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Physical Constraints on Acoustic Communication in the Atmosphere: Implications for the Evolution of Animal Vocalizations

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Summary. 1. Acoustic communication requires not only detection of the signal but also discrimination of differences among signals by the receiver. Attenuation and degradation of acoustic signals during transmission through the atmosphere will impose limits on acoustic communication. Attenuation of sound during atmospheric transmission results primarily from atmospheric absorption, ground attenuation, scattering of a sound beam, and deflection of sound by stratified media. For maximum range of detection, therefore, animals should favor optimal positions in their habitat and optimal weather conditions. Frequency-dependent attenuation seems not to differ consistently among major classes of terrestrial habitats, such as forests and fields. Increased scattering of higher frequencies from vegetation in forests is in part matched by scattering from micrometerological heterogeneities in the open.

2. In addition to frequency-dependent attenuation, two kinds of degradation during atmospheric transmission will limit a receiver's ability to resolve differences among acoustic signals: the accumulation of irregular amplitude fluctuations from nonstationary heterogeneities, often atmospheric turbulence, and reverberation. Both types of degradation affect temporal patterns of amplitude or intensity modulation more than patterns of frequency modulation. Both effects should increase with carrier frequency, as they depend on the relationship between wavelength and the dimensions of scattering heterogeneities. Irregular amplitude fluctuations are more severe in open habitats and primarily mask low frequencies of amplitude modulation; reverberations are more severe in forested habitats and primarily mask high frequencies of amplitude modulation and rapid, repetitive frequency modulation. This difference between forested and open habitats could explain previous reports that birds in the undergrowth of tropical forests avoid rapid frequency modulation in their long-range vocalizations.

3. Maximum range of detection is probably not the primary selection pressure on many animal vocalizations, even for territorial advertisement, except perhaps in tropical forests. Instead, acoustic signals might incorporate features that degrade predictably with range to permit a receiver to estimate

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the signaler's distance. Future investigations might explore the propagation of animal vocalizations in relation to the usual spacing of animals in their habitat. Features that encode different kinds of information, such as individual and species identity, might propagate to different distances.

4. Measurements of the transmission of sound in natural environments have often not controlled several important parameters. First, the effects of ground attenuation and scattering are not linear with range; consequently measurements of excess attenuation over different ranges in the same environment might differ. Second, the directionality of speakers and microphones will affect measurements of attenuation and reverberations in scattering environments. Third, as stationary waves shift with frequency, any single microphone placement will lie in a null for some frequencies and in a maximum for others.

Introduction

A review of sound transmission in the atmosphere will help to clarify the adaptations for acoustic communication by animals in terrestrial environments. The distance over which an acoustic signal carries information depends on the amplitude and structure of the sound at the source, the characteristics of the medium and its boundaries, and the receiver's mechanism for detecting the signal. Our task is to specify the attenuation and degradation of sound during transmission as a function of the properties of the sound and the characteristics of the medium and its boundaries.

Morton (1970, 1975) and Chappuis (1971) have pioneered the study of sound propagation in terrestrial environments with a view to understanding the evolution of acoustic communication in the atmosphere. Their principal concern was the attenuation of sound as a function of frequency and the general nature of the vegetation in the communication channel. Waser and Waser (1977), Marten et al. (1977), and Marten and Marler (1977) have pursued this line of research. Our own interests in this problem arose from a separate question: the consequences of an accumulation of irregular fluctuations in amplitude and reverberations during the transmission of acoustic signals (Wiley, 1976; Richards and Wiley, in prep.).

Acoustic engineers and physicists have placed primary emphasis on the wave properties of sound and attenuation during transmission. Practical interests in sound transmission in the atmosphere have focused on the use of vegetation and other barriers to attenuate undesirable noise (Lyon, 1973) and on military applications for locating and detecting sounds. There has been little systematic experimentation on atmospheric transmission of sound in relation to signal detection and discrimination. As a result, there is no convenient review of these problems for biologists interested in animal communication with sound in terrestrial environments.

We have restricted our discussion to atmospheric communication at sonic frequencies. The physical properties of sound transmission in water, coherently reviewed elsewhere (Tolstoy and Clay, 1966), differ substantially from atmospheric transmission. Griffin (1971) discusses some special features of ultrasonic transmission in relation to echolocation and communication by animals.

Before considering the atmospheric transmission of sound, a brief discussion of some general principles of communication will clarify basic questions about the transmission of signals.

I. Signal Discrimination as a Basic Process in Communication

Communication, in the most fundamental terms, is an association between a signaler's and a receiver's behavior as a consequence of a signal, a specific pattern of energy, transmitted between them (Shannon and Weaver, 1949; Raisbeck, 1963; Cherry, 1966; Altmann, 1967; Klopfer and Hatch, 1968; Schleidt, 1973). The information contained in a signal results from the association of each signal with a particular referent, which could include the identity, behavioral tendencies, or external circumstances of the signaler. The information in a signal at the source (broadcast information) is always greater than the information obtained by a receiver (received information). The received information is the reduction in the receiver's uncertainty about the possible referents as a consequence of receiving the signal. While broadcast information depends on the diversity of signals and their associations with referents, received information depends on the receiver's ability to discriminate signals from other perturbations of its sense organs that comprise background noise, to discriminate differences among signals, and to decode the associations between signals and possible referents. The signaler thus produces distinguishable variants or categories of signals associated with referents, and, for effective communication, the receiver must discriminate these differences and decode them.

For effective communication, when the received information approaches the broadcast information, it is not enough for a receiver simply to detect a signal. It must discriminate the relevant variations in signal structure. Noise is any error in associating variation in received signals with variations in broadcast signals. Thus anything that hampers the receiver's ability to discriminate differences among signals or to discriminate signals from background perturbations constitutes noise.

Noise is a property of the communication channel. Although in animal communication the nature of the channel differs strikingly according to the sensory modalities employed, a general definition of channel is the aggregate of all paths by which the energy of the broadcast signal is transmitted to the sensory receptors of the receiver.

Errors of reception are conveniently separated into two types: errors in detecting signals; and errors in discriminating among variant signals. The first error involves the receiver's failure to discriminate between a perturbation of its sense organs caused by a signal in the channel and other similar perturbations of its sense organs. This error becomes more likely when the signal power is low, so that the perturbation of sense organs by a signal approaches the perturbations from other sources (low ratio of signal power to noise power), and when the structure of signals closely resembles the structure of other perturbations. Attenuation and degradation of a signal during transmission through the channel make errors of detection more likely.

Random degradation of signals during transmission also increases the second kind of error, the receiver's errors in discriminating significant variations in signals. For signals that propagate through space, attenuation and degradation of signals will normally increase with increasing distance between the signaler and the receiver. The receiver's ability to detect signals and discriminate relevant variations will thus decrease with distance from the signaler.

II. Transmission of Sound Through the Atmosphere

In this section a review of the physical principles of atmospheric transmission of sound will identify the determinants of attenuation and degradation of acoustic signals under different environmental conditions. We intend to provide a guide for biologists interested in acoustic communication by animals, not a formal statement of the relevant physics. Helpful treatments of acoustical physics, including fundamentals, are Kinsler and Frey (1962), Wood (1966), Morse and Ingard (1968), and Beranek (1971). After this review, we shall summarize the sources of attenuation and the kinds of degradation in acoustic signals during propagation through the atmosphere and consider their consequences for acoustic communication.

1. Spherical Spread

The energy in a sound wave consists of approximately elastic expansion and compression of the gases in the medium. In isotropic media, for a simple source (dimensions of the vibrating source much less than the wavelength of sound produced) and for radii much larger than one wavelength, surfaces of equal density of acoustic energy are spherical. The intensity of a sound wave (its power density) is the average rate of energy flow per unit area perpendicular to the direction of propagation, or the density of energy multiplied by the velocity of sound (Wood, 1966: 295). Because the density of energy at a distance r from the source decreases with the surface area of a sphere with radius r, intensity varies inversely with r^2, which corresponds to a decrease of 6 dB for each doubling of distance ($10 \log (2r/r)^2 = 6$ dB). Sound pressure level (SPL) is an estimate of relative intensity based on a measurement of RMS sound pressure (Kinsler and Frey, 1962: 123; Wood, 1966: 290, 295). For spherically diverging waves, SPL thus decreases by 6 dB for each doubling of distance.

Most studies of sound transmission in natural environments subtract the effects of spherical divergence from their determinations of attenuation. The resulting attenuation is usually termed excess attenuation. Some authors, in contrast, subtract *both* spherical divergence and molecular absorption (Wiener and Keast, 1959; Aylor, 1971; see below) in order to obtain excess attenuation.

Acoustic communication by animals rarely involves spherical spread of sound through isotropic media. Sounds produced near a plane boundary, even in an isotropic half-space, would only diverge spherically if the boundary were completely absorbing. As we review below, sound propagation may differ substantially from spherical divergence for other reasons as well.

2. Absorption

Absorption, as the term is used in acoustics, includes (1) the dissipation of sound energy as other forms of energy either in the molecules within the medium itself or in substances that form the boundaries of the medium and (2) the reduction of sound energy in a particular medium by transmission into other media at the boundaries.

The dissipation of acoustic energy by the transmitting medium, air or other gases, has received intensive treatment by acoustic physicists (Kinsler and Frey, 1962, Chapter 9). Absorption in the transmitting medium falls into three categories: viscous losses, losses by heat conduction, and molecular absorption. Losses from viscosity and heat conduction are sometimes termed the classical component of absorption, which increases in direct proportion with temperature and with frequency squared. The classical component of atmospheric attenuation at 8 kHz and 20° C approximates 0.02 dB per meter. Molecular absorption depends on the chemical composition of the medium and in atmospheric transmission is affected in particular by the percent water vapor. For frequencies below 8 kHz except in extremely cold or dry air, attenuation increases approximately linearly with decreasing humidity (Griffin, 1971). For example, total atmospheric attenuation of an 8 kHz sound at 20° C and 1% water vapor (approx. 40% relative humidity) reaches 0.2 dB per meter. At 20° C and 2.4% water vapor (100% relative humidity), total attenuation approximates 0.07 dB per meter.

Absorption at the boundaries of the medium results from the transmission of acoustic energy to the boundary medium in addition to dissipation of acoustic energy as heat or molecular processes. The events are so complicated that empirical measures of absorption by boundary substances are usually required. A sound wave transmitted into a solid may propagate effectively only at right angles to the surface, or refract into two waves, longitudinal waves and transverse shear waves, or refract in the familiar way of waves passing from one fluid to another (Snell's law). In architectural acoustics, boundary substances are assigned absorption coefficients by determining the change in reverberation time in a room as a result of adding a known area of the material to the walls (Kinsler and Frey, 1962: 424). An ideal absorbing surface reflects no sound.

Sound waves can induce oscillations in objects in contact with the medium. When a driving force, such as sound, induces oscillations in a mechanical system, the power supplied to the system is dissipated as work against frictional forces. Such induced oscillations in objects exposed to sound waves thus dissipate acoustic energy in the medium. The mass and compliance of a mechanical system determine a resonant frequency at which the average power supplied to the system by the driving force is a maximum (Kinsler and Frey, 1962: 22–26). The vibration of branches and trunks of trees act as forced oscillators with resonant frequencies between 200 and 2000 Hz (Embleton, 1963). This process, however, is insignificant in natural environments. Embleton's calculation of the attenuation of sound in this band owing to resonant absorption by a plantation of pine indicated that resonant absorption accounted for only 10^{-4} dB/m attenuation, far less than the precision of measurements in natural environments. Embleton's results from transmission experiments showed appreciably greater excess attenuation at frequencies below 1000 Hz than at medium frequencies between 1000 and 2000 Hz. Because his speaker was one meter above ground, ground attenuation might well explain the higher attenuation at low frequencies (see below). Aylor's (1971) calculations indicate, in addition, that acoustic energy is not dissipated appreciably by heat conduction into vegetation or oscillations of foliage against the viscosity of air.

3. Refraction, Reflection, and Diffraction

These phenomena pertain to the propagation of waves at or near interfaces between media of different characteristic impedences. The characteristic impedence of a substance $\rho_0 c$ ($\mathrm{N \cdot s/m^3}$, mks rayls), also termed specific acoustic impedence or resistance, is the product of the average particle density of the substance, ρ_0, and the velocity of sound in the substance, c (Kinsler and Frey, 1962: 122). Refraction is the deflection of waves as they move between media of different $\rho_0 c$; reflection is the return of waves from a boundary between media of different $\rho_0 c$; and diffraction is the deflection of waves in a medium at the edge of an object of different $\rho_0 c$. In addition, students of wave propagation refer to scattering, the complicated deviation of waves by refraction, reflection and diffraction from objects entirely within a medium of different $\rho_0 c$.

All of these phenomena depend strongly on the relationship between the wavelength of sound and the dimensions of the boundary between zones of different characteristic impedence. Objects much smaller than a wavelength produce little refraction, reflection, diffraction or scattering of waves (Morse and Ingard, 1968: Chapter 8). Such objects if numerous enough might change the acoustic properties of the medium but do not deflect the propagation of sound waves. When wavelength approximates the dimensions of an object in the medium, sound fields are complicated and irregular functions of wavelength, depending on interactions of the effects of diffraction and reflection. Refraction, reflection, and diffraction become easily separated properties of transmission at surfaces that are large in relation to wavelength.

Spatial Variation in the Sound Field. Reflections from objects or surfaces within or on the boundaries of the medium have two effects that introduce spatial heterogeneity into the sound field. First, the waves arriving at any point in the sound field have traveled by different paths, depending on the complexity of surfaces and reflections, and thus can interfere constructively or destructively, depending on differences in the lengths of the paths and wavelength. The net result of such interference at one point will often differ from that at another point even nearby.

In addition, reflection establishes a spatial pattern of interference between the incident wave and the reflected wave. When the wavelength of the incident sound remains constant for a sufficient period this spatial pattern of interference remains stationary for this period and is termed a standing or stationary wave. The spatial pattern of sound intensity depends on the wavelength of the sound. The minimum time required to establish a stable pattern of interference at a specified distance from a reflecting surface depends on the speed of sound in the medium. For a distance of 1 m in the atmosphere (in which the speed of sound approximates 330–345 m/s for temperatures between 0 and 20° C), the minimum time required is about 0.06 s. Briefer sounds would not establish such interference patterns.

It is a common experience during experiments on the transmission of pure tones in natural environments to find that slight shifts in the location of a microphone result in substantial changes in the level of the received sound. Such differences in level associated with different locations would result from spatial patterns of interference as a consequence of reflections. Refraction and diffraction from heterogeneities in the atmosphere will also generate spatial patterns of interference and consequently stationary patterns of intensity (Chernov, 1960). To reduce the effects of standing waves on received levels of sound, some experimenters have broadcast frequency sweeps or warbling, rather than constant, tones or octave-wide bands of white noise; these procedures yield received intensities averaged over a band of frequencies.

If objects in the environment, such as branches or leaves, or the source and receiver, moved slowly (with periodicities of 0.1 s or greater) the resultant standing waves from a constant source would also shift and add slow temporal fluctuations to the received signal at one location. This situation, however, involves nonstationary heterogeneities, which are discussed below. Stationary heterogeneities in a medium establish stationary patterns of intensity in space.

Reflection also distorts the spectrum and amplitude patterns of incident signals. The reflected signal acquires a frequency-dependent aftereffect (Tolstoy and Clay, 1966: 47; Morse and Ingard, 1968: 264). Such frequency-dependent propagation is termed dispersion. As a result, a pulse is reflected with more gradual onset and termination.

Stratified Media. When reflecting or refracting layers are arrayed parallel in a sound field, these surfaces act as wave guides. Sound produced between two such surfaces would reflect from the surfaces and propagate in the medium between them. An approximation to this situation might arise in natural circumstances, for instance, in the space between the ground and the canopy of a forest, providing neither the ground nor the canopy is totally absorbing. As we shall see below, certain temperature and wind gradients might also reflect sound waves and thus contribute to the formation of wave guides for sound propagation.

The simplest consequence of propagation in a wave guide is the absence of spherical divergence of sound energy. Experimental measurements of sound attenuation in forests have sometimes yielded 'negative excess attenuation' for certain frequencies (Morton, 1975; Waser and Waser, 1977). In other words, sound intensity decreases less than in proportion to the inverse square of range. A wave-guide effect under a forest canopy or between strata of vegetation might explain such phenomena. Because the strata of vegetation in natural environments never create regular, completely reflecting surfaces, natural environments will never form ideal wave guides. The effects of irregular and discontinuous boundaries would increase attenuation in a wave guide (Tolstoy and Clay, 1966: Section 6.9).

Sound propagation in wave guides has another important feature (Tolstoy and Clay, 1966: Chapter 2; Morse and Ingard, 1968: Section 9.2). The waves reflected from the two boundaries of the wave guide establish interference patterns within the wave guide. The presence of a second boundary permits only a limited set of values of wave number (oscillations/m) in the direction perpendicular to the boundaries. The number of permissible values increases as the distance between boundaries increases. Owing to these constraints on perpendicular wave number, only certain angles of incidence at the boundaries are allowed for any one frequency of sound within a wave guide. The horizontal phase velocity (the propagation of points of constant phase along the length of the wave guide) thus varies with frequency: horizontal propagation in a wave guide is dispersive. The practical consequence of such dispersive propagation is the alteration of transients. The propagation of pulses in a wave guide is attended by a spreading of the onsets and terminations of the pulses.

A continuously stratified medium will also reflect and refract waves traveling obliquely with respect to the stratification. In the atmosphere, temperature and wind gradients often produce continuous changes in the velocity of sound and characteristic impedence of the medium with height above the ground. Sound traveling from a zone of cooler air into a zone of warmer air, where the velocity of sound is higher, is refracted and reflected along a curved path back into the zone of cooler air. The theory of reflection in continuously stratified media is summarized by Tolstoy and Clay (1966: 28–33).

This effect produces a shadow zone for sound propagation above the ground and vegetation on sunny days. The sun warms the ground or vegetation and thus indirectly heats the air closest to the ground or vegetation. This process establishes a temperature gradient with warm air close to the ground and progressively cooler air higher. Such temperature gradients are established on sunny days above the canopies of forests and above the vegetation of open fields. Sound generated above the surface of the vegetation is then refracted and reflected upward, which results in greatly diminished transmission of sound to even moderate distances horizontally above the vegetation. Wiener and Keast's (1959) measurements show that excess attenuation increases by 25 dB as the receiver moves into the shadow zone. To increase the transmission distance under such circumstances, either the source or the receiver must increase its height above the vegetation (Fig. 1).

The deflection of waves in a stratified medium increases as the gradient of characteristic impedance increases. Thus a steeper thermoclime results in the formation of a shadow zone closer to the source. For horizontal propagation in a constant temperature gradient, l, at a distance, z, from a boundary or layer of maximum temperature, T_0, the distance from the source to the shadow ⊖ zone is approx. $4(zT_0/l)^{\frac{1}{2}}$, where T_0 is absolute temperature and l the lapse rate (degrees/m) (Pridmore-Brown and Ingard, 1955).

The warming of air in a forest during the morning establishes a temperature gradient that has consequences for sound transmission within the forest. In the first few hours after sunrise, the air at the top of the canopy and above warms up before much change in temperature begins within the forest (Geiger, 1950). The zone of warm air above the canopy, sandwiched between cooler air, refracts and reflects sound downward from sources located below the top of the canopy. Thus for an animal within the forest, particularly one in the canopy, warm air above the canopy would reflect sound back into the canopy and thus increase the intensity at certain distances from the source (Fig. 2a). Waser and Waser (1977) have measured sound transmission in the canopy of Kibale Forest in Uganda and demonstrate that sound propagates through the canopy especially well several hours after sunrise when the temperature gradient above the canopy is well established.

This effect requires both a layer of warm air above the canopy and homogen- b eous temperatures within the forest (Fig. 2a). Under these conditions the direct propagation of sound from the source to the receiver within the canopy will interfere constructively or destructively, depending on wave length, range, and characteristics of reflection from above the canopy, with the sound reflected from warm air above the canopy. Such conditions develop around midmorning, while the temperature within a forest is still nearly homogeneous (Geiger, 1950; Waser and Waser, 1977).

As the morning progresses, air within the canopy warms up. Under these conditions temperature gradients extend from the ground into the canopy (Geiger, 1950; Heckert, 1959; Haddow and Corbet, 1961). Such gradients within a forest would create a shadow zone for animals attempting to communicate a in the canopy (Fig. 2b). Sound generated within the gradient would be refracted and reflected into zones of cooler air and create shadow zones for horizontal propagation. Because temperature gradients in forests at midday are small (ca. 0.1–0.3° C/m; Eyring, 1946; Haddow et al., 1947; Geiger, 1950; Haddow and Corbet, 1961), the shadow zone for a source in the canopy might lie several hundred meters away.

Temperature gradients in tropical forests need further investigation. In some forests, the large amount of moisture on the leaves appears to retard the warming of air in the canopy after sunrise (Baynton, 1963). In addition, some tropical forests retain appreciable temperature gradients through the night (Richards, 1952).

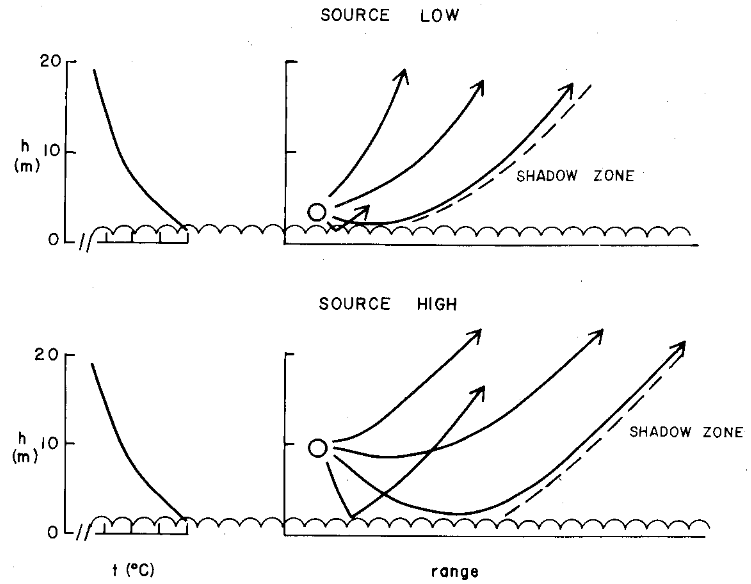

Fig. 1. Effects of the height of a source (h) on sound propagation in a temperature gradient above vegetation or the ground. Left, temperature gradient; right, rays perpendicular to the wave front from the source. Source, o. Upper limit of vegetation, scalloped line

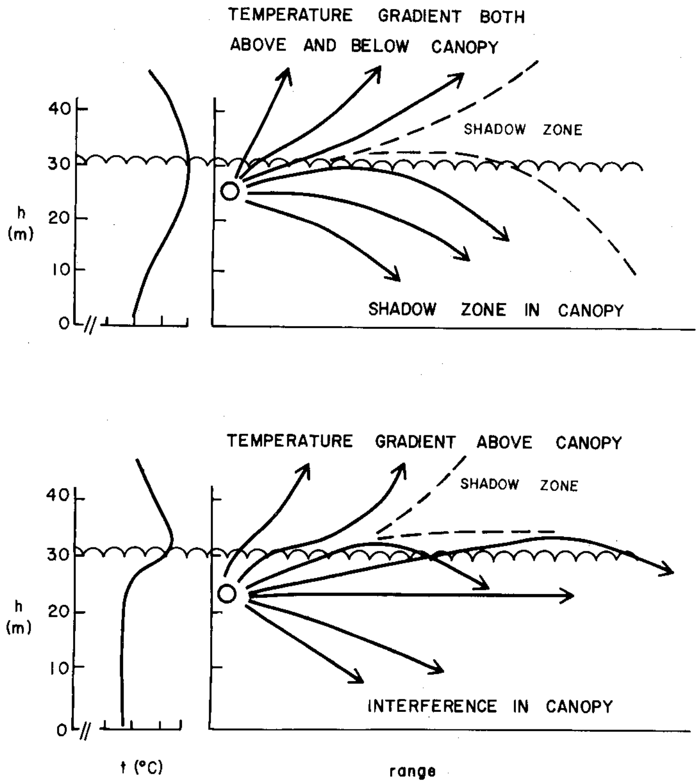

Fig. 2. Effects of two temperature gradients on sound propagation in forest canopies. See Figure 1 for further explanation

Gradients of wind velocity also deflect sound, and the effects resemble those from true refraction (Wood, 1966: 161–166). The horizontal velocity of sound is the sum of the velocity of sound in air and the velocity of the air. Wind gradients near the surface of the earth are normally positive with altitude, owing to friction between the air and the ground. Consequently an obliquely ascending wave front is deflected downward when traveling downwind and upward when traveling upwind. For a wavelength proceeding at a given angle with respect to horizontal, there exists a difference in wind speed, independent of the distance between layers with these speeds, for which total reflection of the wave front occurs. Wood (1966) argues that since the downwind propagation of sound is kept close to the ground and is thus subject to ground attenuation, whereas upwind propagation of sound is deflected away from the ground, the intensity of sound at a given distance from the source might actually be greater upwind at a suitable height above the ground than downwind near the ground. Deflection of sound waves away from the ground upwind creates a shadow zone as a consequence of the wind gradient.

Wind gradients and temperature gradients often counteract each other in open areas on sunny days (Ingard, 1953; Wiener and Keast, 1959). A negative temperature gradient and positive wind gradient reinforce each other in creating a shadow zone upwind but counteract each other in producing shadow zones downwind. The radial distribution of a shadow zone around a source thus depends on the relative values of the wind and temperature gradients.

Boundary Interference. Several studies in natural environments have demonstrated greater attenuation at low frequencies (below 1 kHz) than at medium frequencies for transmission at less than a few meters above ground (Embleton, 1963; Linskens et al., 1976; Marten and Marler, 1977; Marten et al., 1977). This greater attenuation of lower frequencies at heights of a few meters arises from effects of the ground.

Ground attenuation, caused by interference between direct and reflected waves at the receiver, depends on the height of the source, the distance of the receiver in relation to the wavelength of the broadcast sound, and on the impedance of the boundary (Ingard, 1951, 1953; Aylor, 1971). Ingard's (1953) calculations suggest that attenuation by the ground reaches a peak for wavelengths between 0.1 and 0.7 times the height of the source and decreases for both shorter and longer wavelengths. The wavelength for peak attenuation varies less with the boundary impedance. Thus for transmission approx. 1 m above ground, ground attenuation is likely to be greatest for frequencies from 300–3000 Hz. The higher the source, the lower the frequency for peak ground attenuation. Thus in experiments by Waser and Waser (1977) in Kibale forest, Uganda, at 15 m above ground, increased attenuation at low frequencies appeared only below 125 Hz.

Because ground attenuation depends on the phase relationships of direct and reflected waves at the receiver, ground attenuation is not a linear function of the distance from the source, the wavelength, or the height of horizontal transmission above the ground. Certain combinations of wavelength, height, and range could result in enough constructive interference to produce 'negative' excess attenuation (Ingard, 1951). Aylor (1971) calculates that, at long ranges in relation to the height of transmission, ground attenuation should increase approximately in proportion to the square of distance (6 dB per doubling of distance). When ground attenuation is appreciable, excess attenuation will not vary linearly with distance from the source. Consequently, separate measurements of excess attenuation (in dB/m) for a particular frequency are comparable only when transmission height and distance are constant.

The characteristic impedance of the surface affects both the frequency for peak attenuation and the level of attenuation. Aylor (1971) studied attenuation of sound broadcast across open ground. With the source and receiver 1 m above ground, bare ground attenuated frequencies of 200–1000 Hz. Tilling the soil, which increased its permeability to air, reduced the frequency of peak attenuation from 700 to 350 Hz. In addition, tilling increased maximum attenuation at a range of 52 m from the source by almost 80%. Linskens et al. (1976) found that low frequencies (less than 500 Hz) in temperate forest communities usually attenuated somewhat less (roughly 5 dB) in winter in comparison to summer, a difference that might result from changes in the litter on the surface of the ground. Marten and Marler (1977) found clear effects of ground attenuation below 2 kHz for transmission within 2m of the ground both in forests and open environments.

Scattering. Scattering of sound by refraction, reflection, or diffraction from objects or heterogeneities within the medium will generate reverberations and standing waves as described above. In addition, when a source produces a beam of sound that passes through a medium with many heterogeneities, scattering will increase the attenuation of sound propagating in the direction of the beam.

Deflection of sound energy will result in a spreading of the beam and thus reduce the energy density within the beam. However, after several scatterings, sound energy will also re-enter the center of the beam, but only after some of the energy has been absorbed by any of the processes discussed earlier. In a scattering medium, at great distances from the source, energy reaching the receiver is almost all scattered sound, which will arrive at the receiver from a variety of directions. Givens et al. (1946) demonstrate that a plot of excess attenuation (attenuation in excess of spherical divergence) against range is convex upward in scattering media. The greater the distance from the source the more sound energy is received as reflection. Consequently, in scattering environments excess attenuation will not increase linearly (constant dB/m) with increasing range. Brief pulses, however, should attenuate linearly, as scattered sound re-entering the beam would arrive later at the receiver than direct sound.

The degree of attenuation as a result of scattering is affected by the directionality of both the source and the receiver. A receiver with a narrow beam of sensitivity will not detect much of the arriving scattered sound. One procedure for estimating the importance of scattering in the propagation of sound is thus to compare the attenuation for directional microphones aimed at the source and normal to the source. Wider radiation of sound from a source in a scattering environment should result in less attenuation along the axis of propagation than from a more narrowly beamed broadcast. Because a wider beam would have a lower surface-to-volume ratio, the proportionate dissipation of energy from the beam would be less over a given distance.

These effects might explain some of the divergent results from transmission experiments in natural environments, as no investigator has determined the directionality of his speakers or microphones nor their effects on measurements of attenuation. The problem is particularly serious, because both speakers and microphones are generally more directional at higher frequencies, an effect that would confound measurements of frequency-dependent attenuation.

Scattering will depend strongly on the relationship between the wavelength of sound and the dimensions of heterogeneities. Heterogeneities that produce scattering of sound in the atmosphere include micrometerological heterogeneities from turbulence or thermals and objects distributed in the medium such as leaves, limbs, and trunks of trees. Because foliage consists of surfaces with dimensions mostly less than 10 cm, it will scatter sound most effectively at frequencies above 3 kHz.

The effects of foliage in forest on the attenuation of sound by scattering become apparent when sound transmission in temperate forests is studied in summer and winter. Linskens et al. (1976) report that attenuation of high frequencies is less in winter than in summer, but they do not present convincing data for this conclusion. Marten and Marler (1977) found lower attenuation at most frequencies between 1 and 10 kHz for transmission at 10 m above ground in deciduous forests without leaves in comparison to the same forests with leaves. In addition, attenuation was less for transmission at 10 m above ground over open fields in comparison to through the canopies of coniferous or deciduous forests. Deciduous forests with leaves had higher attenuation than open fields for most frequencies above 1 kHz. Aylor (1971) found greater attenuation of high frequencies by dense second growth during summer than during autumn after the leaves had fallen. In addition, he measured the attenuation of sound by a cornfield as a function of the density of plants. Excess attenuation of 2 and 4 kHz tones exceeded that for 1 kHz tones and increased with an increase in plant density.

Nonstationary Heterogeneities. So far our discussion has centered on the effects of stationary heterogeneities within the sound field, which produce spatial patterns of intensity that depend on the characteristics of the sound at the source and the nature and distribution of the heterogeneities and boundaries. Fluctuating heterogeneities in contrast have effects that vary in time and thus introduce temporal fluctuation in a received sound even when the source is constant (Fig. 3). Nonstationary heterogeneities could include moving objects, such as swaying vegetation, but atmospheric turbulence is probably most important. Turbulence would include local variations in the density, temperature, and velocity of air, such as eddies created by air movement or thermals of various dimensions produced by temperature gradients. These volumes of air with different characteristic impedance from the surrounding medium will refract, reflect, and diffract sound waves when the dimensions of these volumes approximate or exceed the wavelength of sound. Prominent fluctuations in a received signal from a constant source are noted by several students of sound transmission

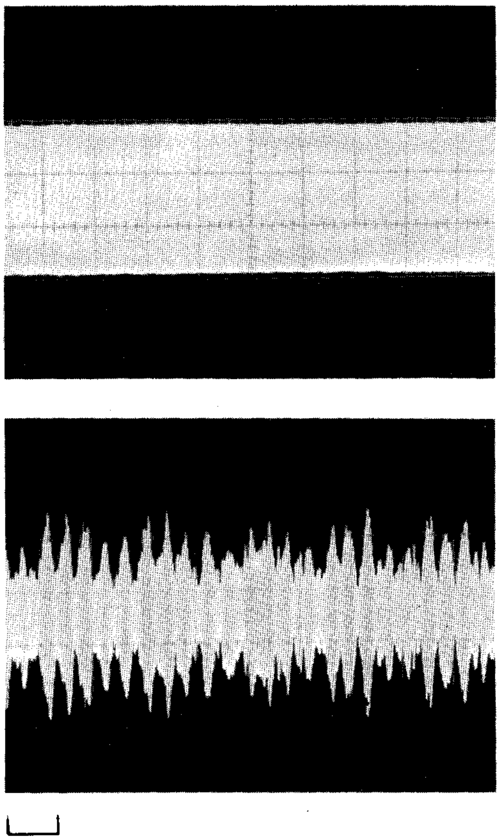

Fig. 3. Oscillograms of a 2.5 kHz signal as broadcast (upper) and as recorded at a distance of 60 m in a hardwood forest in leaf (lower). Speaker and microphone 1.5 m above ground; weather clear with barely perceptible air movement near ground; noon May 10, 1975. Time mark, 1.0 s

(Knudsen, 1946; Rudnick, 1947; Richardson, 1950; Ingard, 1953; Wiener and Keast, 1959; Jilka and Leisler, 1974; Morton, 1975; Waser and Waser, 1977; Marten and Marler, 1977; Marten et al., 1977).

Formal analysis of the effects of such nonstationary heterogeneities predicts that the relative fluctuations (RMS intensity/mean intensity) should increase linearly with range and with the square of frequency for any one medium (Chernov, 1960) when the dimensions of the heterogeneities (indicated by the spatial correlation parameter) greatly exceed the wavelength. Chernov quotes Krassilnikov, whose experiments on fluctuations during sound transmission in a few experiments in the atmosphere confirm the linear increase with range. Experiments in the ocean suggest the same results (Tolstoy and Clay, 1966). Jilka and Leisler (1974) report that fluctuations increase monotonically with frequency in transmission experiments in terrestrial environments. Our own experiments with broadcasts at constant intensity in a forest (Richards and Wiley, in prep.) have confirmed a linear increase in fluctuations with range and with the square of frequency, when measurements are made within short time intervals

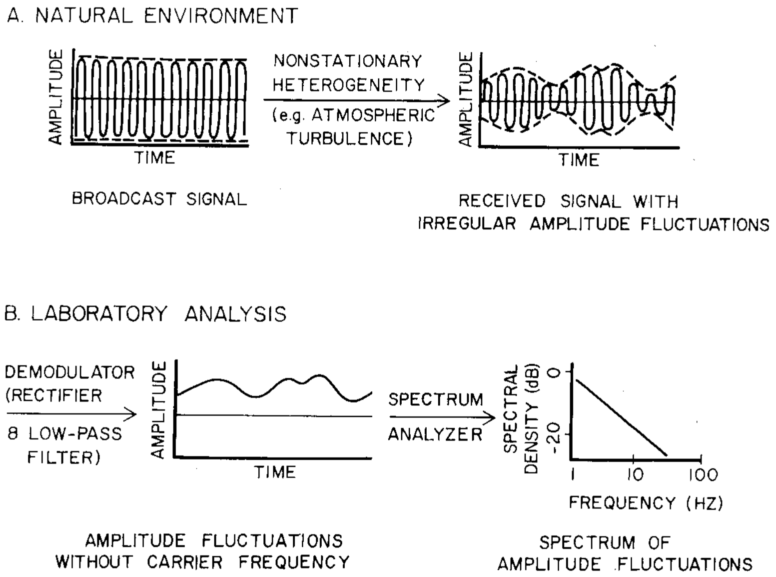

Fig. 4A and B. Origin of irregular amplitude fluctuations during the propagation of sound through a medium with nonstationary heterogeneities (**A**) and analysis of the spectrum of these fluctuations (**B**)

without substantial changes in micrometeorological conditions. However, both of these effects are less than the effect of wind speed. The turbulence from even the slightest wind creates tremendous fluctuations in the received signal at moderate distances (Fig. 3).

In addition, we measured the spectra of these fluctuations for constant-intensity broadcasts of single frequencies. These fluctuations constitute amplitude modulation of the carrier signal, which in spectral analysis appear as side bands or spreading of the carrier frequency. We demodulated the received signal in order to isolate the amplitude modulation (Fig. 4). The spectra of these fluctuations showed a nearly monotonic decrease in spectral density with increasing modulation frequency. The spectra varied only slightly under different conditions in which the amplitude of fluctuations differed considerably. Almost all of the energy in the spectra of amplitude fluctuations was below 50 Hz (Richards and Wiley, in prep.); spectral density dropped 20–30 dB from near 0 to 50 Hz.

These amplitude fluctuations as a result of nonstationary heterogeneities have an important effect on a receiver's ability to discriminate amplitude modulations in the received signal. Amplitude fluctuations with a period greater than the analysis period of the receiver's ear, or any other frequency analyzer, will appear as temporal changes in the intensity of the received signal. Amplitude fluctuations with periods less than the analysis period of the receiver will appear as side bands of the carrier frequency. The analysis time-constants of mammalian ears lie between 0.01 and 0.05 s, so that amplitude fluctuations less than 20 Hz are perceived as temporal changes of intensity while those greater than 100 Hz are perceived as side bands; between 20 and 100 Hz a mixed perception

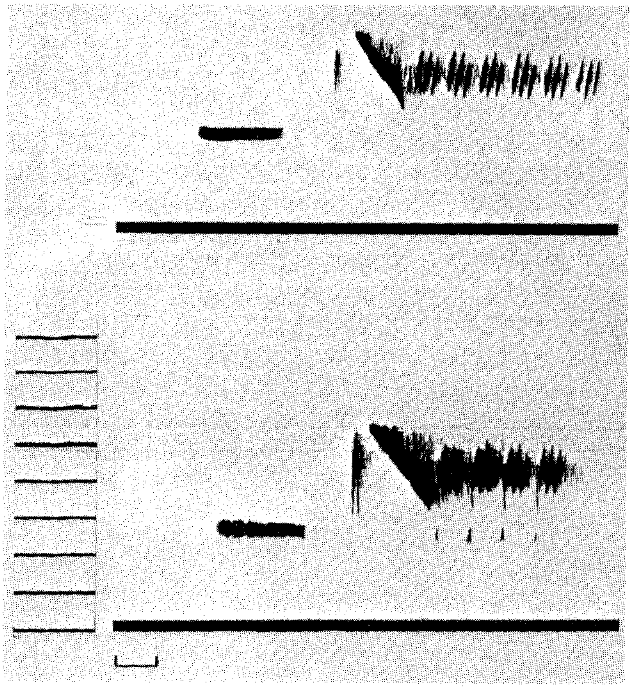

Fig. 5. Spectrograms of two recordings of the same song theme by a male rufous-sided towhee (Pipilo erythrophthalmus) to illustrate the effects of reverberations on the reception of amplitude modulation and rapid, repetitive frequency modulation. The upper spectrogram shows a recording from closer to the singing bird than the lower spectrogram. Note particularly the effects of reverberations on the reception of rapid trills. Some of the fluctuations in the intensity of the introductory whistle might result from amplitude fluctuations from nonstationary heterogeneities. Male towhees do not always repeat song themes exactly; note the differences in the length of the trill and the intensity of a low-frequency component in the trill. Time mark, 0.1 s. Frequency intervals, 1 kHz

occurs (Littler, 1965; Gerber, 1974). Because the amplitude fluctuations accumulated during atmospheric transmission of sound have most of their energy in frequencies below 50 Hz, they are perceived as intensity fluctuations by a listening animal and tend to mask intensity changes in the broadcast signal. Amplitude fluctuations greater than 100 Hz create side bands in the received signal, and these would tend to mask similar sidebands from amplitude modulation in the broadcast signal.

Reverberations. Transients in acoustic signals are also distorted by reverberations caused by the superposition at the receiver of direct waves and reflected waves. In an environment with complex distributions of reflecting surfaces, such as a forest, the variety of possible paths for reflected waves often results in very substantial distortion of transients in sound waves. A tone pulse with sharp onset and termination arrives at the receiver with progressive onset and long reverberations, and complex fluctuations in between. This phenomenon is familiar to everyone who has spectrographed animal sounds recorded in a forest (Fig. 5).

Reverberations are affected by the directionality of the source and receiver and by the wavelength of the sound in relation to the dimensions of scattering surfaces. Narrowly beamed sources and directional receivers would reduce the superposition of waves from different paths at the receiver and thus reduce the effects of reverberations. As discussed for scattering, frequencies above 3 kHz are probably subject to greater scattering during transmission through forests than are lower frequencies. Consequently, reverberations should increase for higher frequencies.

In summary, intensity changes encoding information for long-distance transmission by sound through the atmosphere are masked in the following ways: sharp changes in intensity, which would include high-frequency components in the transients, become obscured during transmission owing to reverberation and pulse dispersion in environments with numerous reflecting, refracting, and diffracting objects; low-frequency components of intensity modulation in a signal are masked by the accumulation of random amplitude fluctuations from nonstationary heterogeneities in the medium.

III. Consequences for Animal Communication

1. Range of Detection: General Considerations

One of the receiver's problems in effective communication is detecting the presence of a signal. In part, this ability depends on the power of the received signal in relation to the power of similar perturbations of the channel, in other words the signal/noise ratio. Attenuation of sound during transmission is thus critical for this consideration. Our review has indicated that attenuation of sound during transmission results from (1) absorption, both by the medium and boundaries, (2) deflection of sound waves by stratified media, (3) ground attenuation, and (4) scattering of a sound beam.

Absorption, ground attentuation, and scattering are strongly frequency-dependent. Much experimental work on sound transmission has aimed at identifying frequency-dependent attenuation. Virtually all results show increasing attenuation with increasing frequency, probably as a result both of increasing molecular absorption by the atmosphere and increasingly effective scattering of higher frequencies by small objects and heterogeneities in the medium. Some studies have also shown greater attenuation of low frequencies (less than 1 kHz) and have attributed this to ground attenuation. The effects of stratified media can produce less attenuation than expected with spherical divergence; probably for this reason, a number of studies have shown some 'negative excess attenuation' for certain frequencies in some environments.

In some studies excess attenuation has not increased linearly with distance, although most of the effects listed here are linear with distance. In a scattering environment, however, excess attenuation will not increase linearly with range. In addition, the effects of ground attenuation are not linear with range. When scattering or ground attenuation are appreciable, excess attenuation will not have constant dB/m.

2. *Locatability*

All deflections of sound waves will create problems for a receiver interested in locating the source. Particularly in scattering environments, where numerous surfaces and heterogeneities create great complexity in the sound field, a receiver at a distance from a source will receive most of the sound energy of a signal in the form of scattered sound. The directionality of the received sound will be substantially degraded.

In addition, irregular amplitude fluctuations, reverberations, and pulse dispersion will interfere with a receiver's ability to detect the directionality of arriving sound. These effects will reduce binaural differences in phase (instantaneous amplitude) or timing of transients in acoustic signals. Amplitude fluctuations and reverberations have less effect on binaural differences in the intensity of high frequency sounds, which result from the sound shadow cast by the receiver's head. High frequency sounds, however, arrive at the receiver with less directionality, as they are scattered more effectively than low frequencies.

3. *Weather*

The pronounced effects of temperature gradients, wind gradients, and atmospheric turbulence on the propagation of sound would favor acoustic communication at times of day and under weather conditions that permit most effective transmission. Atmospheric turbulence increases during winds and pronounced temperature gradients. Reduced turbulence early in the morning and during still weather favors acoustic communication at these times. Animals could use thermal and wind gradients to their advantage. Waser and Waser (1977) suggest that canopy monkeys in tropical forests give their long-distance vocalizations primarily in the few hours after sunrise, when the advantageous temperature gradient above the canopy is likely to be best developed.

4. *Position of the Signaler and Receiver in the Environment*

The location of the signaler and the receiver with respect to boundaries, objects, and gradients in the environment will have important effects for the transmission of sound between them. Shadow zones created by temperature or wind gradients are best counteracted when the signaler is located at a height above the ground or the receiver is located above the signaler. Animals in open environments will often have to contend with shadow zones. Birds of open fields standardly deliver their advertising vocalizations during song flights, which has the double advantage of increasing their visual conspicuousness and extending the range of communication with receivers on the ground (Morton, 1975). It would be interesting to know whether these species sing from higher altitudes above the ground during the middle of the day than at dawn before thermal gradients are established.

Ground attenuation is also strongly influenced by the height of the source above the ground. The frequency of maximum attenuation and the magnitude of attenuation decrease with increasing height of the source. Since ground attenuation primarily affects frequencies below 1 kHz, the use of such frequencies near the ground would not permit maximum range in communication for a source of given power. Most avian vocalizations for long-range communication employ frequencies above this range. Mammals that use vocalizations with low frequencies for long-range communication are mostly primates that call from a height above the ground (Waser and Waser, 1977). The lion is a striking exception (Schaller, 1972).

Animals in forested environments might also concentrate their long-range communication in a horizontal stratum that permitted the use of wave-guide effects between layers of vegetation. To employ this effect, the signaler and receiver would have to occupy the same stratum. Species of birds in forests often have characteristic heights for singing, which do not necessarily match the heights for other activities such as feeding. There seem to exist no systematic studies of the heights of vocalizing animals above ground. Whether there actually exist certain strata within forests that act as wave guides, owing to reflections from horizontally arrayed vegetation, is a question that needs investigation.

5. Resolution

The amount of information transmitted between a signaler and a receiver depends in part on the diversity of signals produced by the signaler and discriminated by the receiver. Variations in signal structure that become degraded during transmission through the atmosphere will not allow the receiver to make the necessary discriminations. Communication can employ two tactics to combat such degradation of signals or noise during transmission: coding of signals in patterns that have minimal similarity to the patterns of other perturbations in the medium; and redundancy, serial or instantaneous correlations in the temporal or spatial organization of signals, which allow the receiver to predict the entire signal from a part of it or to average signals over time. Redundancy in acoustic signals would include stereotyped temporal sequences of sounds, often simple repetitions.

The most important sources of noise produced by physical effects of transmission in acoustic channels include pulse distortion on reflection, the accumulation of amplitude fluctuations, and reverberations. All of these effects will produce the greatest degradation of signals in which information is encoded by amplitude (or intensity) modulation.

6. Wide and Narrow Spectrum Signals

Tonal signals, those that focus energy in a narrow band of frequencies at any instant, presumably permit an animal to broadcast greater power per Hz band width. For animals with tuned or frequency-analyzing receptors, like the ears of all terrestrial vertebrates, such signals would permit greater signal/noise ratios on reception and thus extend the range of effective transmission. The tympanal organs of insects, on the other hand, only permit coarse frequency resolution at most (Schwartzkopff, 1974; Michelsen and Nocke, 1974). For such receptors, the masking band-width is wide even for tonal signals.

Tonal signals have some additional advantages for long-range communication. They permit both frequency and amplitude modulation for encoding information. In contrast, when signals have energy spread over a wide band of frequencies that covary in time, frequency variations within this band become unavailable for encoding information, and amplitude changes must be used. Independent modulation of the frequency components in wide-spectrum signals is probably not possible for most animals, so that in practice the choice is between wide-spectrum signals with limited frequency modulation and signals with few frequency components that permit extensive frequency modulation. Thus signals with energy in a wide band of frequencies usually must emphasize amplitude modulation for encoding information.

Wide-spectrum signals with sharp changes of intensity would have advantages in locating the source, because the receiver could make binaural comparisons of many frequency components (Gulick, 1971; Konishi, 1973). However, wide-spectrum signals have disadvantages for long-range communication. Reverberations and temporal fluctuations in amplitude from nonstationary heterogeneities will degrade or mask patterns of amplitude modulation in the broadcast signal. Because wide-spectrum signals must rely on amplitude modulation to encode information, such signals would permit the transmission of little information in long-range communication.

Temporal fluctuations in the amplitude of received signals are sometimes less for bands of white noise than for continuous tones (Morton, 1970; Wiener and Keast, 1959; Waser and Waser, 1977). Such an effect might result if the different frequency components in a wide-spectrum signal propagated independently, so that the received signal would represent an average of random amplitude fluctuations in a number of frequency bands. When the wavelength is either considerably greater or considerably smaller than the heterogeneities of the medium, different frequency bands should be affected similarly and have highly correlated propagation. In contrast, when wavelength approximates the dimensions or correlation parameter of the heterogeneities, the effects of refraction and diffraction are so strongly frequency-dependent that wide-spectrum signals in this range would indeed show some averaging of the different propagation of narrow frequency bands.

If this effect is confirmed with more systematic experiments, long-range communication with wide-spectrum signals that encoded information as amplitude modulation would do best to match the frequency band to the dimensions of heterogeneity in the environment in order to reduce the amplitude fluctuations in the received signal. To use this strategy, either the dimensions of heterogeneities must remain roughly stable or the signaler must shift the location of its frequency band to match environmental conditions.

All things considered, however, frequency modulation to encode information would prove most advantageous for long-range communication; amplitude modulation to encode information would normally require enough redundancy, usually repetition, to counteract the accumulation of random fluctuations and reverberations. In fact, animals that employ long-range acoustic signals either emphasize frequency modulation over relatively wide frequency ranges, or incorporate considerable redundancy in amplitude modulations, often by exact repetition of sound pulses, or by a combination of the two. The advertising songs of many passerine birds exemplify the first and third alternatives; the long-range acoustic signals of forest primates and many Orthoptera exemplify the second (Dumortier, 1963; Alexander, 1967; Marler, 1969, 1972, 1973; Waser and Waser, 1977).

At short range, where random amplitude fluctuations are much less likely to interfere with correct reception of signals, sharp intensity transients offer the advantage of easy locatability (see above). Perhaps for this reason some colonial birds that communicate over distances of a few meters employ broad-spectrum sounds with sharp amplitude modulations in complex patterns (White and White, 1970; Wiley, 1976).

7. Directionality of Source and Receiver

The directionality of both the source and the receiver influences the effects of scattering on attenuation, reverberations, and the ease of locating the source by the receiver. Communication in environments with many scattering surfaces might require some compromises in the choice of directionality of the source and receiver.

Because a source is inherently more directional for higher frequencies than lower frequencies, narrowly beamed broadcasting would probably prove possible only for wavelengths appreciably shorter than the dimensions of the source. A narrowly beamed source would increase the signal intensity within the sound beam and thus might increase the range of detection, provided the source was aimed toward the receiver. This effect might not hold in scattering environments, where, as discussed above, attenuation from scattering in the axis of propagation at a given range is greater for narrowly beamed than for widely beamed broadcasts. In addition, the greater difficulty of producing narrowly beamed broadcasts at lower frequencies is offset by lower attenuation by atmospheric absorption and scattering of these frequencies. The optimal directionality for a source in a scattering environment, in order to permit maximum range of detection, will depend on the counterbalancing effects of directionality on attenuation from scattering and spatial concentration of acoustic power.

Narrowly beamed broadcasting would permit a signaler to limit its signals to a specific receiver. On the other hand, a narrow beam would prove disadvantageous if the signaler did not know the approximate location of potential receivers or needed to communicate in many directions at once.

For a receiver, greater directionality would increase the signal/noise ratio of the received sound. By aiming toward the source, a directional receiver could exclude some of the background noise. This effect, however, would be reduced in a scattering environment, in which both the signal and background noise would arrive from many directions.

For resolving temporal patterns in acoustic signals in a scattering environment, narrowly beamed broadcasts and directional reception offer clear advantages. Both would serve to reduce the superposition of direct and scattered waves by the receiver and thus reduce reverberations.

8. Open and Forested Habitats

One of the initial hopes in studying atmospheric transmission of sound was to identify reliable differences in frequency-dependent attenuation among natural habitats and correlate these differences with the frequencies employed by animals in long-distance communication. Available results, however, have failed to demonstrate consistent differences in frequency-dependent attenuation associated with gross features of habitat structure.

Often intermediate frequencies (1–4 kHz) propagate with least attenuation regardless of habitat and overall attenuation differs little between habitats. Linskens et al. (1976) directly compared transmission at a height of 1 m through forested habitats and over, bare, sandy ground at ranges of 4 and 8 m. Their results in general show an increase in attenuation below 1 to 2 kHz and above 4 kHz in both situations. The open habitat differed in having very low attenuation of the lowest frequencies (below 200 Hz) and much higher attenuation of high frequencies. Between 2 and 4 kHz overall attenuation was similar in the open and in forests.

Marten and Marler (1977) report differences between open and forested habitats for transmission over a distance of 100 m at 10 m above ground. For transmission at lower elevations open and forested habitats are more similar. In contrast to Linskens et al., Marten and Marler report less attenuation of high frequencies in open environments than in forests. Although these two studies used different methodologies, including different heights above ground and different ranges for transmission, it is not clear what might explain this discrepancy.

The lack of consistent differences in acoustic transmission through open environments and forests presents something of a paradox in view of the clearly different acoustic environments in a forest and in the open, yet closer consideration of these differences suggests that they might have similar effects on frequency-dependent attenuation. Forests, with their complex distribution of vegetation, are characterized by a large degree of relatively stationary heterogeneity (SH), which increases scattering of sound, reverberations, and pulse dispersion from reflection. Open environments, particularly during midday, have greater micrometeorological instability and stronger winds; consequently nonstationary heterogeneity (NH) is probably much greater in the open, which increases the accumulation of random amplitude fluctuations and scattering of sound in the open. Thus the additional scattering of sound and consequent attenuation by foliage in the forest is often compensated by additional scattering from micrometeorological heterogeneities in the open. Both effects increase as carrier frequency increases. Consequently, frequency-dependent attenuation from scattering might not differ consistently between open and forested habitats, as it would depend on the dimensions of both NH and SH in the environment.

Might an environment with large SH affect the transmission of acoustic signals in ways different than a habitat with large NH and small differences of characteristic impedance? The first environment produces pronounced reverberations and pulse distortion by reflection, while the second environment produces pronounced amplitude fluctuations. Reverberations are in a sense the converse of irregular amplitude fluctuations: reverberations result from the propagation of an amplitude-modulated signal through an environment with SH, while irregular amplitude fluctuations accumulate in propagation of a constant signal through NH. The exponential decay of reverberations means that high rates of amplitude modulation in signals are masked and lower rates progressively less masked. In contrast, the spectrum of amplitude fluctuations from NH shows the greatest spectral density at low frequencies, so that low rates of amplitude modulation in a signal are masked more than higher rates.

These considerations suggest that low frequencies of amplitude modulation of a carrier frequency should propagate with less degradation in forests than in the open, while high frequencies of amplitude modulation should propagate best in the open. Pulse modulation of a signal is essentially extreme amplitude modulation; the transients at onset and termination of a pulse generate high frequency components in a spectral analysis. Reverberations and pulse dispersion in forests should interfere with the transmission of information by variations in pulse width and interval, while these variations should propagate better in the open. Sharp onsets and terminations of pulses and high rates of amplitude modulation of continuous signals will generally propagate with less degradation in open environments. Information coded in repetitions of pulses at relatively low rates might transmit better in forests. However, as stated before, it seems that frequency modulations would be better for long-range transmission of information in either environment.

Reverberations impose limitations, in addition, on the rate of repetitive frequency modulation. To the extent that frequency modulation involves rapid recurrence of particular frequencies, reverberations will hinder the receiver's resolution of patterns of frequency modulation (Fig. 5). Environments with large SH might thus favor signals that avoided rapid, repetitive frequency modulation as well as rapid amplitude modulation.

Birds of the understory in tropical forests generally do avoid rapid frequency modulation in their vocalizations (Morton, 1975). In addition, they emphasize frequencies around 2 kHz, lower than those of species in edge habitats or grasslands. Chappuis (1971) reports similar contrasts between birds of tropical forests and open habitats in Africa. The lower emphasized frequencies of birds in the understory of tropical forests would reduce reverberations in a habitat with high SH. However, lower frequencies are advantageous in any environment, as discussed above, owing to lower attenuation from atmospheric absorption and scattering.

There are some striking exceptions to these generalizations about the vocalizations of tropical birds in open and forested habitats. Possibly the reason that many birds of the undergrowth in tropical forests use vocalizations with simple structure and moderate frequencies is that they are so widely spaced in their habitat that their communication is under extreme selection for maximum range. It would be interesting to know whether these species encode as much information about individual identity and behavioral tendencies in their long-range vocalizations, in addition to species identity, as do temperate-zone passerines of forest undergrowth.

9. *Use of Degradation for Ranging*

It seems likely that individuals of many species of birds are not spaced far enough apart to place strong constraints on the structure of their signals for long-range communication. An individual might do better to produce a signal that degraded during transmission in ways that allowed the receiver to judge its distance. Without definite information about the signaler's distance, a receiver would have to approach the signaler in order to locate it by comparing intensities at different locations or by visual contact. If a signal included information about the distance of the signaler, a receiver could avoid the signaler without risking an interaction. Rather than assuming that animal signals have adapted for maximum range, one might instead, as Schleidt (1973) has suggested, look for features of signals that correlated with the expected spacing of individuals in relation to the degradation of signals in a particular habitat.

African forest primates provide an example of such a relationship. Among four species in the Kibale forest, Uganda, the dominant frequencies of long-range, intergroup vocalizations are related to the typical spacing of groups (Waser and Waser, 1977). The mangabey *Cercocebus albigena*, groups of which are rarely less than 500 m apart, uses a long-range vocalization, the 'whoop-gobble', with most of the emitted energy below 500 Hz. The Wasers' experiments demonstrated that this vocalization attenuates less during propagation through the forest canopy than do the usual long-range vocalizations of *Colobus guereza*, *Cercopithecus mitis*, and *C. ascanius*, which emphasize higher frequencies. Neighboring groups of the latter species are closer than mangabey groups. *Mitis* does produce a low-pitched 'boom' that attenuates even less than the mangabey's 'whoop-gobble'. Although *mitis* uses this vocalization infrequently, several west African *Cercopithecus* species have similar calls that they use regularly in intergroup communication. The west African species maintain wider spacing of groups than does *mitis* in east Africa. The Wasers' measurements suggest that the intensities of long-range calls are similar at the source for all species. Greater attenuation of high frequencies during propagation through the canopy explains the different attenuations of their long-distance vocalizations. In effect, the structure and consequent attenuation of the intergroup vocalizations of each species seems adapted to the usual spacing of groups.

To permit a receiver to judge the source's distance, animals could include features in their vocalizations that degrade predictably with distance from the source. The overall attenuation of the received signal, however, is probably not the best cue for the distance of the source, because changes in the weather would strongly affect atmospheric absorption and scattering from microclimatic heterogeneities. Much more reliable ranging would result from comparing separate features of the received signal, either different frequency bands or different periodicities of intensity in any one band.

One possibility for ranging would involve comparing the received intensities of high- and low-frequency components of a signal. Because high frequencies attenuate faster, owing to higher absorption and scattering, a receiver that knew the spectral structure of a signal at the source could judge its distance by the relative attenuation of high frequencies. In addition, because reverberations and random amplitude fluctuations increase with the carrier frequency, a receiver might compare reverberations or amplitude fluctuations of a high and a low frequency component in the signal. Alternatively, because both reverberations and amplitude fluctuations mask high and low rates of amplitude modulation respectively, a receiver might determine which rates of amplitude modulations in a known signal were more degraded and which rates were less.

To allow such ranging, a signal should include either a variety of rates of amplitude modulation or variation in the carrier frequency. This reasoning suggests an experiment to test for the use of degradation in ranging during long-range communication by animals. Played back vocalizations at controlled intensity should evoke less response when artificially degraded, for instance, by introducing reverberations or passing the signal through a voltage-controlled amplifier that would artificially introduce irregular amplitude fluctuations.

Conclusions

A basic conclusion from this review of the physical properties of sound transmission through the atmosphere is the disadvantage of encoding information in amplitude modulations of a carrier frequency for long-distance communication. When the receiver must discriminate a variety of signals, for instance, to obtain information on individual identity or behavioral tendencies associated with acoustic structure, signal variations used to encode this information must reliably propagate the necessary distance. Although our review has suggested that amplitude modulation of a carrier frequency, including pulse modulation, might prove possible at long-range depending on the nature of heterogeneities in the channel, frequency modulation of the carrier seems like a much more reliable strategy. Information encoded solely in amplitude modulations would normally require considerable redundancy, in the form of repetition, to ensure accurate transmission.

Consequently, for rapidly transmitting large amounts of information to the maximum range, signals should consist of tones modulated in frequency. In forests, frequency modulations that result in rapid repetitions of any one frequency, particularly high frequencies, would be masked by reverberations. In the open, this constraint on the nature of frequency modulation is relaxed.

For maximum range of transmission, acoustic communication within a few meters of the ground should employ neither high (>4kHz) nor low (<1kHz) frequencies, regardless of habitat. Low frequencies become less disadvantageous when the source is higher above the ground, because attenuation of low frequencies results primarily from ground attenuation. The signaler and receiver should also position themselves to avoid the effects of shadow zones and to make use of wave-guide effects in forests.

This review has also emphasized that the degradation of signals during transmission would allow individuals to judge a signaler's distance. For this reason, acoustic signals in animal communication might evolve to incorporate features that degraded in predictable ways during transmission in relation to the usual spacing of individuals, rather than simply to maximize the range of transmission.

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