, this means that for plane waves a path close to the ground represents a *forbidden mode of propagation* (Piercy et al., 1977), except at close distances. The magnitude of the "shadow zone" close to the ground may reach values around 30 dB as the sound propagates outwards from the sound source. Consequently, the range of communication of the field cricket in the absence of temperature- and wind gradients is likely to be about 10 times lower than the value calculated by Nocke, if one allows for the magnitude of the shadow zone. The field measurement of cricket song performed by Popov et al. (1974) show that the sound pressure close to the ground does in fact fall off much faster than expected from geometric spreading alone. Unfortunately, the wind- and temperature gradients were not measured in this study.

The sound pressure likely to reach a listening cricket at a distance of, for example, one metre from a singing cricket is very difficult to calculate. At close range the sound waves are not plane, but spherical. In equations assuming local reaction and homogeneity of the ground, the interaction between a spherical wave and the ground impedance gives rise to a *ground wave*. These assumptions have been questioned by Carlson et al. (1977), but the existence of the ground wave seems well supported by experimental observations (Donato, 1976; Embleton et al., 1976).

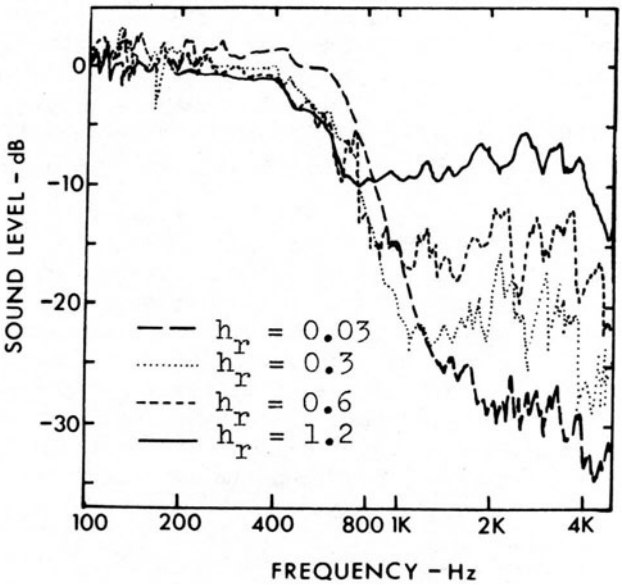

FIG. 13. Propagation of sound over grass. The sound source was 0.03 m from the ground, and the receiver at heights (h_r) between 0.03 and 1.2 metres from the ground. The horizontal distance was about 4.6 m. The reference sound level is that expected from geometric spreading (6 dB/dd) alone. From Embleton et al., 1976 (changed).

The range of the ground wave depends upon the frequency, the grazing angle, and the impedance of the ground. For a constant grazing angle and impedance, the ground wave propagates a certain number of wavelengths away with only the attenuation due to geometric spreading (6 dB/dd). Above this range, however, the ground wave suffers an additional 6 dB/dd attenuation. The ground wave therefore behaves as a *low-pass filter*. Fig. 13 shows the result of measurement over grass, where the distance between the sound source (3 cm over ground) and the receiver (3 to 120 cm over ground) was about 4.6 m. Frequencies below 500 Hz are seen to suffer only the attenuation expected from geometric spreading, whereas higher frequencies sustain an excess attenuation. The attenuation above 500 Hz increases with frequency and decreases with the distance from the ground.

STRATEGIES FOR SOUND COMMUNICATION

It is interesting to compare Fig. 13 with Fig. 3, where both the sound source and the receiver were about 1.2 m above ground.

We can use these results to speculate about the optimum strategy for sound communication in terrestrial animals. From Fig. 13, one can see that animals on the ground may communicate over long distances, if they use low frequencies. This is possible for large animals. Small animals like insects are, however, unable to produce much sound below a few kHz (see Michelsen and Nocke, 1974).

With frequencies of several kHz, the range of communication is limited, if both the singing and the listening animal is on the ground, although the range may be several metres, if the animal produces very loud sounds. The intensity of the sound signals is limited by the muscle power available, but higher intensities may be obtained by means of a resonator. For example, the cricket produces long, pure tones of considerable intensity by driving the sound emitting structure (a part of the wing called the harp) at its resonance frequency. Molecrickets go one step further. They use a horn-shaped burrow for "amplifying" their calls (Bennet-Clark, 1970).

The use of resonators (mechanical oscillators, horns) is an efficient way of producing large sound intensities. The "price" for this solution is that the animals are limited to the resonance frequency (-ies) of the resonator. They cannot signal their message

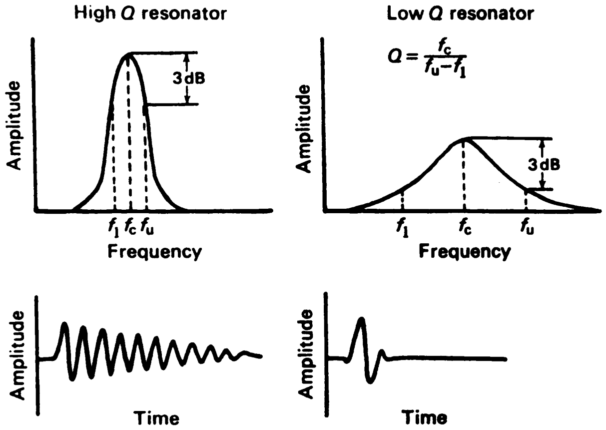

FIG. 14. The behaviour of a lightly (left) and a heavily (right) damped mechanical oscillator. The upper figures show the frequency response of the two systems. The lower figures show the impulse response (the waveform produced when the oscillator is excited by a sudden shock of broad band energy). The degree of damping is often indicated by the Q-value (a high Q means a small amount of damping). From Sales and Pye, 1974.

by means of, say, frequency sweeps. Furthermore, lightly damped resonators are mechanically "slow" systems (Fig. 14). Such systems cannot be used for transmitting rapid modulations (Michelsen and Nocke, 1974). The message communicated by the calling song of the field cricket is rather simple (I am here, I belong to species X, females are welcome, males are not).

Many species of frogs, toads and birds also produce rather pure tone sounds, which are subjected to a slow amplitude modulation (1-20Hz). The parameters available for carrying the information are limited to frequency and (slow) rhythms. Since the frequency band is limited to one to two decades in small animals (lower frequencies cannot be produced efficiently; higher frequencies do not travel far enough), only a limited number of species can coexist in the same habitat. The use of slow amplitude modulation for carrying information may also be limited by air turbulence, which causes amplitude modulations of similar frequencies (see above).

Some insects (shorthorned grasshoppers, most bushcrickets) are non-resonant singers. The primary vibration is, as in the cricket, produced by the stridulatory organ, where a scraper on one part of the body (leg or wing) hits a series of teeth (the "file") on another appendage. The sound emitting structure (parts of the wings) do not have any lightly damped resonances and generally appear to have a large frictional damping. (The degree of damping can be estimated from the shape of the sound impulses produced by the impacts of the scraper on individual teeth in the file). The sound emitted from such a system is a broad-band noise of rather low intensity. But the system is much faster than the lightly damped, highly tuned sound emitter in the cricket. This means that the animals can use faster rhythms for communication, and thus be undisturbed by the lower-frequency amplitude-variation due to atmospheric turbulence. The "price" is the lower sound intensity, which means a shorter range of communication, and which forces the animals to have higher population densities.

The range of communication may become much greater, if the singing animal and/or the listening animal climbs up the vegetation. Many grasshoppers sing about half a meter above ground, while bushcrickets are often one, two or more metres from the ground. But, as shown in Fig. 3 the price for this longer range of communication may be a large and variable frequency filtering of the sound signal. Unfortunately, very little is known about the magnitude of this frequency filtering in natural habitats.

For many years the insects were considered to be unable to discriminate sound frequencies, and the information was thought to be coded only as amplitude modulations of the carrier sound (Pumphrey, 1940). In 1965 Andrej Popov (Leningrad) and I independently found that the ear of the migratory locust (a short-horned grasshopper) is able to perform some frequency discrimination. Further studies demonstrated that the four anatomical groups of receptor cells have different frequency sensitivities (Michelsen, 1971a; Römer, 1976) and revealed the physical basis for the frequency discrimination (Michelsen, 1971,b). Later, a less detailed discrimination, based on only two groups of receptor cells, has been found in crickets (Nocke, 1972) and molecrickets (Zhantiev and Korsunovskaya, 1973). The physical mechanism has been studied in the latter case (Michelsen, 1978). A much finer frequency discrimination has been found in bushcrickets (Rheinlaender, 1975). Here, 33 receptor cells are situated in a serial arrangement, and their accessory structure become progressively smaller from the proximal to the distal end of the receptor organ. The frequency of maximum sensitivity differs among the cells, probably in a systematic way corresponding to the anatomical arrangement.

Until recently, recordings of insect song were studied (and published) with a time scale, which was suitable only for demonstrating slow amplitude modulations. Finer details in the song did not attract interest, partly because such details are often blurred in tape recordings (either for technical reasons, or because the two sound producing mechanisms in short-horned grasshoppers may be playing slightly different songs, see Elsner, 1974). Elsner's study, however, suggested that specific information may be signalled as changes in the repetition rate for the very short impulses, which are produced during stridulation. This theory will be considered in the following section.

IMPULSE RATE AS CARRIER OF INFORMATION

The song produced by males of the short-horned grasshopper *Omocestus viridulis* L. was studied by Elsner (1974). He noticed that the song of one-legged males contains more details than songs from normal males (in which the two legs do not follow each other precisely, thus leading to the aforementioned blurring). In particular individual impulses lasting about 0.2 msec could be observed (Fig. 15,B). These impulses are caused by the impact of the "scraper" upon a tooth in the "file" of the stridulatory organ. A plot of the time intervals between the impulses demonstrated large and very fast sweeps of impulse frequency (Fig. 15,C). For about half of the song the impulse rate is low (around 300 Hz), but at the end of each chirp the impulse rate reaches 8 kHz. At first sight, such high impulse rates are not likely to be of much interest, since the ears are not fast enough to respond to the individual impulses (the "flicker fusion frequency" for clicks is about 300 Hz; Michelsen, 1966). There is, however, another possibility, which I proposed some years ago (in Elsner, 1974): The impulse frequency could be received by the ear as a frequency, that is, it could be modifying the frequency spectrum of the song, and the grasshoppers could use their ability for frequency discrimination to detect spectral features caused by the impulse rate. This hypothesis has now been confirmed in behavioural experiments (Skovmand and Pedersen, 1978).

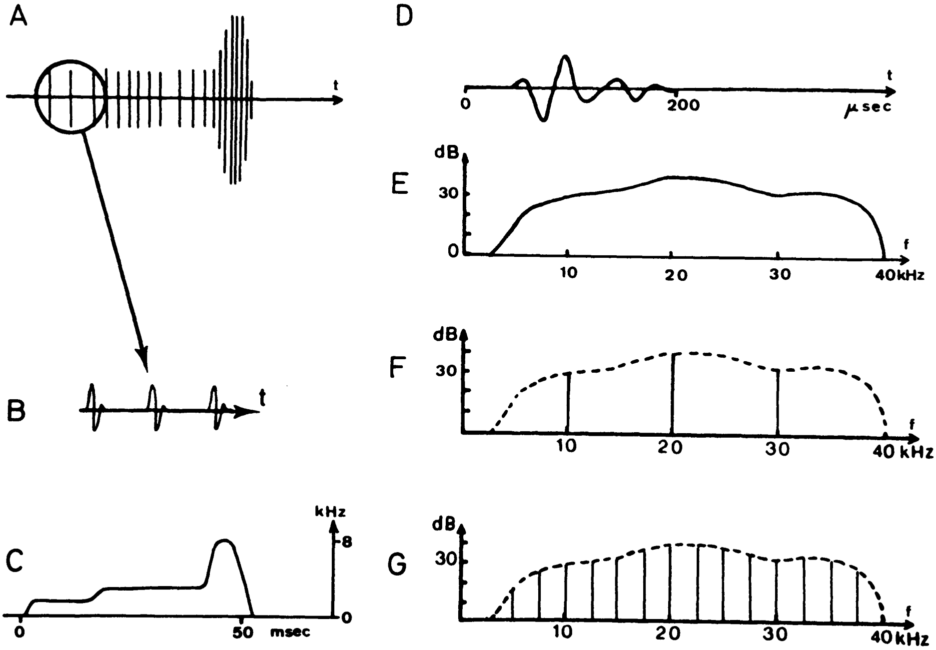

FIG. 15. Analysis of the song of the short-horned grasshopper *Omocestus viridulus*. A. Schematic diagram of one chirp in the song. B. Individual impulses in the chirp. C. The impulse rate during a chirp (schematically). The time scale applies to A and C. D. An impulse shown in more detail. E. One impulse has a continuous frequency spectrum. F and G. The frequency spectrum of a series of impulses with constant repetition rate consists of a number of discrete frequencies (lines). The intensity of each of these frequencies is determined by the spectrum of the individual impulse. The frequency of the lines depends upon the impulse repetition frequency (10 kHz in F, 2.5 kHz in G). From Skovmand and Pedersen, 1978 (changed).

Physically, the situation is rather complicated. The spectrum of a series of impulses (Fig. 15,F-G) differs from the spectrum of one impulse (Fig. 15,E) in being a line spectrum, which is contained in the (broad) spectrum of the single impulse. If the impulse repetition is quite regular, the spectrum of a series of impulses will consist of some discrete frequencies. The lowest of these frequencies is the impulse repetition frequency, and the other frequencies are higher harmonics of this frequency. If the impulse repetition frequency is, for example 5 kHz, the frequency spectrum will have components at 5, 10, 15, 20, -- kHz. When the impulse repetition frequency varies during a chirp, the spectral lines will move.

This is a very complicated pattern of FM-sweeps, but apparently the simple frequency discriminating mechanism of the grasshopper auditory system is able to extract the necessary information. This was shown in experiments, in which behaviourally receptive females were given the choice between various artificial songs (Skovmand and Pedersen, 1978). The songs were generated on a computer in such a way that the individual parameters of the song could be varied and controlled. The variation in (root mean square) sound pressure amplitude appeared to be the most important parameter, but signals with "correct" impulse rate modulation were significantly more attractive than signals without this feature.

These experiments show that frequency information can be coded as the repetition of very short (0.2 msec) impulses. The frequency spectrum of the individual impulses is very broad (1-40 kHz). This means that a considerable part of the impulse will get through the "environmental filter", even in environments with a substantial frequency filtering. No information is presently available about the magnitude of environmental filtering in the habitats of short-horned grasshoppers. From the behaviour one gets the impression of an enormous redundancy in the signal. The males may court a female for many minutes, repeating their chirps several thousand times.

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