

Acoustic Communication in Birds

Volume 1

Production, Perception, and
Design Features of Sounds

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Adaptations for Acoustic Communication in Birds: Sound Transmission and Signal Detection

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I. INTRODUCTION

Birdsong typically serves for communication at long range, over distances of 50–200 m. In contrast, humans use their enormous capability for acoustic communication predominantly at short range. As a consequence, engineers have devoted little attention to the problems of long-range acoustic communication, and most people have little intuitive feel for its difficulties. Nevertheless, many distortions of acoustic signals during propagation through natural environments, such as frequency-dependent attenuation, boundary interference, reverberations, and irregular amplitude fluctuations, are easily detected by ear. Just in the last decade, as a result of initiatives for noise control in human environments, our understanding of the acoustics of sound transmission in the atmosphere has developed rapidly.

This review considers adaptations in acoustic signals that can improve the efficiency of transmitting information to a receiver. For this task, we first need to consider some general features of communication, in particular the concepts of information transfer and noise. Next, this review turns to the physical processes that affect sound as it propagates through the atmosphere. Our aim is to compare the optimal acoustic signals for communication in natural circumstances with the signals actually used by birds. We focus primarily on communication at long range, but consider some adaptations for short-range communication as well. Finally, a look at the theory of signal detection in a noisy environment identifies some basic compromises that any receiver must make and some adaptations in birdsong that could improve the performance of receivers.

II. INFORMATION TRANSFER IN COMMUNICATION

In seeking adaptations of acoustic signals for efficiency of information transfer, we presuppose that communicatory signals usually evolve to increase this efficiency, the ratio of the amount of information transmitted to energy or time necessary. This premise appears to contradict a suggestion that signals often evolve to manipulate receivers while transmitting as little information as possible about the sender (Dawkins and Krebs, 1978). The confusion arises over use of the term "information." This review, like much previous ethological literature

(Altmann, 1965; Hazlett and Bossert, 1965; Dingle, 1972; Hazlett and Estabrook, 1974a,b; Wilson, 1975), uses the term "amount of information," or "information" for short, as defined in information theory by Shannon's measure of uncertainty or entropy (Shannon and Weaver, 1949; Woodward, 1953; Quastler, 1958; Raisbeck, 1963; Pfeiffer, 1965; Cherry, 1966). For a set of discrete events, the average uncertainty of the next event, H , equals

$$-\sum_i P(i) \log_2 P(i)$$

where the $P(i)$ are the probabilities of each event. For continuously variable events, measurement of H requires an integration rather than a summation over the field of events, or H can be approximated by classifying events into discrete categories. Information received from a signal is then the reduction in the uncertainty of the receiver's responses after receiving the signal. This definition presupposes a nonparticipant observer, who records received signals and responses of the receiver. The *received* or *transmitted information*, H_T , equals $H_R - H_{R|S}$ where H_R is the uncertainty of the receiver's actions without regard to the occurrence of signals and $H_{R|S}$ is the uncertainty of a receiver's responses after a signal occurs.

The necessary condition for concluding that a signal transmits information to a receiver is $H_T > 0$. This condition is an exact statement of the usual criterion for communication: a change in the receiver's behavior after receiving a signal, where a signal is any pattern of energy or matter that reaches the receiver without providing the power to effect a response directly (Cherry, 1966; Altmann, 1967; Klopfer and Hatch, 1968; Hailman, 1977; Green and Marler, 1979). The measurement of any of these uncertainties involves a number of difficulties in classifying signals and in detecting subtle, delayed, or tonic responses (Schleidt, 1973; Smith, 1977), all of which lead to underestimates of the information transmitted by a signal (see Beer, Chapter 9, Volume 2). Nevertheless, to conclude that communication has occurred, an investigator must document some change in the receiver's behavior as a consequence of a signal.

Another measure of information in communication is the amount of *broadcast information*, the information included in a signal about a sender. Broadcast information, H_B , is the reduction in the uncertainty concerning the behavioral states and external circumstances of the sender as a result of the emission of a signal: $H_B = H_0 - H_{0|S}$, where H_0 is the uncertainty concerning the sender's states or external circumstances. Here the nonparticipant observer focuses on the broadcast signal and sender, rather than the received signal and receiver. Again, measures of the amount of broadcast information in a signal require judgments about the classification of variants of signals and the sender's states or circumstances. Ethologists, however, have long recognized that signals are often associated with particular states or circumstances of senders, such as species identity,

individual identity, general motivational state, specific behavioral tendencies, and even events in the external environment, such as the presence of a predator or food (Marler, 1961, 1967; Smith, 1977; Green and Marler, 1979). Smith's (1963, 1969, 1977) concept of the *message* of a signal corresponds to a subset of the broadcast information, since he restricts the message to the association between signals and the sender's behavioral states and excludes associations between signals and external circumstances.

Although $H_T > 0$ is a necessary criterion for communication, $H_B > 0$ is not. Some communicatory signals could conceivably contain no information about a sender. In this case no association would exist between the sender's behavioral states or external circumstances and the occurrence of a signal. It is difficult to imagine that natural selection could favor responding to such signals, however.

Dawkins and Krebs (1978) emphasize that senders might include "misleading information" in signals. The distinction between "misleading" and "correct information" has no relation to the amount of transmitted or broadcast information. Instead, this distinction depends on changes in the fitnesses of the sender and receiver as a consequence of the receiver's responses. Signals contain "misleading information" when they evoke responses to the advantage of the sender and disadvantage of the receiver. The sender thus manipulates the receiver by exploiting the receiver's rules for interpreting signals. The separation of manipulative communication with "misleading information" from mutualistic communication with "correct information" depends entirely on whether or not the receiver's responses benefit the receiver, the sender, or both (Fig. 1).

Regardless of changes in the receiver's or sender's fitnesses, the criterion for communication is always $H_T > 0$. Furthermore, natural selection should favor senders that tend to maximize the efficiency of information transmission whenever interactions of individuals are either mutualistic or manipulative (Fig. 1). In either case, signals should evolve to produce responses by the recipient with the minimal commitment of the sender's time and energy. Receivers, on the other hand, should tend to minimize H_T in manipulative communication. As much as possible, receivers should ignore signals with "misleading information." Instead, receivers should tend to maximize H_T for mutualistic or altruistic communication (Fig. 1). In general, the evolution of manipulative and altruistic communication poses the same problems as the evolution of cheating in any mutualistic social interaction (Dawkins, 1976).

Owing to the attenuation and degradation of signals and the mixing of signals with background noise, there always exists some equivocation in the association between the properties of received (R) and broadcast (B) signals: $H_{S(B)|S(R)} > 0$ (Shannon and Weaver, 1949; Quastler, 1958; Wilson, 1975). This conditional uncertainty is noise. It is a property of the communication channel between the sender and the receiver; in fact, it defines the channel. Like H_T and H_B , it is available only to a nonparticipant observer. Noise as a result of degradation and

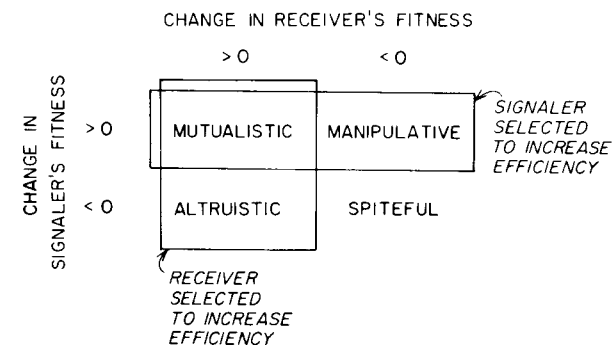


Fig. 1. Classification of communication according to changes in the sender's and the receiver's fitnesses. For senders, selection tends to increase the efficiency (see text) of mutualistic and manipulative communication, while for receivers selection tends to increase the efficiency of mutualistic and altruistic communication.

attenuation of signals and mixing with background sounds affects manipulative as well as mutualistic communication. All forms of communication must confront the difficulties of communication through a noisy channel.

Our primary concern in this chapter is the nature of noise in the channel for acoustic communication in terrestrial habitats. From a receiver's point of view, noise interferes with two tasks in the reception of signals, detection and recognition. *Detection* requires discrimination between the presence and absence of a signal, while *recognition* requires discrimination among classes and variants of signals as well as between signal and no signal. Detection and recognition are both affected by noise in the channel, by equivocation in the association between broadcast and received signals. Communication at long range strains a receiver's capabilities for both detection and recognition of signals, since attenuation of the intensity and degradation of the structure of signals increase with the distance between the sender and the receiver. Note that degradation of the structure of signals can affect a receiver's ability to discriminate among variants of signals even when detection is little problem, while attenuation always affects both detection and recognition.

III. FREQUENCY-DEPENDENT ATTENUATION

In the pioneering studies of sound transmission in natural environments in relation to properties of birdsong, one goal was to identify the optimal frequencies for long-range acoustic communication in different habitats (Morton, 1970, 1975; Chappuis, 1971). These studies showed greater attenuation of high frequencies in forests than in open habitats. Furthermore, a "sound window"

existed for transmission near the ground. Frequencies around 1–2 kHz attenuated less than either lower or higher frequencies (Marten and Marler, 1977; Marten *et al.*, 1977).

To understand the attenuation of sound in the atmosphere, we need to consider four processes: spherical spread, atmospheric absorption, scattering, and boundary interference. The latter three produce frequency-dependent attenuation and thus determine the optimal frequencies for long-range acoustic communication. However, these processes should not produce any consistent differences in optimal frequencies among natural habitats. Furthermore, “sound windows” should vary in complex ways that depend on the exact locations of the sender and receiver with respect to the ground and on features of the ground and the atmosphere.

A. Spherical Spread

As a result of the spherical spread of sound energy radiating from a source, intensity decreases in proportion to $1/r^2$, where r is the distance between source and receiver, a decrease of 6 dB for a doubling of r . This spherical spread of sound energy holds only for a homogeneous medium. We shall see that scattering, vertical gradients in temperature and wind, and reflective layers such as the ground or strata of vegetation interfere with spherical spread of sound. Spherical spread thus provides a standard against which other forms of attenuation are compared. Studies of sound propagation in the atmosphere concentrate on excess attenuation, attenuation in excess of the 6 dB per doubling of distance from spherical spread of sound energy. Some authors also subtract attenuation from atmospheric absorption in calculating excess attenuation.

Sound does not attenuate with $1/r^2$ in the immediate vicinity of a sound source, even in a homogeneous medium. In the near field of a source, intensity goes through a series of maxima and nulls with increasing distance from the source. Only when $r > 2a^2/\lambda$, where a = the radius of a cylindrical piston source (approximately similar to a circular cone loudspeaker) and λ = wavelength, does intensity decrease inversely with the square of the distance. Thus the inverse square law of spherical spreading can be used to extrapolate sound intensity back to approximately $r = 2a^2/\lambda$ but not any closer to the source (Kinsler and Frey, 1962, pp. 175–177; Gaunaurd and Überall, 1978). For a small animal this distance is only a few centimeters, but for many speakers it is about one meter.

B. Atmospheric Absorption

The absorption of sound energy by the atmosphere increases with frequency as a result of two processes (see Kinsler and Frey, 1962; Evans *et al.*, 1971; Beranek, 1971a). Energy dissipated as heat owing to the viscosity of the atmo-

sphere (the classical component of atmospheric absorption) is proportional to absolute temperature and the square of frequency. Energy dissipated in rotational and vibrational relaxation of oxygen molecules in the presence of water molecules (the molecular component) is strongly influenced by the percentage of water vapor in the atmosphere as well as by frequency. Harris (1966) presents detailed measurements of the absorption of sound in air as functions of temperature and relative humidity for frequencies between 125 Hz and 4 kHz, and Pöhlmann (1961) presents values for higher frequencies (see Griffin, 1971).

For any value of temperature and relative humidity, atmospheric absorption increases monotonically with frequency. For frequencies between 100 Hz and 10 kHz, except in very cold or dry air, absorption is proportional to frequency raised to a power between 1 and 2. In natural environments, measurements of sound attenuation invariably reveal greater attenuation of higher frequencies. At least some of this effect results from greater atmospheric absorption of higher frequencies. For instance, in Marten and Marler’s (1977) measurements of excess attenuation over open fields at a height of 10 m, attenuation increased with frequency approximately as expected from Harris’ data. Attenuation closer to the ground and in forested habitats is generally higher than expected for absorption alone, although increased absorption of higher frequencies affects the attenuation of sound in all environments.

Attenuation by absorption decreases as humidity increases, at least for conditions that apply to birdsong (frequencies below 8 kHz and percentage water vapor greater than 0.5%). In practice, this effect is small. A change in relative humidity from 50 to 90% reduces attenuation by absorption by less than 1 dB/100 m for frequencies below 2 kHz and temperatures greater than 5°C. For a frequency of 4 kHz, the effects of humidity are more appreciable in the range of temperature from 0° to 15°C, conditions that apply to songbirds in early spring. However, humidity and temperature have counteracting influences on attenuation by absorption. Since humidity often drops as temperature rises during a morning, attenuation by atmospheric absorption of sound might not vary in a regular pattern during a diurnal cycle.

C. Scattering

Scattering refers to the multiple reflection, diffraction, and refraction of sound by objects or heterogeneities in the atmosphere. It depends on the wavelength of sound in relation to the dimensions of objects or heterogeneities. As a consequence, scattering in natural environments is strongly dependent on frequency.

In acoustics the actual wave in a scattering medium is treated mathematically as if it were the result of a scattered wave interfering with the incident wave. The scattered wave is thus the difference between the actual wave and the undisturbed wave that would occur if the object were absent, and the total power of the

scattered wave is the power removed from the incident wave by scattering from the object (Morse and Ingard, 1968, Chapter 8). The scattered wave normally has two components, a reflected portion consisting of energy radiating in all directions from the object, and an interfering portion producing a shadow along the line of propagation of the incident wave behind the object. When the object is large in relation to the wavelength of the incident sound, the interfering and reflected components are equal. In other words, the energy reflected from the object equals the energy removed from the shadow behind the object. For wavelengths that approximate the radius of the object (within a factor of two or three) the spatial distribution of the scattering wave becomes extremely complicated with lobes extending in many directions. When the wavelength of the incident sound is large in relation to the object, the total scattered power is small, and no distinct shadow is formed behind a relatively rigid object. Most calculations of scattered waves assume an incident plane wave rather than a spherical wave. However, for a small source, propagating sound approaches the conditions of a plane wave, at least for relatively small areas of the wave front and at long distances from the source.

Near a small source, such as an animal or a loudspeaker, sound often radiates in a beam. Under these conditions one effect of scattering is to reduce sound intensity along the axis of the beam by deflecting energy outward; in effect, the angular spread of the beam increases progressively. Since the ratio of circumference to cross-sectional area decreases with distance from the source, a beam of sound in a scattering environment should attenuate more over a given distance near the source, where a greater proportion of the scattered sound leaves the beam, than at a great distance (Givens *et al.*, 1946; Schilling *et al.*, 1947). As a consequence, description of excess attenuation in scattering environments requires measurements at several distances from the source.

To evaluate sound attenuation in natural environments as a result of scattering, we need to consider scattering from two sorts of heterogeneities, (1) vegetation and (2) variations in the velocity and temperature of the air as a result of turbulence.

1. Scattering from Vegetation

Vegetation presents surfaces that are approximately cylindrical or spherical, since roughly circular objects like leaves in random orientations have average effects similar to those of spheres. Scattering of sound by a single cylinder or sphere and by an array or cloud of cylinders or spheres has received considerable attention in the acoustic literature (Morse and Ingard, 1968, Chapter 8; Johnson, 1977; Embleton, 1966). In all of these cases, scattering is a function of the frequency of the incident sound, but scattering can either increase or decrease with frequency depending on the surface impedance of the objects. Acoustical impedance is analogous to electrical impedance in circuits with alternating current. It includes resistance and reactance that impede the propagation of sound.

Embleton has calculated the attenuation of a plane wave by an array of cylinders to illustrate the dependence of scattering on surface impedance. For rigid cylinders (impedance approaching infinity), attenuation by scattering increases as a sigmoid function of frequency. The inflection point occurs at the frequency corresponding to a ratio $d/\lambda = \pi$, where d is the diameter of the cylinders and λ is the wavelength. In contrast, soft cylinders (impedance approaches 0) scatter less sound as frequency increases. At very high frequencies ($d/\lambda > 10\pi$), regardless of the surface impedance of the cylinders, scattered power converges on a value of $8.8 \text{ dB}(Na)/100 \text{ m}$, where N is the number of cylinders per unit area and a is the mean radius of the cylinders. In other words, the asymptotic attenuation at high frequencies is proportional to the density of objects times their average radius. Thus for approximately rigid objects, like the trunks and large limbs of trees, attenuation of sound by scattering depends primarily on the density of objects with radii substantially larger than 1λ . As frequency increases (shorter wavelengths), smaller objects become effective scatterers of sound. The density of effective scatterers thus increases with frequency in forests.

The only attempts to compare theoretical expectations for attenuation from scattering and actual measurements of excess attenuation in natural environments are Aylor's (1971) studies in hemlock and pine forests. For 8-kHz tones, he measured attenuation of 28 dB through 69 m of hemlock and 18.5 dB through 92 m of pine. These values agree nicely with Aylor's calculated values of 25 and 16 dB, respectively. However, his approximate expression for attenuation of high frequencies as a result of scattering from an array of rigid cylinders yields results somewhat different from those of Embleton's procedure, discussed above. The latter, including the corrections for the asymptotic attenuation at the high-frequency limit, yields expected values of about 15 dB for both of Aylor's measurements. Unlike Embleton's calculations, in which attenuation of sound by scattering is directly proportional to Na , at least for values such as those that apply to natural forests, Aylor's calculations do not yield values of attenuation directly proportional to Na (see also Morse and Ingard, 1968, p. 441). The resolution of these discrepancies must await further research. However, the available information suggests that we can expect attenuation by scattering in forests to reach at least 10 dB/100 m for frequencies above 1 kHz.

The effects of foliage on attenuation by scattering are clear in Aylor's (1971) measurements of excess attenuation in fields of corn with different densities of plants. Attenuation at 1 kHz increases less steeply as foliage density increases compared to attenuation at 4 kHz. Attenuation of sound by dense second-growth brush before and after the leaves had dropped in autumn showed similar effects. At 10 m above ground in a deciduous forest, Marten and Marler (1977) found that foliage increased attenuation of frequencies between 2 and 11 kHz by about 10 dB/100 m (Fig. 2). In this case, foliage had approximately the same effect on attenuation for all frequencies above 2 kHz. Deciduous forests have rather uniform leaf sizes, roughly 3–5 cm in radius. Frequencies above 2–3 kHz would

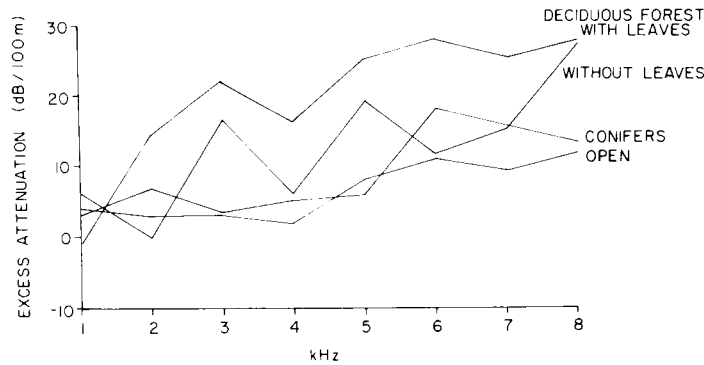


Fig. 2. Excess attenuation as a function of frequency in four natural habitats over a distance of 100 m at a height of 10 m above ground (after Marten and Marler, 1977): a deciduous forest with and without leaves; a coniferous forest; and an open field with little wind. Frequencies between 1 and 8 kHz are those used most for long-range communication by passerine birds.

thus have uniform attenuation by scattering. In coniferous forests at 10 m above ground, attenuation was lower than in a deciduous forest with leaves (Marten and Marler, 1977). Evidently conifer needles scatter little sound at frequencies below 10 kHz. Thus trunks, large limbs, and the broad leaves of dicotyledonous trees are important in attenuating sound above 1–2 kHz, well within the frequency range used by singing birds.

2. Scattering from Turbulence

Attenuation of sound by scattering from atmospheric turbulence results from the refraction of sound by cells of air that differ in temperature or velocity from the surrounding medium. Interference between the scattered and undisturbed waves can attenuate sound in the direction of propagation. Just as for scattering from solid objects, scattering from atmospheric heterogeneities in turbulent air becomes more pronounced at higher frequencies and thus shorter wavelengths in relation to the scale of the atmospheric heterogeneity. In addition, at higher frequencies the scattered wave is more narrowly concentrated in the forward direction, where it produces interference with the undisturbed wave, just as in scattering from solid objects.

The effects of turbulence in attenuating sound by scattering have not received experimental study. Nevertheless, theory suggests that it is worth serious consideration. For frequencies corresponding to wavelengths less than the scale of the turbulence, scattered power from a unit volume increases with the square of frequency (Lighthill, 1953):

$$\text{Attenuation} = 2k^2LM^2$$

where $k = 2\pi f/c$, L is the scale of the turbulence, and M is the Mach number of the fluctuations (RMS velocity in the direction of propagation divided by c , the velocity of sound). With $L = 1$ m and $v = 1$ m/sec, attenuation of a 1-kHz tone would amount to 2.6 dB/100 m. On the other hand, at 10 kHz attenuation would reach 3.8 dB/m, more than 100 times greater than at 1 kHz. Even moderate atmospheric turbulence should result in severe attenuation of the higher frequencies used by birds for singing. Scattering from atmospheric turbulence should thus have much the same effect on the attenuation of sound as scattering from vegetation and atmospheric absorption. All three processes in general produce increasing attenuation with increasing frequency, particularly in the range between 1 and 10 kHz. Attenuation by turbulence and vegetation should often exceed attenuation by absorption.

Atmospheric turbulence can result from wind shear over irregular surfaces and also from temperature gradients near the surface of the ground or the top of a forest canopy (Munn, 1966; Stringer, 1972, Chapter 3). Temperature gradients that exceed the adiabatic lapse rate for air (about $-10^\circ\text{C}/\text{km}$) result in cells of warmer air rising from the surface and expanding. Over irregular surfaces wind shear produces vortices and thus fluctuations in wind velocity. Although any wind in a forest is likely to be highly turbulent, wind velocity is normally lower inside forests than in open areas. Thus heterogeneity in the atmosphere caused by turbulence primarily affects open habitats, where the effect is usually strongest during midday when the sun heats the surface. We can expect that on calm days open habitats attenuate sounds above 1–2 kHz less than forested habitats. Under windy conditions, scattering of sound should become much more comparable in open and forested habitats.

D. Boundary Interference

A reflecting boundary near the path of transmission affects sound in two ways: (1) as a result of interference between the direct wave from the sender to the receiver and the reflected wave from the boundary; and (2) as a result of additional waves propagating in and near the ground. In natural environments, this situation frequently arises for acoustic communication between individuals near the ground. Like all interference phenomena, this effect depends strongly on frequency. Thus it is the third major source of attenuation that varies with frequency.

1. Reflected Waves

The nature of interference between the direct and reflected waves depends on three factors: the difference in path length; the acoustical impedance of the surface (Embleton *et al.*, 1976; Donato, 1976; Chessell, 1977; Thomasson, 1977); and irregularities in the medium or the surface which affect the coherence

of the direct and reflected waves (Ingard and Maling, 1963; Daigle *et al.*, 1978; Daigle, 1979).

The importance of the difference in path length is easily appreciated. For a perfectly homogeneous medium and a smooth rigid surface, the difference in the lengths of the direct and reflected paths in relation to the wavelength of the propagating sound completely determines the nature of interference at the receiver. When the difference in path lengths equals one-half wavelength (or an odd multiple of $\lambda/2$), destructive interference at the receiver would reach a maximum and intensity at the receiver would approach 0. When the path length difference equals one wave length (or an integer multiple of λ), constructive interference would double the intensity at the receiver.

The difference in path length, ΔR , between a sender and a receiver at the same height above ground equals

$$\sqrt{4h^2 + r^2} - r$$

where h is the height and r is the horizontal distance between sender and receiver. As height increases the difference in path length increases approximately proportionately. Thus for transmission over a given distance, the lowest frequency for maximal destructive interference decreases as height increases. As range increases from 0 to very large distances, the path length difference decreases from $2h$ to nearly 0. The lowest frequency for maximal destructive interference also increases, although very slowly when r is large in comparison to h .

For several reasons, these simple calculations of differences in path length do not permit an exact prediction of the frequencies for maximal destructive interference in natural habitats. First, reflection from a surface of finite impedance, like the ground, introduces a phase change in the reflected wave which shifts the frequencies for maximal interference. Second, measurements under field conditions usually do not reveal evidence of destructive interference at frequencies above 1 or 2 kHz (Marten and Marler, 1977; Marten *et al.*, 1977). This lack of clear interference patterns for higher frequencies results from irregularities in the medium and the surface, which scatter the propagating waves and thus destroy their coherence. Third, propagation of sound with angles of reflection close to grazing involves two additional modes of propagation, a ground wave in the ground itself and a surface wave coupled to the ground but in the air immediately above the surface. To understand the effects of boundary interference, we must consider these three features in turn (see Rudnick, 1947b; Ingard, 1951, 1953, 1969; Embleton *et al.*, 1976; Donato, 1976; Thomasson, 1977; Piercy *et al.*, 1977).

Comparisons of sound attenuation at 1.2 m above asphalt and closely mown grass show how a phase shift in the reflected wave can change the frequencies for maximal destructive interference (Embleton *et al.*, 1976). The grass introduces a large phase change in the reflected wave at frequencies above about 1 kHz. In

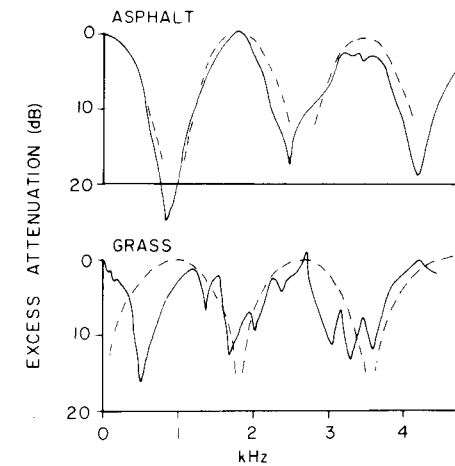


Fig. 3. Excess attenuation as a function of frequency above two surfaces over a distance of 15 m at a height of 1.2 m above ground (solid lines; after Embleton *et al.*, 1976). Dashed lines represent waves with no phase change on reflection (asphalt) or 180° phase change on reflection (grass).

contrast, the asphalt surface has an impedance large enough that phase changes on reflection are negligible. In fact, the phase change on reflection by the grass approaches 180° to judge from Embleton *et al.* (1976). The lowest frequency for destructive interference shifts from about 900 Hz for propagation over asphalt ($r = 15$ m, $h = 1.2$ m) to approximately 1800 Hz for propagation over grass (Fig. 3).

Note, however, that grass also attenuates frequencies around 500 Hz (Fig. 3). Below 1 kHz, the acoustic impedance of mown grass increases sharply. The impedance varies approximately inversely with the square root of frequency (Embleton *et al.*, 1976) and increases fivefold between 1 kHz and 100 Hz. This dependence of acoustic impedance on frequency introduces a major peak of attenuation at about 500 Hz, for a difference in path length (ΔR) about equal to $\frac{1}{4}\lambda$ (Fig. 3). A similar peak of attenuation at 300–800 Hz often appears in studies of sound propagation in natural habitats (Morton, 1975; Aylor, 1971; Marten and Marler, 1977; Marten *et al.*, 1977; Waser and Waser, 1977). The location of this peak is primarily determined by the frequency-dependent acoustic impedance of the ground below 1 kHz and the consequent frequency-dependent phase change on reflection. Changes in ΔR with changes in height or range have little effect on this attenuation.

We can see how this frequency-dependent change in impedance produces attenuation below 1 kHz as follows (Fig. 4). Recall that the surface changes from low to high impedance as frequency drops from 1 kHz toward 0. A low impedance surface, inducing a large phase change on reflection, produces *destructive*

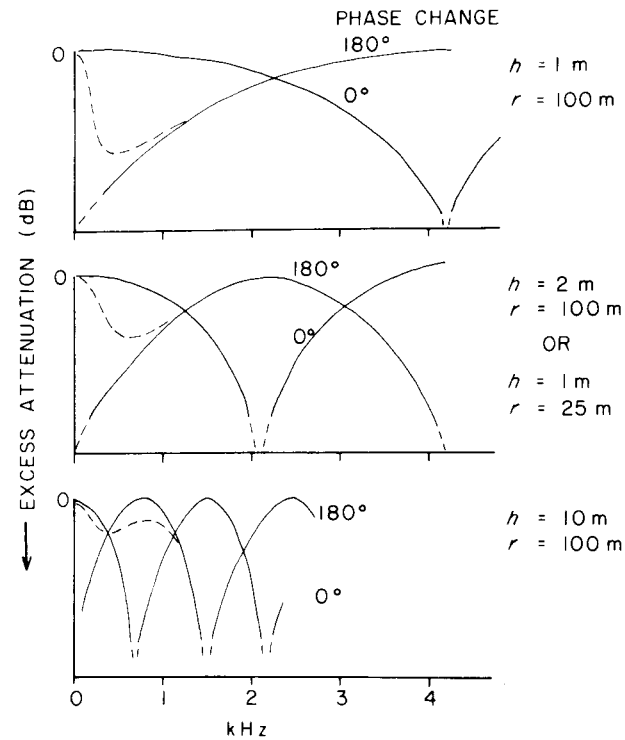


Fig. 4. Schematic representation of excess attenuation expected for frequencies below 1 kHz, when the acoustic impedance of the ground varies inversely with frequency below 1 kHz. For each combination of height (h) and horizontal range (r), two solid lines show the attenuation expected from interference between direct and reflected waves with 0° and 180° phase changes on reflection. The dashed line in each case indicates the attenuation expected when the phase change increases from 0° to 180° as frequency decreases from 1 to 0 kHz. Note that the peak in excess attenuation becomes less pronounced as height increases or range decreases.

interference for $\Delta R/\lambda$ near 0. In contrast, a surface of high impedance, inducing little phase change on reflection, produces *constructive* interference for $\Delta R/\lambda$ near 0. Thus as frequency decreases below 1 kHz (wavelength increases), attenuation passes through a maximum value and then decreases as frequency approaches 0 (Fig. 4). The maximal attenuation reached depends on the height of propagation above ground and the range, but the location of this peak changes little (see Piercy *et al.*, 1977, for more details).

In measurements of sound attenuation in natural environments, little evidence of interference appears for frequencies above 2 kHz (Marten and Marler, 1977; Morton, 1975; Waser and Waser, 1977). In the experiments by Embleton *et al.*

(1976) the interference maxima are irregular at higher frequencies. Also the maxima for destructive interference do not reach infinite attenuation as predicted from coherent interference between direct and reflected waves. This smoothing of the interference peaks particularly at higher frequencies results from turbulence in the atmosphere and irregularities of the surface which reduce the coherence of the propagating waves (Daigle *et al.*, 1978; Daigle, 1979). Recall that turbulence affects higher frequencies and correspondingly smaller wavelengths more than it does lower frequencies. Thus at long range under even mild conditions of turbulence and irregularity in the environment, the interference peaks at high frequencies largely disappear.

2. Ground and Surface Waves

When the wave reflected from a boundary travels at near grazing incidence, propagation of sound includes some additional properties (Embleton *et al.*, 1976; Piercy *et al.*, 1977; Chessell, 1977). Reflection at grazing incidence occurs when the height of the sender and receiver is small in relation to the range of propagation, so that the same considerations apply to insects or other small animals communicating over distances of a few meters just above the surface of the ground (Michelsen, 1978) and to larger animals communicating over longer distances at a height of several decimeters or even a meter.

For surfaces with finite impedance, such as grass or soil, reflection at grazing incidence involves essentially a 180° phase change. The reflection coefficient for a locally reacting surface equals

$$\frac{\sin \theta - \rho c/Z}{\sin \theta + \rho c/Z}$$

where ρc is the characteristic acoustic impedance of the air, Z is the normal specific impedance of the ground, and θ is the angle of incidence of the reflected wave. As θ becomes small, $\sin \theta$ becomes small in relation to $\rho c/Z$ and the reflection coefficient approaches -1 . The consequence, in this first approximation of interference between direct and reflected waves at grazing incidence, is essentially complete destructive interference between direct and reflected waves; essentially no sound would propagate between the sender and the receiver. Actual measurements show that this first approximation is far from accurate. In fact, in this situation low frequencies propagate with little excess attenuation, while frequencies above some cutoff attenuate rapidly; the effect is rather like communication through a low-pass filter.

The propagation of low frequencies in spite of near cancellation between the direct and reflected waves results from two additional terms in the wave equations, usually termed a ground wave and a surface wave. These two terms describe the interaction of a curved wave front with a surface of finite impedance. For a spherically spreading wave, the ground wave and surface waves

become negligible as the range of propagation becomes large. For transmission at grazing incidence above real surfaces for moderate distances, the ground wave in particular results in propagation of low frequencies. Under these conditions, the cutoff frequency above which sound is severely attenuated decreases as range increases. In practice, long-range propagation of sound close to the ground is effectively limited to frequencies below 1 kHz.

For a source near the ground, as the receiver moves higher above the ground, progressively more sound above the cutoff frequency reaches the receiver (Embleton *et al.*, 1976). If both source and receiver move upward away from the ground, the spectrum of received sound transforms into the pattern of interference peaks, discussed above.

3. Applications

In summary, boundary interference has complex effects on sound. Attenuation results from interference between direct and reflected waves from the sender to the receiver, which in turn depend on the height, range, surface impedance, and turbulence in the medium. In natural environments, destructive interference primarily affects a band of low frequencies, approximately 0.5–1 kHz, especially for propagation about 1 m above ground and ranges on the order of 100 m. Attenuation in this band of frequencies results primarily from the sharp increase in the acoustic impedance of the ground as frequency decreases below 1 kHz. Attenuation by destructive interference between direct and reflected waves is much less pronounced at frequencies above 1–2 kHz, since scattering of sound destroys the coherence of direct and reflected waves. In addition, for very low height/range ratios sound propagation is effectively restricted to low frequencies, with the cutoff frequency increasing as the h/r ratio increases.

The acoustic impedance of the ground, critical for understanding boundary interference in natural environments, has not received extensive study. Technical difficulties make precise measurements difficult. Apparently the surface impedance of closely mown grass and that of forest floor do not differ greatly (Piercy *et al.*, 1977). The porosity of the soil as a result of root action seems to determine the acoustic impedance (Aylor, 1971; Piercy *et al.*, 1977). Other surfaces, snow, water, and sand for instance, might differ more. In addition, a surface covered with relatively deep vegetation, such as an old field or a forest canopy, would act like an absorbing baffle and reflect little sound, at least at frequencies above 0.5–1 kHz. It seems possible that birds singing from shrubs projecting from an old field might encounter little boundary interference. In fact, in some measurements of sound propagation above tall grass, there is little evidence of boundary interference (Morton, 1975; Marten and Marler, 1977).

Interference between direct and reflected waves is unlikely to have much effect on frequencies above 1–2 kHz at moderate or long distances from the source. The coherence of these waves is lost during transmission as a result of

scattering. The suggestion that such interference could create pronounced patterns of frequency-dependent attenuation at distances of 50–200 m from the source (Roberts *et al.*, 1979) needs further verification.

Most measurements of attenuation in natural environments are not easily compared with predictions concerning the effects of boundary interference. It has become standard procedure to use a microphone close to the speaker to determine the output of the speaker. The response from a more distant microphone is then compared to the response from this reference microphone. However, it is clear that both microphones are affected by interference between direct and reflected waves. Owing to the differences in the distances of the two microphones from the speaker, interference differs at the two microphones. To avoid this problem, Embleton *et al.* (1976) used a single microphone and determined the frequency response of their speaker independently.

Furthermore, attenuation by boundary interference, like attenuation of a beam of sound by scattering and attenuation by spherical spread, is not a linear function of the distance between source and receiver. A determination of excess attenuation at a single distance from the source does not permit conclusions about excess attenuation at other distances, whenever scattering or boundary effects are appreciable. In these circumstances, it is necessary to determine excess attenuation at two or more distances from the source in order to extrapolate attenuation at other distances (Michelsen, 1978; Wiley and Richards, 1978).

E. Differences between Habitats

The preceding review leads to no clear prediction for differences among natural habitats in the optimal frequency for long-range acoustic communication. Consider the possibilities for such differences from each of the sources of attenuation. Atmospheric absorption results in increasing attenuation as frequency increases, regardless of habitat. Scattering also increases attenuation as frequency increases. In forests, scattering from vegetation has the greatest effect, while in open habitats, scattering from atmospheric turbulence predominates. Thus attenuation from scattering is probably lower in open habitats under conditions of low atmospheric turbulence, such as at night or in early morning with little wind. The absolute level of attenuation from absorption or scattering could differ between open and forested habitats, depending on the humidity and turbulence of the atmosphere, but both processes have a similar dependence on frequency under all conditions. To reduce attenuation by absorption and scattering, it is always best to use the lowest frequencies possible.

Boundary interference has more complicated effects. It primarily influences possibilities for acoustic communication within 1–2 m above ground. Again, these effects should not differ with habitat in any systematic way. For sound transmission over deep vegetation, such as old fields or marshes, boundary

interference would decrease as a result of absorption of the reflected wave by the vegetation. In this case there is no restriction on the use of the 0.5- to 1-kHz band close to the surface. To summarize, lower frequencies attenuate less in all habitats, with the exception that sound propagation near the ground is subject to destructive interference. For maximum efficiency, long-range acoustic communication in any habitat should employ the lowest frequencies possible.

In spite of these considerations, several studies have reported that the average frequencies of songs differ in forested and open habitats. In particular, birds in tropical forests average lower frequencies in their long-range songs than do birds of open habitats (Morton, 1970, 1975; Chappuis, 1971). On the other hand, in a survey of birds in open habitats and forests in North Carolina, we could find no differences in the frequencies of songs (Richards and Wiley, 1980). We thus confront two problems: no clear reason why birds in forests and open habitats should emphasize different frequencies; and a possible difference between tropical and temperate habitats.

These problems are perhaps resolved in part by one striking feature of birds in tropical forests: some species habitually sing very close to or actually on the ground. Singing on or near the ground rarely occurs in temperate forests, as indicated by our information for a North Carolina deciduous forest (Fig. 5). Even those species that feed on the ground rarely sing any lower than 3 m. The Wood Thrush (*Hylocichla mustelina*) and Ovenbird (*Seiurus aurocapillus*), which feed almost exclusively on the ground, usually sing about 10–20 m above ground. This avoidance of long-range communication close to the ground reduces the effects of boundary interference.

In contrast, in tropical forests some species sing while actually walking on the ground. In neotropical forests, species in several genera of the family Formicariidae (antbirds) regularly sing either on or within 1 m of the ground (particularly genera like *Formicarius* and *Grallaria*; Slud, 1960; Ridgely, 1976). These songs are long-range signals, as individuals of these species are often widely separated in the forest. They have the striking features that we associate with birdsong in neotropical forests: steady tones of unusually low frequencies for a passerine (1–2 kHz). Because propagation of sound at grazing incidence with respect to the ground is subject to stringent low-pass filtering, frequencies above 1–2 kHz are effectively useless. It is not possible to predict the exact cutoff frequencies for these antbirds without further study. Simply standing on a log would make a substantial difference in the attenuation of an antbird song.

A number of non-passerine birds produce remarkably low frequency sounds for long-range communication from positions near the ground. The booming calls of many grouse (Tetraonidae) are prime examples, often clearly audible more than a kilometer away (Greenewalt, 1968; Hjorth, 1970; Wiley, 1973). Ground-dwelling curassows (Cracidae), a neotropical gallinaceous group, also produce sounds of extremely low frequency (100–200 Hz) (Delacour and

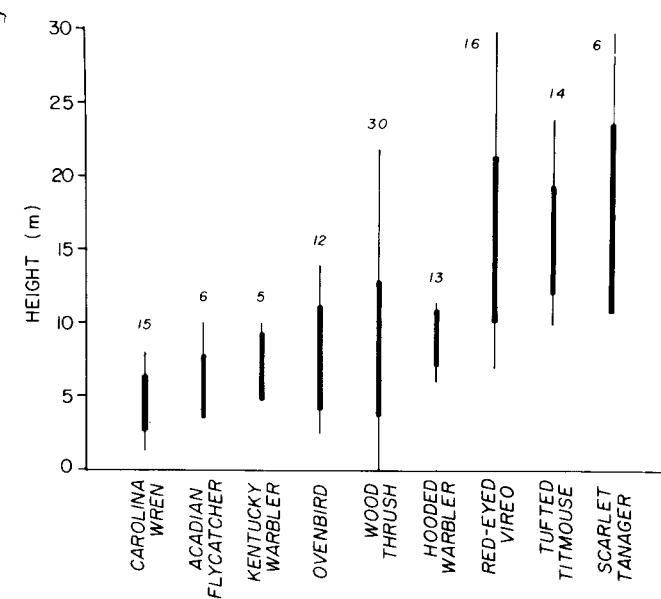


Fig. 5. Heights of undisturbed singing birds in a deciduous forest in North Carolina during May. For each species, the plot shows the mean, 1 SD on either side of the mean, and the range of observed heights. Above each bar is the sample size (number of separate perches on which uninterrupted singing continued for at least 30 sec); samples included two to eight individuals of each species. Wood Thrushes and Ovenbirds feed on the ground; Carolina Wrens feed primarily within 2 m of the ground. The remaining species forage at approximately the same heights at which they sing. Species listed are *Thryothorus ludovicianus*, *Empidonax virescens*, *Oporornis formosus*, *Seiurus aurocapillus*, *Hylocichla mustelina*, *Wilsonia citrina*, *Vireo olivaceus*, *Parus bicolor*, and *Piranga olivacea*, respectively.

Amadon, 1973). The Ruffed Grouse (*Bonasa umbellus*) uses its wings to produce mechanical sounds of very low frequency (Hjorth, 1970). All of these apparently bizarre acoustic signals seem ideally adapted for long-range communication at grazing incidence with the ground.

Aside from interference near the ground, patterns of attenuation in all habitats favor low frequencies for long-range communication. Many owls, doves, and cuckoos employ frequencies below 1 kHz for long-range acoustic signals (Greenewalt, 1968). Why, then, do passerines rely on frequencies above 1 kHz for long-range communication (Fig. 6)? The answer probably lies partly in the small sizes of most songbirds. Sound sources with small dimensions, regardless of the exact method of sound production, cannot efficiently produce low-frequency sounds (Kinsler and Frey, 1962). In general, the frequencies emphasized in loud vocalizations vary inversely with a bird's size (Konishi, 1970a; Bowman, 1979).

One technique for increasing the efficiency of a sound radiator at low frequencies is to couple it with an exponential horn (Kinsler and Frey, 1962). At low

frequencies, a horn serves to match the radiation impedance to the relatively large impedance of the large volume of air outside. In addition, a resonating air sac, crop, esophagus, gular pouch, or tracheal sac could increase the radiation efficiency of low-frequency sounds. However, most passerines have no anatomical structures large enough to serve as effective horns for frequencies below 5–10 kHz nor large enough to resonate at frequencies below about 2 kHz. The tropical antbirds that sing on the ground are undoubtedly under the strongest selection to lower the frequencies of their songs; perhaps they have gone as far in this direction as a small bird can. The grouse and curassows already noted for the extremely low frequencies in their long-range signals could use resonating esophageal sacs of trachea for producing these sounds, although acoustical studies have not established this point. Woodpeckers, even small ones, can use hollow trees for this purpose.

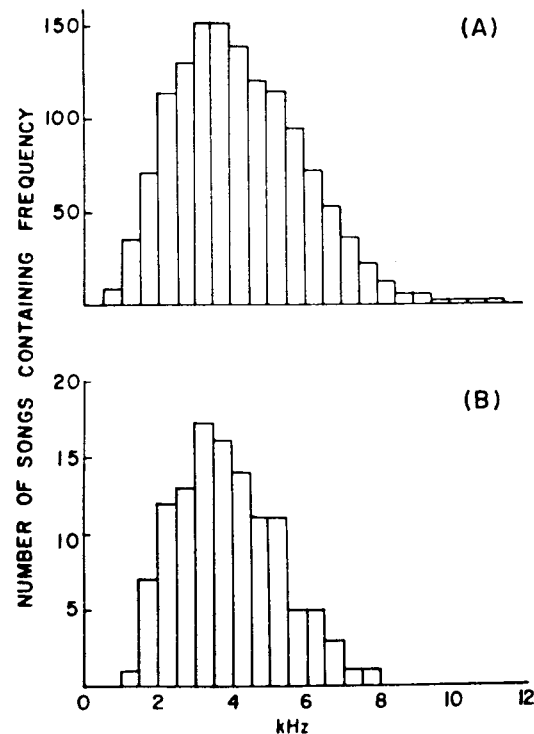


Fig. 6. Numbers of species of birds that use each 500 Hz band of frequencies in their songs. (A) All North American species; (B) species that breed in a deciduous forest in North Carolina. (Both based on measurements of maximum and minimum frequencies on the sonagrams in Robbins *et al.*, 1966.)

An additional limitation on the use of low-frequency acoustic signals for long-range communication is the threshold for hearing, which in passerines rises steeply below 2 or 3 kHz (Konishi, 1970b, 1973b; Dooling *et al.*, 1971, 1978; Dooling, Chapter 4, this volume). The frequencies in the long-range songs of passerines (Fig. 6) are roughly the mirror image of hearing thresholds for passerines.

At present, we are left with questions. Do grouse and curassows have unusual thresholds for hearing at low frequencies? Or does the reduced attenuation of low frequencies compensate for the higher thresholds of hearing? What limits the evolution of greater sensitivity to low frequencies in those passerines that use long-range acoustic communication? Or do the constraints on radiation of low-frequency sounds alone explain the reliance on frequencies above 1 kHz?

Although the best frequencies for long-range propagation of sound probably do not differ much among natural habitats, there still might be differences in the bands of acceptable frequencies. In open habitats, at least during periods of calm weather, frequencies above 3–4 kHz attenuate less than in forests, so that in the open these frequencies might prove acceptable, even though not optimal. In forests, scattering from foliage would always attenuate these frequencies regardless of weather. Perhaps a difference in the acceptable bandwidth for long-range songs explains why songs of Great Tits (*Parus major*) average lower frequencies in forests than in open woodland (Hunter and Krebs, 1979). In any habitat, the upper limit of the band of acceptable frequencies is also constrained by auditory thresholds. Since auditory thresholds of passerines rise 25 dB between 4 and 8 kHz (Konishi, 1970b; Dooling *et al.*, 1971, 1978), frequencies much higher than 4 kHz would not permit long-range communication in any case. Bowman (1979) presents some suggestive examples of Darwin's finches (Emberizidae) with bandwidths of song that match the patterns of attenuation in natural habitats. It is not yet clear how general these patterns are, nor how they relate to differences in vegetation.

In studies of attenuation in natural environments, measurements are often obtained for only one location within each habitat and even then not replicated. Furthermore, most such studies have intentionally measured attenuation in open habitats at times when atmospheric turbulence is slight, such as early in the morning in the absence of wind. Birds of open habitats as well as forests sing more at such times than later in the day or during windy weather, but nevertheless long-range communication in open habitats must often contend with turbulence, which as we have seen would attenuate higher frequencies more than lower ones. To compare attenuation of sound in open and forested habitats definitively, we need repeated measurements within each habitat, at different locations, heights above ground, distances, times of day, and weather conditions.

IV. DEGRADATION OF ACOUSTIC SIGNALS

So far we have focused on attenuation, the progressive reduction in the intensity of sound in the course of propagation through natural environments. In most cases, communication requires more than simple detection by the receiver of the presence or absence of sound of a given frequency. The receiver must discriminate among signals with different acoustic structures, in other words different patterns of frequency and intensity in time. Consequently, degradation of these patterns during the propagation of a signal is another major limitation on long-range communication, in addition to any attenuation of the signal.

If we turn to two processes that degrade the structure of acoustic signals, a clear difference between habitats emerges. Communication through dense vegetation, for instance, between birds in a forest, must contend with strong reverberations, while communication through a turbulent atmosphere, as between birds in an open field at midday, must contend with strong fluctuations in the amplitude of signals. Reverberations and irregular amplitude fluctuations have different consequences for communication.

A. Reverberation

Reverberations, which result from multiple reflections and scattering of sound during propagation, are often apparent in sonagrams of sounds recorded in a forest (Fig. 7). When a source produces a square pulse of sound at a given frequency, a receiver some distance away in a forest detects a pulse that rises to its maximal amplitude and then decays gradually. In environments with many reflecting surfaces, like a forest, the decay of received energy results from sound

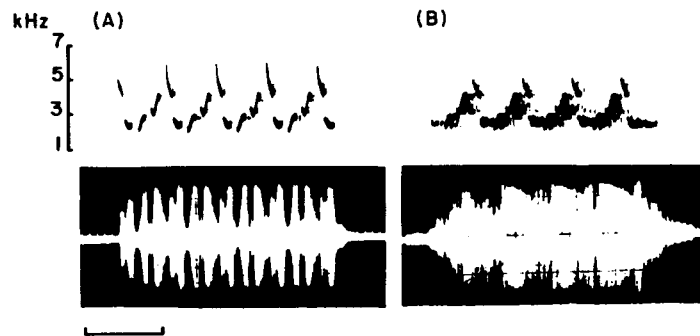


Fig. 7. Songs of Carolina Wrens (*Thryothorus ludovicianus*) recorded 10 m (A) and 50 m (B) from the singing bird to show the effects of reverberation. Upper, sonagram; lower, oscillogram. Time mark, 1.0 sec. Note that the basic pattern of frequency is preserved at a distance of 50 m although the pattern of amplitude is completely lost.

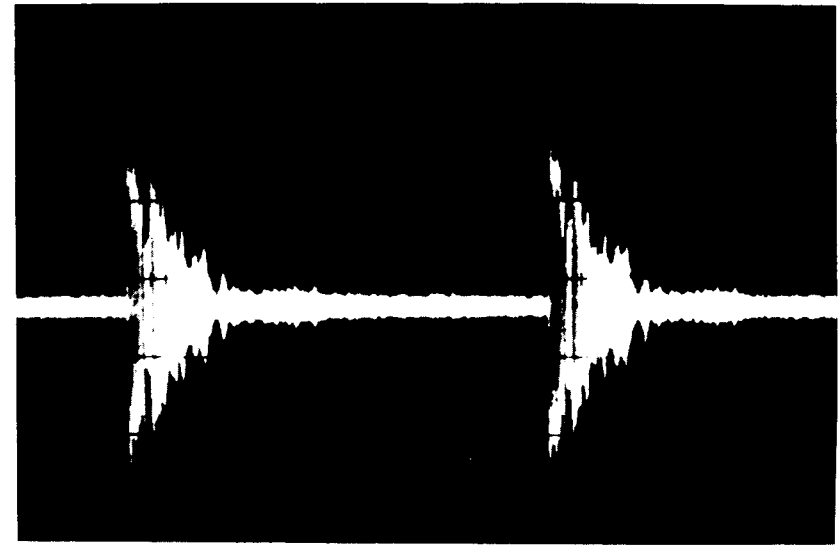


Fig. 8. Reverberations of two 25-msec square pulses of 8 kHz sound recorded 25 m from a speaker in a deciduous forest. Time mark, 100 msec. (After Richards and Wiley, 1980.)

that has traveled over progressively longer paths in the course of multiple reflections and scatterings. For environments with numerous reflecting surfaces in complex arrangement, the decay is roughly exponential (Kinsler and Frey, 1962; Beranek, 1971b; Embleton, 1971). The increase in sound intensity on the leading edge depends on the relative intensity of the direct wave in relation to reflected and scattered waves. At a distance of 25 m in a mixed deciduous forest, a pulse of 8 kHz has a relatively sharp leading edge but decays slowly (Fig. 8) (Richards and Wiley, 1980).

Since reverberations depend on multiple reflections and scattering, they should vary in intensity with frequency and the presence of foliage. In a mixed deciduous forest, reverberations for frequencies above 4 kHz are stronger with leaves on the trees than without leaves. Reverberations are essentially absent in an open field at a distance from any forest edge on a calm day. In addition, at least at moderate distances between the source and the receiver, reverberations should depend on the directivity of the source. Reverberations are substantially greater for an omnidirectional speaker than for a much more directional horn speaker (Richards and Wiley, 1980). Reverberations should also increase markedly as the range of communication increases, although this effect has not yet been measured. The dependence of reverberations on frequency provides

another reason for long-range acoustic communication in forests to avoid signals with high frequencies.

Reverberations create difficulties for a receiver attempting to resolve rapid amplitude modulations at a given frequency. Reverberations decay rapidly (>3 dB/50 msec) in a forest even at high frequencies. Consequently, reverberations primarily interfere with the separation of rapidly repeated pulses of sound. For instance, in the presence of reverberation, the trills in some birds' songs blend into a sound of almost constant intensity.

In contrast, reverberations have little effect on recognition of frequency modulation. For receivers that can discriminate frequencies, like all birds and mammals, reverberations at one frequency do not interfere with the reception of a pulse of sound at another frequency (outside the masking bandwidth of the first frequency). Signals that avoided rapid repetition of any one frequency would minimize interference from reverberations. The song of the Carolina Wren (*Thryothorus ludovicianus*) provides a good example of a complex acoustic structure that avoids rapid repetitions of a given frequency (Fig. 7).

Reverberations thus primarily mask rapid amplitude modulation (AM) and rapid, repetitive frequency modulation (FM) in acoustic signals. Since forested and open habitats clearly differ in reverberation, forest birds should, in general, avoid rapid, repetitive FM in comparison to birds of open habitats. Morton (1970, 1975) and Chappuis (1971) reported just this trend for birds in tropical forests and open habitats. Even populations of the same species differ in this way: Rufous-collared Sparrows (*Zonotrichia capensis*) sing slower trills in wooded than in open habitats (Nottebohm, 1975). Among passerines breeding in North Carolina, more than 40% of forest birds lack rapid, repetitive FM (minimum time between repetitions of the same frequency greater than 0.1 sec) while only 15% of birds in open habitats lack such rapid repetitions (Richards and Wiley, 1980).

Nevertheless, most birds in forests (60%) did include some rapid, repetitive FM in their territorial songs. Properties of signals that degrade rapidly with distance can serve for communication between individuals nearby. In addition, acoustic signals can incorporate some degradable features in order to permit a receiver to judge the source's distance (see below).

B. Amplitude Fluctuations

Sound propagating through turbulence acquires irregular amplitude fluctuations. While reflections from stationary objects always produce standing patterns of amplitude in space, moving or nonstationary heterogeneities in the medium produce nonstationary amplitude patterns at any one locus. A constant tone at the source thus acquires irregular amplitude fluctuations after propagating through a turbulent atmosphere or in the presence of irregularly moving objects (Fig. 9)

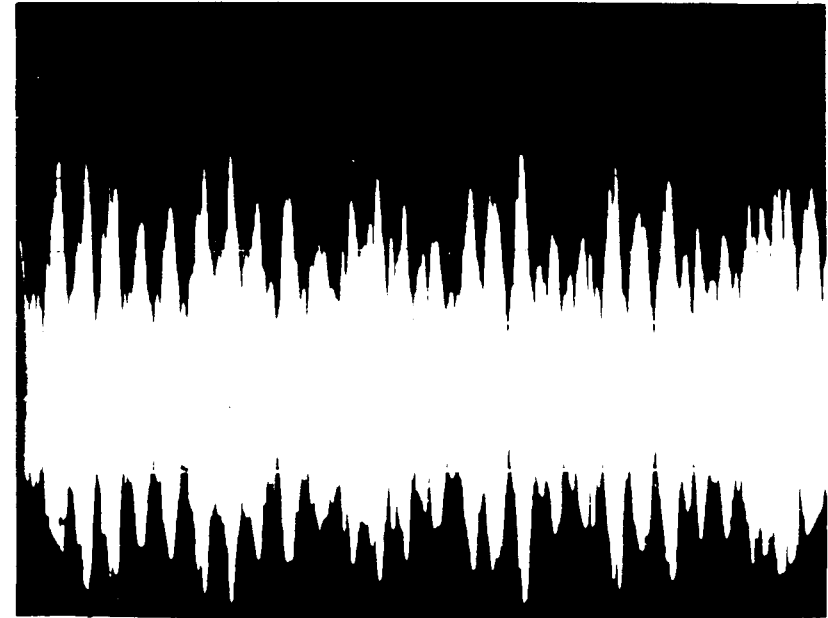


Fig. 9. Amplitude fluctuations of a 2-kHz tone recorded 60 m from a speaker in a deciduous forest. Total duration, 1 sec. (After Richards and Wiley, 1980.)

(Knudsen, 1946; Rudnick, 1947a; Richardson, 1950; Wiener and Keast, 1959; Kriebel, 1972; Embleton *et al.*, 1974; Marten and Marler, 1977; Marten *et al.*, 1977; Waser and Waser, 1977).

The theory of wave propagation through a randomly varying, isotropic medium is well developed (Chernov, 1960; Tatarski, 1961; Tolstoy and Clay, 1966; Ishimaru, 1978). In general, amplitude fluctuations increase in direct proportion to the square of frequency, the distance of propagation, and two parameters of the turbulence, the mean square fluctuations of refractive index and the dimensions of the largest scale of eddies or heterogeneities. Amplitude fluctuations of sound in a forest are appreciable even during light breezes (Richards and Wiley, 1980). Peak values of amplitude fluctuations for pure tones exceed 36 dB under all conditions except barely perceptible breezes. These fluctuations generally increase with frequency and distance, but turbulence as a result of even a light wind near the ground is the principal determinant of the intensity of the fluctuations.

These amplitude fluctuations mask amplitude modulation in a signal. To know which rates of AM are masked, we need to know the spectrum of the amplitude fluctuations caused by turbulence. Fluctuations recorded under various conditions of wind speed all have similar spectra (Richards and Wiley, 1980). In all

cases, spectral density decreases approximately exponentially with frequency more than 30 dB between 1 and 50 Hz. Thus, random amplitude fluctuations induced by turbulence mask primarily low rates of AM (less than 10–20 Hz). High rates of AM, including high-frequency components in AM as a result of sharp onsets and terminations of pulses of sound, should thus propagate through turbulence with little degradation.

Irregular amplitude fluctuations have no appreciable effect on the frequencies of propagating sound. Amplitude modulation changes the frequency spectrum of a signal by adding side bands above and below the carrier frequency, with the difference in frequency between the carrier and the side band equalling the frequency of amplitude modulation. Thus random amplitude fluctuations from turbulence produce an exponentially decreasing envelope of side bands on either side of the carrier frequency. This envelope drops to more than 30 dB below the carrier frequency for frequencies 50 Hz on either side of the carrier and thus would have no appreciable effect on perception of frequency. Owing to the temporal resolution of hearing by birds and mammals, irregular amplitude fluctuations from turbulence are primarily perceived as fluctuations in intensity.

C. Frequency-Modulated Tones in Long-Range Communication

The combined effects of reverberations and irregular amplitude fluctuations suggest that long-range acoustic signals should not encode information in patterns of amplitude modulation. Reverberations and amplitude fluctuations have complementary effects in degrading the structure of AM in acoustic signals. Reverberations primarily interfere with reception of rapid AM; amplitude fluctuations primarily mask low rates of AM. In contrast, patterns of frequencies should prove much less susceptible to degradation during propagation.

Information can be encoded in frequency patterns in two ways: either as simultaneous combinations or as sequences of independently selected frequencies. In practice, the vocal tracts of animals cannot produce more than two or three simultaneous, independently variable frequency components. Differentiation of vowels in human speech by formants is probably the closest approach to this sort of system among animals. Any one human language differentiates less than 10 sounds by this means. In some birds, the syrinx can produce two independent frequencies (Greenewalt, 1968). Encoding information in more complex patterns of frequencies usually requires frequency modulation, the use of successive tones of different frequencies, or tones of continuously varying frequency.

Tonal signals have an additional advantage in long-range communication. When receivers can discriminate frequencies, the concentration of power in a single tone increases the receiver's signal/noise ratio. Thus, for animals that can

analyze or discriminate frequencies, tonal frequency-modulated signals provide the optimal arrangement for long-range acoustic communication.

Long-range advertising songs of birds almost invariably consist of frequency-modulated tones (for an exception, see Wiley and Cruz, 1980). In addition, some long-range signals of mammals also fit the expectation of frequency-modulated tones. Prime examples include the howls of wolves (Harrington and Mech, 1978), the whistling of bull elks (Struhsaker, 1967), the songs of gibbons (Tembrock, 1974; Tenaza, 1976), and the whoop component of the mangabey's whoop-gobble (Waser, 1977a).

For effective use of amplitude modulation in long-range signals, the amplitude patterns must incorporate enough redundancy, usually simple repetition, to counteract degradation during propagation through the environment. The trills of many passerine birds and the long-range vocalizations of some primates show this sort of repetitive amplitude modulation (Marler, 1969, 1973). For a variety of passerine birds, playbacks in the field of artificially modified recordings of songs have shown that recognition of conspecific songs does not depend on amplitude patterns (Falls, 1963; M. Schubert, 1971; G. Schubert, 1971). The North American Ovenbird is particularly striking in this respect, since human observers standardly use the pattern of increasing amplitude to identify this species' songs, although the Ovenbirds themselves appear unaffected by this feature (Falls, 1963).

V. STRATIFIED ENVIRONMENTS

Since the velocity of sound depends on the temperature and velocity of air, vertical gradients of temperature and wind velocity refract sound (Wood, 1966; Eyring, 1946; Ingard, 1953; Pridmore-Brown and Ingard, 1955; Wiener and Keast, 1959; Piercy *et al.*, 1977). In warmer air, sound travels faster. In moving air, the velocity of sound equals the resultant of the velocity of sound in stationary air of the same composition and temperature and the velocity of the air itself. When temperature decreases with height above the ground, a shadow zone exists for horizontal propagation of sound above the ground as the wave front is refracted upward into zones of lower sound velocity. Likewise, when wind velocity increases with distance above ground, a shadow zone exists for upwind propagation of sound horizontally above the ground.

The exclusion of sound energy from the shadow zone is not absolute. Some energy is refracted into the shadow zone as a result of turbulence in the atmosphere. In addition, sound propagating near the ground includes ground and surface waves (Pridmore-Brown and Ingard, 1955), which transmit energy into the shadow zone. Nevertheless, a shadow zone has a marked effect on horizontal propagation of sound. Attenuation can increase by 20–30 dB at the boundary of

the shadow zone (Wiener and Keast, 1959; Piercy *et al.*, 1977). Piercy *et al.* (1977) report that excess attenuation in the shadow zone is largely independent of frequency or distance. This finding suggests that most of the energy in the shadow zone derives from energy scattered by turbulence.

The horizontal distance from the source to the shadow zone equals

$$-4(hT/\gamma)^{1/2}$$

where T = temperature, h = height, and $\gamma = dT/dh$, the temperature gradient.

Thus one way that a bird can avoid the effects of sound shadows on long-range communication in open habitats is to sing at a height above the ground, since the distance along the ground to the shadow zone increases with the square root of the height of the singer. In fact many birds of open country either select isolated high perches for singing or perform song flights high above ground (see Morton, 1975).

Low frequencies of sound are much less affected by atmospheric temperature gradients than are higher frequencies, since the scale of the strong gradients in wind and temperature close to the ground becomes smaller than the wavelength of sound for low frequencies (Piercy *et al.*, 1977). Experimental measurements suggest that shadow zones do not form for frequencies below 200–400 Hz.

When sound velocity increases with distance above ground, rather than decreases, refraction deflects sound downward toward the ground. At night, as the ground cools by radiating heat to the sky, the layer of air immediately adjacent to the ground cools faster than the air higher above ground. Consequently, temperature often increases with distance above ground, rather than decreases as it does during midday (Munn, 1966; Geiger, 1965). When temperature increases with height, termed an inversion, sound becomes effectively trapped in a layer next to the ground. Under these conditions, sound propagates horizontally with much less attenuation than otherwise. Even at moderate distances attenuation would vary with the first power of range, rather than the square of range as in spherical spreading.

Long-range acoustic communication horizontally above the ground should thus avoid conditions that tend to produce shadow zones and should take as much advantage as possible of temperature inversions. Above open ground or dense vegetation, shadow zones are most likely during midday in sunny weather, when temperature usually decreases with height above the surface and winds tend to be strong. At night temperature inversions would favor long-range acoustic communication.

Temperature gradients inside forests might produce some complex patterns of shadow zones for acoustic communication. The forest canopy absorbs more radiation during the daytime and radiates more at night compared to the lower levels of vegetation. Temperatures below the canopy fluctuate much less from day to night and often vary only slightly with height above ground. Conse-

quently, during midmorning there is a major maximum in temperature in the upper part of the canopy. At night this peak in temperature in the canopy is reduced (Evans, 1939; Schilling *et al.*, 1946; Eyring, 1946; Hales, 1949; Christy, 1952; Heckert, 1959; Geiger, 1965).

A temperature maximum in the upper canopy tends to refract sound upward above the canopy and downward below the canopy. Under these conditions, a position just below the canopy might have advantages for long-range acoustic communication as a result of the temperature inversion immediately above (Fig. 10) (Wiley and Richards, 1978). In measurements of sound transmission in a tropical forest, Waser and Waser (1977) found evidence for just such an effect. Birds in forests might take advantage of such temperature gradients, to judge from the heights of singing birds in relation to the main canopy of a mixed

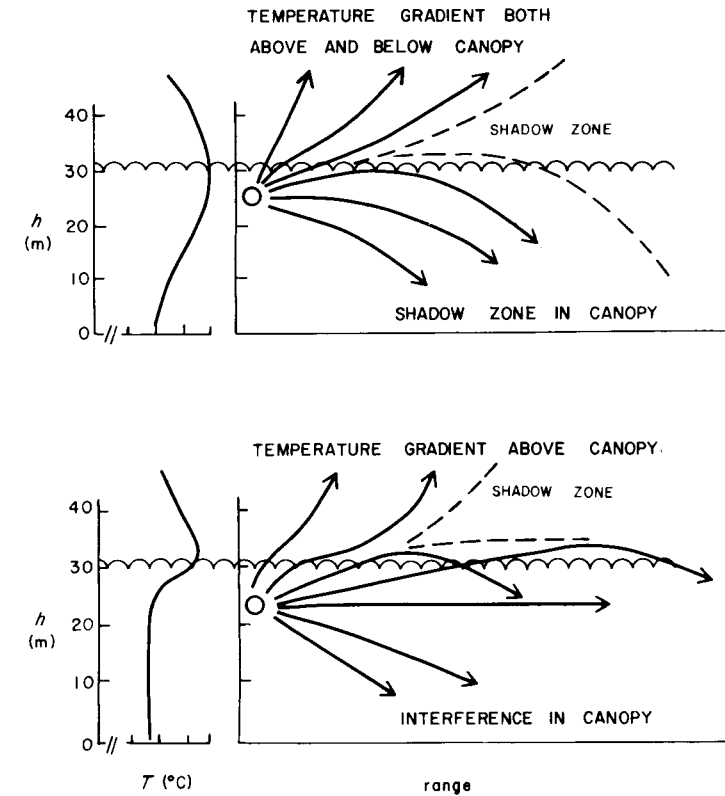


Fig. 10. Possible shadow zones in propagation of sound through the canopy of a forest. Left, representative temperature gradients; right, rays perpendicular to wave fronts for the propagation of sound from a source (circle) in the canopy. Scalloped line, top of canopy. (After Wiley and Richards, 1978.)

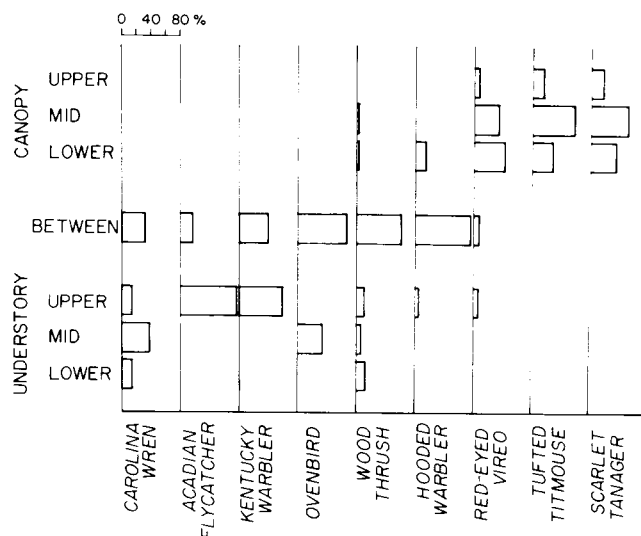


Fig. 11. Locations of undisturbed singing birds in relation to strata of foliage in a deciduous forest. Upper, mid, and lower designate thirds of the range of dense foliage in the canopy and understory. Between designates a zone of less dense foliage between understory and canopy. Ovenbirds and Wood Thrushes (see Fig. 5) actually favored locations just below the canopy in this open stratum.

deciduous forest in North Carolina (Fig. 11). Several species preferentially select singing positions near the lower edge of the canopy.

Another possibility arises in forests that have layers of dense foliage above and below a more open layer, an arrangement that might form a wave guide for sound propagation in the open layer. To evaluate this possibility, we need measurements of excess attenuation at heights corresponding to maxima and minima in density of foliage. For layers of foliage to create this effect, they must reflect a substantial fraction of incident sound.

VI. OTHER CONSIDERATIONS IN LONG-RANGE COMMUNICATION

A. Time of Day

At midday, particularly during sunny weather, the acoustic properties of the atmosphere are particularly unfavorable for long-range acoustic communication. On sunny days, large temperature and wind gradients develop above the ground on layers of dense vegetation. The temperature gradients often exceed the adiabatic lapse rate. Under these conditions turbulence results from cells of rising

air. At night, temperature gradients are much more favorable for sound transmission near the ground. In the absence of strong winds, there should also be little turbulence to scatter sound.

While many nocturnal animals (including birds) call throughout most of the night, diurnal species tend to concentrate their long-range communication in the first hours of day and to a lesser extent in the evening (Henwood and Fabrick, 1979). Since the temperature cycles tend to lag the solar cycle somewhat, atmospheric conditions for long-range sound propagation should usually be more favorable at sunrise than at sunset. It is significant that a dawn chorus is less apparent near the ground inside tall tropical forests. In this environment, winds are rarely strong at any time, and temperature gradients are unusually small.

B. Communication across Water

Acoustic communication across water encounters some conditions that differ from those for communication above the ground or vegetation. The acoustic impedance of water is high in comparison to the relatively porous ground. As a consequence, a still surface of water should create boundary interference for sound propagating near the surface approximating that above asphalt (Embleton *et al.*, 1976). In particular, the prominent peak of attenuation below 1 kHz for propagation over porous surfaces like grass should not appear over water. If waves on the surface are large in relation to the wavelength of sound, they should create a strong spatial variation in the intensity of reflected sound much as a defraction grating does for reflected light.

Another important difference between sound transmission above water and above land would result from differences in temperature gradients above the surface. Water has such a high heat capacity that temperature changes at the surface as a result of solar radiation or radiation to the sky at night are normally much less than the changes in the surface temperatures of ground or vegetation. Consequently, temperature gradients above water probably diverge less from the adiabatic lapse rate than gradients above soil or vegetation. As a result, shadow zones resulting from temperature gradients should have less effect on horizontal communication above water than above soil. In addition, gradients of wind velocity near the surface might be less over water than over land. It is also possible that less turbulence would develop above water at least in the absence of large waves, so that sound would attenuate less by scattering from turbulence than above ground.

C. Directivity of the Source

The angular spread of sound radiating from a source, termed its directivity, influences several of the processes of attenuation and degradation considered above. As a result of scattering, a narrowly beamed sound attenuates more

rapidly with distance than expected for spherical spread alone. On the other hand, by focusing energy into a narrow beam, a source increases the intensity at every position along the axis of propagation. A beamed sound also encounters less reverberation.

All of these considerations suggest that directivity increases the detection and recognition of signals at the distance. However, this advantage accrues only when the sender knows the location of the receiver so that it can aim the beam of sound in the correct direction. Otherwise, a sender would need to produce repeated signals aimed successively in different directions in order to cover all possible locations for receivers. In view of the advantages of directivity, it might well pay for a bird to produce beamed acoustic signals for long-range communication but to aim them in different directions whenever the location of potential receivers was unknown (Richards and Wiley, 1980). There is little information available on the directivity of avian vocalizations (Witkin, 1977).

D. Background Noise

The distance at which an acoustic signal is detectable depends ultimately on the levels of masking background sounds, including sounds generated by physical processes, like wind and rain, and sounds used for acoustic communication by other species.

A receiver confronts somewhat different problems in detecting or recognizing signals in the presence of more or less continuous background sounds in comparison to relatively brief background sounds. As a result of wind and rain, for instance, more or less continuous energy over a wide band of frequencies is mixed with signals from the source. The intensity of this more or less continuous background sound, relatively easily measured in natural environments (Morton, 1970; Waser and Waser, 1977), is highest at midday and early afternoon. In addition, some animals create nearly continuous background sounds for other species, like the cicadas (*Tibicen*) in North American forests in late summer.

For receivers of any one species, brief sounds that serve for communication by other species are also important in masking. These extraneous sounds are more difficult to measure than the continuous sounds. They usually occur too intermittently to affect the mean level of background sound. During the hour or so of dawn chorus, however, the cacophony of singing birds amounts to nearly continuous background sound.

In some communities of frogs, species appear to use distinct frequency bands (Littlejohn and Martin, 1969; Straughn, 1973). In communities of birds, species or individuals can avoid singing simultaneously (Cody and Brown, 1969; Ficken *et al.*, 1974; Wasserman, 1977) but no clear allocations of the frequency dimension occur. In fact, most passerine birds use approximately the same frequency band for their long-range acoustic signals.

VII. ESTIMATING A SIGNALER'S LOCATION

The physical properties of sound in the atmosphere suggest several other adaptations in addition to long-range communication. Consider first those adaptations for indicating the signaler's location with respect to the receiver. A singing bird might find it advantageous to let receivers judge its location. For instance, consider a song that discourages conspecific males from settling near the singer. If the receiver could judge where the singer was, it could settle at a distance that would reduce the chances of competition with a previously established resident. On the other hand, if the song included no cues for locating the signaler, the receiver would have no choice but to approach the singing bird in order to ascertain its location or simply to settle in a location without regard to the singer's location. Including cues for location in a song could thus prove advantageous for both the singer and the receiver, since both could avoid unnecessary confrontations. A singer might find it advantageous to appear closer to a receiver than it actually was. Like all forms of deception in communication, this technique would require some gullibility in the receiver.

To judge the signaler's location, a receiver must estimate its direction and range. To estimate direction, larger vertebrates, whose ears act as pressure receptors, can use binaural comparisons of intensity, phase, or time of arrival of a sound. Smaller animals, including some birds, have ears that appear to behave like pressure-gradient receptors (Lewis and Coles, 1980). Determination of direction by each of these methods depends on differences in the simultaneous amplitudes at the two ears. Consequently, propagation of acoustic signals through scattering environments or turbulence degrades cues for estimating the direction of the signaler. Nevertheless, man and other primates are remarkably good at estimating the directions of sounds in a forest (Eyring, 1946; Waser, 1977b). One way to enhance the locatability of an acoustic signal in the presence of scattering or turbulence is to include highly repetitive amplitude and frequency modulation. With a highly predictable signal, a receiver could extract the precise relationship of the signals received by its two ears by cross-correlating sufficient samples from each ear. Birds can locate wide-spectrum noise better than any pure tone (Konishi, 1973a, 1977; Shalter and Schleidt, 1977; Knudsen and Konishi, 1979) but, as we have seen, such signals have disadvantages in long-range acoustic communication for other reasons.

To judge the signaler's range, a receiver could use cues from most processes of attenuation and degradation considered above (Coleman, 1963; Schleidt, 1973; Griffin and Hopkins, 1974; Wiley and Richards, 1978). Frequency-dependent attenuation can serve to indicate the distance to the source when a receiver can compare the relative intensities in different frequency bands of the signal. The receiver would need to have some knowledge of the intensities in different frequency bands of the signal at the source, or it would need to hear the same

signal at different distances. Reverberations and amplitude fluctuations also increase with range and thus can be used to judge the distance to the signaler. Estimates of range based on reverberations or amplitude fluctuations would not require detailed information about the signal at the source or at different distances. The receiver could make at least a crude estimate on the basis of its own information about the transmission path. Use of reverberations for ranging is easiest if a signal includes a variety of repetition rates of a given frequency. Examples include trills that change continuously in repetition rate or trills of different rates in the same song. Many songs incorporate frequency–time patterns that look like an inverted chevron, a pattern that would provide a continuous range of repetition rates within a limited time period.

It is difficult to obtain experimental evidence that birds use the attenuation or degradation of songs for estimating distance. In most cases, the natural response of a bird to a signal at a greater distance is simply less consistent or intense than to a closer one. An experimenter playing back recorded songs to birds at different distances cannot judge whether a subject fails to hear a song or chooses to ignore it. Carolina Wrens, however, provide an opportunity for differentiating these two possibilities. In natural circumstances, Carolina Wrens respond to songs broadcast within their own territory by silent approach and agonistic calls rather than song. In contrast, a song from an adjacent territory stimulates a wren to sing.

Richards (1981a) compared responses to test tapes of songs recorded at distances of 10 and 50 m from wrens in forests. When played at the same intensity within the territories of Carolina Wrens at distances of approximately 25 m from the subjects, these two tapes evoked different responses from the wrens. The subjects stopped singing and approached the speaker in response to the clean recordings but increased their singing in response to the degraded recordings, a demonstration that Carolina Wrens can use the natural degradation of song to judge a singer's distance.

The assumption that birdsong should evolve to maximize range of communication is unreasonable for many species. In many cases acoustic signals probably evolve for communication with receivers at some optimal distance corresponding to the usual spacing of individuals rather than simply for communication at maximal distances (Schleidt, 1973; Jilka and Leisler, 1974; Wiley and Richards, 1978). Communication at longer distances would waste time and energy, attract predators unnecessarily, and require a territorial resident to respond to individuals answering their songs from unnecessarily great distances. The advantages of restricting communication to an optimal distance are of course closely related to the advantages of including cues for estimating distance in a signal.

To insure effective communication at a distance of approximately one territorial diameter, signals should certainly not attenuate or degrade completely at that distance. Instead a song should reach the limits of detectability at a distance

substantially greater than that required for effective communication. Nevertheless, the properties of songs that resist attenuation and degradation should correlate with the usual spacing of individuals. Evidence along these lines is available for *Cercopithecus* monkeys in Africa (Waser and Waser, 1977). Among Darwin's finches, population density, and thus presumably the usual spacing of individuals, correlates with average frequencies in songs and body size (Bowman, 1979). Small species are more abundant and have higher pitched songs.

VIII. SHORT-RANGE COMMUNICATION

Much vocal communication in birds, particularly between parents and young and between mates, occurs over distances of a few meters at most. In order to avoid attracting predators or sexual competitors, natural selection in many cases favors limitation of such signals to the minimal distance necessary. The characteristics of many such calls seemed designed to increase rather than decrease attenuation. Calls used in parent–offspring communication are not only low in intensity, but they often employ high frequencies (above 6 kHz) which attenuate rapidly. Precopulatory calls also tend to use high frequencies.

In colonial species, short-range communication between mates encounters some special problems. Attraction of predators is not likely. On the other hand, sexual competitors during the days of sexual receptivity pose a greater problem for colonial birds than for isolated pairs. The most pervasive problem for mates in a dense colony, however, is the difficulty of recognizing the mates' vocalizations in the continuous background sounds of other pairs. This problem is analogous to the difficulty of recognizing words in a continuous background of irrelevant speech, termed the "cocktail party effect" in psychophysics (Cherry, 1966).

One way to improve the detectability of signals in this situation is to increase their locatability. In psychophysical experiments, detection of words in irrelevant speech is improved if the two signals have different phase relationships in dichotic presentations, an arrangement analogous to signals from sources located in different directions from the receiver. For communication between mates among colonial birds, selection should thus favor acoustic signals that maximize the precision of locating the sender. Wide-spectrum sounds with sharp changes in amplitude, such as sudden onsets and terminations, result in maximal locatability (Konishi, 1977). In fact this sort of structure recurs in the vocalizations of many colonial birds, both passerine and non-passerine (White and White, 1970; Wiley, 1976).

Mates in dense colonies usually have visual and sometimes tactile signals available as well as many short-range calls for communication of information about the sender's internal states and external circumstances. In this case a

complex stereotyped vocalization serves primarily to establish the signaler's identity and to attract the mate's attention, so that communication with the rich diversity of subtle visual and acoustic signals can begin (Wiley, 1976). Primary requirements for these signals are individuality and ease of locating.

The use of wide-spectrum sounds with sharp amplitude modulation and limited frequency modulation in colonies contrasts with the use of tonal sounds with complex frequency modulation in long-range communication. These two types of acoustic structure are suited for nearly opposite purposes, one for maximal locatability at short-range, the other for maximal resistance to degradation by reverberations and amplitude fluctuations in long-range communication.

IX. DETECTION AND RECOGNITION: MAXIMIZING THE RECEIVER'S PERFORMANCE

So far the distinction between detection, a receiver's judgment concerning the occurrence of a signal without classifying it, and recognition, a classification of a signal by its parameters, has not affected our conclusions. We have noted that attenuation and degradation affect both sorts of tasks. However, recognition of a signal places greater demands on the performance of a receiver than does pure detection. For effective communication in natural circumstances, a receiving individual must usually distinguish among a large number of different signals from the same and other species. In other words, recognition, not simple detection, of signals is crucial.

In the following discussion, we shall see that both detection and recognition of signals by any receiver are subject to some general constraints in a noisy environment. In terms of a receiver's performance, recognition is analogous to detection of signals with unknown parameters. It will develop that complex signals, by proper design, can improve the reliability of detection and recognition by a receiver. To see these points, we need to start with some basics.

A. Signal Detection

The theory of signal detection, developed primarily for electronic applications, like radar, characterizes the properties of the optimal receiver for detecting signals in noise (Woodward, 1953; Selin, 1965; Hancock and Wintz, 1966; Helstrom, 1968; Egan, 1978). The characteristics of an optimal receiver provide a standard against which real receivers are compared. The theorems require a number of simplifying assumptions that make exact application to animals in natural situations difficult. Nevertheless, they establish some very general limitations of signal detection, which have found wide application in psychophysics (Green and Swets, 1974; see also references cited below). Experiments that

utilize this theory often require hundreds of repetitions with subjects that can follow precise instructions and whose motivation can be partially controlled with rewards. Thus methodological difficulties partly explain why this theory has never been applied to animal communication.

Nevertheless, two fundamental concepts from the theory of signal detection have such general application that they suggest some ways that animals might increase the efficiency of information transfer: (1) the distinction between the inherent detectability of a signal in noise and the receiver's criterion for a positive response; and (2) the necessary trade-off for any receiver between the probability of correct detections and the probability of false alarms.

The first step in the theory of signal detection is to establish a basic criterion that any receiver can use to decide whether or not it has detected a particular signal (see Swets *et al.*, 1961; Blachman, 1966). The general form of this criterion is a likelihood ratio. To see this point, we first need to define some probabilities: let $P(SB_1)$ and $P(SB_2)$ equal the prior probabilities that each of two signals are broadcast by a source, where $P(SB_1) + P(SB_2) = 1$. The source does one of two things; for instance, it either emits a signal (SB_1) or does not (SB_2). Alternatively, if we assume that detection of a signal is no problem, SB_1 and SB_2 can represent two different signals that constitute the entire repertoire of the sender. Now suppose that the receiver records an input (SR). The receiver's task then is to decide whether SR indicates that the source emitted SB_1 or SB_2 . Thus $P(SB_1|SR)$ and $P(SB_2|SR)$ are the respective posterior probabilities of each broadcast signal given the received signal, with $P(SB_1|SR) + P(SB_2|SR) = 1$. The posterior odds in favor of SB_1 are $P(SB_1|SR):P(SB_2|SR)$.

The posterior probabilities are related to the *prior* probabilities as follows (by application of Bayes' formula):

$$\frac{P(SB_1|SR)}{P(SB_2|SR)} = \frac{P(SB_1)}{P(SB_2)} \frac{P(SR|SB_1)}{P(SR|SB_2)}$$

The posterior odds in favor of SB_1 thus depend on two terms: (1) the prior odds in favor of SB_1 (the odds that the receiver could guess the broadcast signal without even paying attention to the received input); and (2) a term, called the likelihood ratio, which summarizes the information provided by the input (SR) concerning the broadcast signal. If the two signals degrade so much that they result in identical stimuli for the receiver, then $P(SR|SB_1) = P(SR|SB_2)$, the likelihood ratio equals 1, and the posterior odds in favor of signal SB_1 simply equal the prior odds. At the other extreme, if each received signal is associated with one and only one broadcast signal, the likelihood ratio goes to infinity and consequently the posterior odds go to infinity; in other words the receiver can be almost certain of the broadcast signal upon receiving SR.

The likelihood ratio can thus provide a basis for a receiver's decisions. When

the likelihood ratio is large enough, then the receiver should conclude that SB_1 occurred. The receiver must thus select a threshold value which separates the set of all possible received signals into two subsets, one that leads to the conclusion that SB_1 occurred and the other to the conclusion that SB_2 occurred.

In the simple situation when broadcast signals fall into two exclusive classes, there are exactly four possibilities each time the receiver samples its input and makes a decision: it can correctly decide that SB_1 occurred (a correct detection of SB_1); it can decide that SB_1 occurred when in fact SB_2 did (a false alarm); it can conclude correctly that SB_2 occurred; or finally it can conclude that SB_2 occurred when in fact SB_1 did (a missed detection of SB_1). The second and fourth of these possibilities are errors by the receiver, like errors of the first and second type in statistical tests. To select an appropriate criterion for decisions, a receiver must not only adopt an acceptable probability of false alarm but must also weigh the values (costs or benefits) of detections and each of the two kinds of errors.

B. Receiver Operating Characteristics

A receiver attempting to detect signals in the presence of noise cannot increase its probability of correct detections without inevitably increasing its probability of false alarms. Suppose a signal is simply a pulse of constant frequency, which must then propagate through a channel with the same frequency present as masking noise and with random amplitude fluctuations. The receiver then samples this channel for a specified time at the frequency of the signal and records the varying intensity of the received signal. When the sender is silent, we assume the received signal is a randomly fluctuating intensity with a Gaussian probability density function (PDF; Fig. 12). When the sender emits a signal, the received signal is also a randomly fluctuating intensity with a Gaussian PDF that has a standard deviation equal to that of the previous case but now has a greater mean intensity. The receiver must then select a threshold for deciding whether or not the sender emitted a signal. In the present case, selecting a threshold value of intensity is equivalent to selecting a threshold value of the likelihood ratio.

For any such threshold, the receiver achieves a certain probability of correct detections (P_{CD}), which equals the integral of the PDF of intensities for signal plus noise from the threshold to infinity. In addition, the receiver faces a probability of false alarm (P_{FA}), which equals the integral of the PDF of intensities for noise only from the threshold to infinity (Fig. 12). Now if the receiver selects different values of the threshold in succession, we can construct a graph of P_{CD} versus P_{FA} as the threshold varies. This function is the receiver operating characteristic (ROC).

If the signal attenuates by different amounts during propagation from the sender to the receiver, we can also study ROCs for different signal/noise ratios (Fig. 12). Note several things about these ROCs. First, if the PDF for signal plus

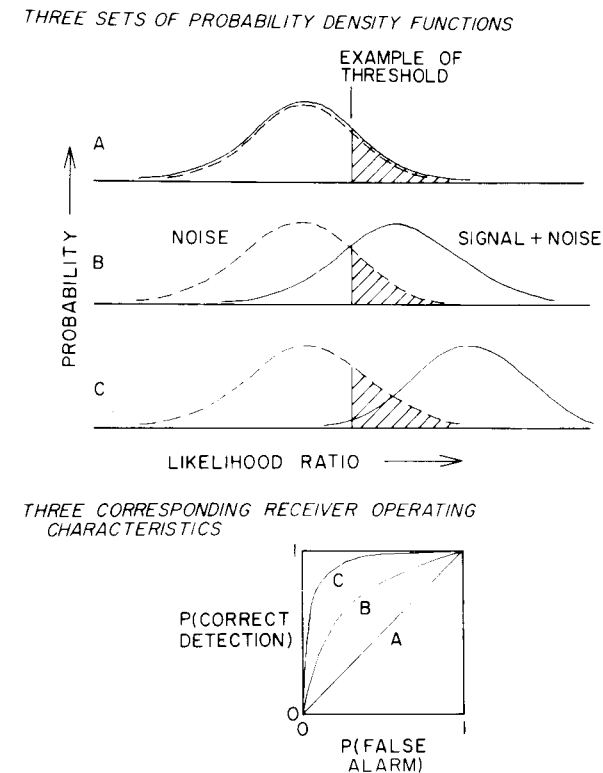


Fig. 12. Schematic demonstration of receiver operating characteristics for simple cases of signal detection. Cases A, B, and C represent increasing signal/noise ratios and hence increasing separation of the probability density functions (PDF) of amplitudes for noise only and noise plus signal. In each case, the probability of a correct detection is the integral of the PDF for signal plus noise from the threshold to infinity; the probability of false alarm is the corresponding integral for noise only. In each case, one can construct the probability of correct detection as a function of the probability of false alarm (the receiver operating characteristic) by letting the threshold vary from $-\infty$ to $+\infty$.

noise and the PDF for noise only are identical, then the probability of correct detection always equals the probability of false alarm, regardless of the threshold. Second, the greater the signal/noise ratio, the more the ROC is displaced away from the positive diagonal and toward the optimal point ($P_{FA} = 0$, $P_{CD} = 1$). Third, when the two PDFs have identical shapes, as in the present case, the ROCs are symmetrical with respect to the negative diagonal. Fourth, for any signal/noise ratio, the probability of correct detection increases monotonically with the probability of false alarm. On the other hand, given a threshold, the probability of false alarm is fixed at all signal/noise ratios, while the probability

of correct detections increases as signal/noise ratio increases. Thus we reach the major conclusion that the receiver's performance depends on two factors: the criterion (threshold) it adopts for deciding that a particular signal has occurred; and the inherent detectability (signal/noise ratio) of the signal.

Although the preceding discussion has dealt with an extremely simplified case, the final conclusion has great generality. A receiver cannot adjust its probability of correct detections and its probability of false alarms independently. The performance of a receiver depends on two factors: its criterion for the presence of a particular signal; and the inherent detectability of signals. These conclusions apply to all communication in noisy environments, ones in which the broadcast signals result in overlapping distributions of inputs sensed by the receiver. Birds attempting to differentiate complex acoustic structures at long range in natural environments provide a good example.

C. More Complex Tasks for a Receiver

A receiver reaches maximal performance when it knows in advance the precise form of the signal, including the exact time of onset. In this case, theory shows that the likelihood ratio for the presence of a signal is a monotonic function of the cross-correlation of the received input and the signal (see general references above). This situation of course occurs rarely even in engineering applications.

Uncertainty on the part of the receiver concerning the exact form of the signal has an effect equivalent to decreasing the signal/noise ratio for a known signal. Likewise, the problem of detecting several different signals also results in an ROC similar to those for lower signal/noise ratios with one signal. Finally, recognition of several different signals, in addition to detection, once again resembles a decrease in the signal/noise ratio for detection alone. All three of these comparisons—detection of a single signal with unknown parameters versus detection of a single completely known signal, detection of several different signals versus detection of a single signal, and recognition versus detection of several signals—follow the same pattern: the ROC moves toward the positive diagonal, analogous to a decrease in signal/noise ratio or detectability.

In contrast, repetition of the same signal has the opposite effect, namely, an increase in signal/noise ratio; the ROC shifts away from the positive diagonal. This result conforms with predictions from information theory that increased redundancy in signals improves the probability of receiving a message in a noisy channel (Shannon and Weaver, 1949; Cherry, 1966). Of course, repetition and other forms of sequential redundancy increase the time required for communication.

These effects of unknown parameters of signals, multiple signals, recognition, and repeated signals have all been established in psychophysical studies on humans (unknown parameters: Creelman, 1960; Egan *et al.*, 1961a,b; Watson

and Nichols, 1976; multiple signals: Veniar, 1958; Pollack, 1959a; Green, 1960; Pollack, 1964; Moray and O'Brien, 1967; Ahroon *et al.*, 1977; recognition: Tanner, 1956; Clarke *et al.*, 1959; Lindner, 1968; Green *et al.*, 1977; Swets *et al.*, 1978; repetition: Pollack, 1959b; Swets and Birdsall, 1978). We can expect that all of these results apply to animal communication just as to human or electronic communication.

D. Adaptations to Improve a Receiver's Performance

The effects of multiple signals, repeated signals, and uncertainty in the time of arrival of signals on the probability of correct detection suggest three adaptations that birds could use to improve a receiver's probability of detecting an acoustic signal: reduction in the diversity of alternative signals, repetition, and alerted detection.

The effect of multiple signals might pertain most clearly to problems of species recognition of songs. One would expect that in ecological communities with greater species diversity, species should use smaller repertoires of song types in order to permit more reliable detection of conspecific songs in the midst of a more complex background of heterospecific signals. Such an effect has been reported for North American wrens (Kroodsma, 1977). This effect should be most apparent among the rare species in diverse communities or species represented by widely scattered individuals, which confront the most extreme signal/noise ratios in long-range communication.

Repetition of an identical signal also improves a receiver's performance. Once again, this technique would have the greatest advantages for communication in ecologically diverse communities, particularly for the rarer species, and for communication at especially long ranges between widely spaced individuals. Exact repetition of a phrase occurs in the songs of many species. In addition, many species repeat the same song pattern a number of times before switching to a new one. The Carolina Wren, for instance, does both.

Alerted detection requires that some easily detectable signal precede, in a defined temporal relationship, a signal that carries important information (Raisbeck, 1963). Easy detection of the alerting component requires a high signal/noise ratio, as a result of low attenuation and degradation, and a simple predictable structure. This component need not carry any essential information, in the sense that the receiver need not make decisions on the basis of classifying (recognizing) this component. In the case of birdsong for instance, the alerting component need not include information on species identity or individual identity. Instead the alerting component serves to define for the receiver the period of time in which it can expect the message component. Since this latter component conveys information to the receiver, it must have enough complexity of structure to permit the receiver to distinguish among alternatives. In summary, the alerting

component permits easy detection; the message component permits classification (recognition).

A variety of species of birds begin their territorial songs with one or a series of relatively simple tones. The songs then become progressively more complex in acoustic structure during their course. Shiovitz (1975) has noted that the song of the Indigo Bunting (*Passerina cyanea*) fits this pattern. He feels that the introductory portions serve as a signature to identify the species while later portions convey more detailed information. Theory of signal detection suggests that the initial portions of a signal should in fact convey less information than the final portions, but this consideration could apply to species identification as well as other kinds of information.

Experiments with Rufous-sided Towhees (*Pipilo erythrophthalmus*) have provided evidence that the initial tones in this species' characteristic songs have an alerting effect, while the final trill carries most of the information that permits territorial towhees to recognize a conspecific song (Richards, 1981b). Realizing that the effect of an alerting note would resemble an increase in signal/noise ratio, Richards compared the responses of territorial towhees to a series of tape recordings of complete songs, introductory notes, and final trills, which in each case were either artificially degraded with reverberations or not (Fig. 13). All recordings came from towhees beyond hearing of the subjects. He found that either clean or degraded recordings of the entire song (introduction plus trill) evoked strong responses. The introductory note alone, either clean or degraded, evoked little response. In contrast, when he tried the final trill alone, he found a dramatic difference between clean and degraded recordings (Fig. 14). Degraded trills evoked little response while clean recordings of trills evoked nearly a full response. Thus the trill provides the information that territorial towhees use to

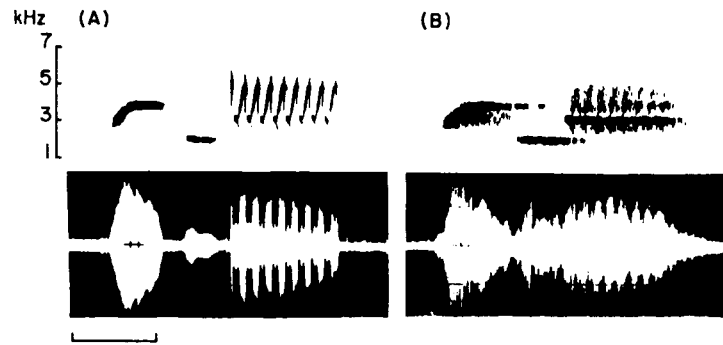


Fig. 13. Example of Rufous-sided Towhee songs used for experiments to demonstrate alerted detection. (A) Clean recording of an entire song without significant reverberation; (B) artificially reverberated version of the same song. Time mark, 1 sec. Above, sonograms; below, oscillograms. (After Richards, 1981b.)

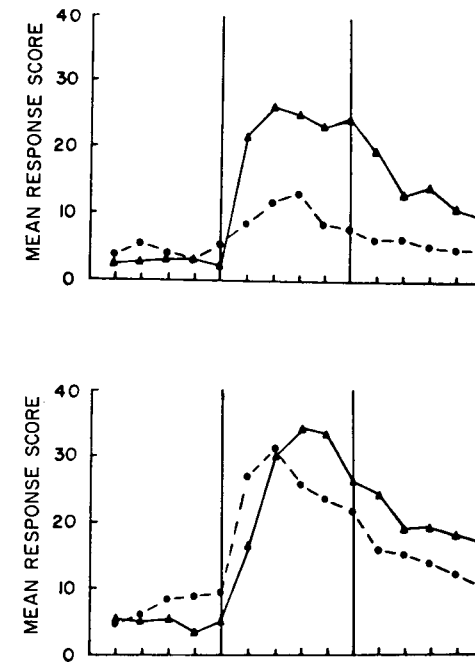


Fig. 14. Reactions of Rufous-sided Towhees to playbacks of clean and artificially reverberated songs and trills (songs without the initial notes). Ordinate, composite response score averaged over all subjects. Abscissa, 1 min blocks before (first five), during (middle five), and after (last five) playback. Dashed lines, response to reverberated recordings; solid lines, response to clean recordings. Above, playback of trills without initial notes; below, playback of entire songs (trills with initial notes). Initial notes alone, both clean and degraded, evoked little response. Thus two degraded components, initial notes and trills, each ineffective alone, combine to make an effective stimulus. (After Richards, 1981b.)

identify a conspecific song. On the other hand, the simple introductory notes, which had little effect alone, had a major effect in increasing the response of towhees to a degraded trill, inasmuch as the degraded trill alone had little effect, while the degraded entire song, complete with introductory notes, had a strong effect. The introductory notes thus allow towhees to recognize degraded trills.

E. Other Applications of Signal Detection Theory

The theory of signal detection has implications for the interpretation of playback experiments with birds under natural conditions. In some circumstances, a reduced response by subjects does not allow the investigator to decide whether the subjects have changed their criterion for a response or whether the signals

differ in detectability. The large number of experiments on species recognition confront this problem. When subjects respond less intensely to artificially modified songs, the inference is usually drawn that the birds no longer recognize these songs as conspecific. In other words, the inference is usually that the songs now fall below the subject's criterion. An alternative possibility, however, is that the modified songs are inherently less detectable.

Detailed application of the theory of signal detection to animal communication requires measurements of ROC curves, including false alarm rates in birds' responses. A problem arises in distinguishing the birds' spontaneous responses from reactions to an experimental stimulus like a playback. Unless one can arrange a response that occurs only in an experiment, in which a signal is either presented or not within a defined time interval, it will prove impossible to separate false alarms from spontaneous response. This caveat, however, need not preclude the application of ROCs to studies of birdsong in the field. Even though probabilities of correct detection and probabilities of false alarm both include a constant probability of spontaneous response, ROCs should still permit experimenters to decide whether or not responses to different conditions of playback result from changes in the detectability of the signals or changes in the subjects' criterion for a response. For methods of determining ROCs that might apply to field studies of birds, see Egan *et al.* (1961c), Pollack *et al.* (1964), Swets and Kristofferson (1970), and Watson and Nichols (1976).

X. CONCLUSIONS

Signals evolve for efficient transfer of information whether the interaction between sender and receiver is mutualistic or manipulative. One way to increase the efficiency of acoustic communication is to minimize attenuation and degradation of signals during propagation. In all habitats, both forested and open, attenuation from absorption and scattering increases monotonically with increasing frequency. Scattering from vegetation and from atmospheric turbulence primarily affects frequencies above about 2 kHz. Thus, provided there is little wind, these frequencies attenuate less in open habitats than in forests. Nevertheless, except near the ground, lower frequencies always attenuate less. Near the ground in any habitat, interference primarily attenuates frequencies between 0.5 and 1 kHz. Thus, there is no clear reason to expect systematic differences in the optimal frequencies for long-range communication in different natural environments.

Degradation of acoustic signals by reverberations and amplitude fluctuations, on the other hand, differs systematically between environments with dense vegetation, such as forests, and open environments. Reverberations are usually more severe in the former and amplitude fluctuations in the latter. In forests, birds tend to avoid rapid repetition of any one frequency, as one would expect in rever-

berant environments. The general character of long-range signals in birds, frequency-modulated tones, avoids the effects of reverberations and amplitude fluctuations on acoustic signals.

Attenuation and degradation of acoustic signals can serve to encode information about the distance to the sender. Attenuation can also help to limit acoustic signals to nearby partners, for instance in communication between mates and between parents and young, when attraction of predators or sexual competitors has disadvantages. In the noisy environment of dense colonies, the principal problem in acoustic communication by mates is the "cocktail party effect." Here, use of wide-spectrum sounds with sharp amplitude modulation, in spite of minimal frequency modulation, has the advantage of increased locatability, which in turn helps a receiver to detect a signal in the high levels of background noise.

The theory of signal detection reaches two general conclusions that apply to birds as well as all other receivers: a distinction between the receiver's criterion (threshold) for a positive response and the inherent detectability of a signal; and an inevitable covariation between a receiver's probability of a correct detection and its probability of a false alarm. These features of signal detection are best summarized in a receiver operating characteristic (ROC), a plot of the probability of correct detection versus the probability of false alarm at different thresholds for a positive response. Certain complexities in a receiver's task, when compared to the task of detecting a single known signal, all have effects that resemble a decreased signal/noise ratio: detection of signals with unknown parameters; detection of one-of-several different signals; and recognition (classification) of signals in addition to detection. On the other hand, repetition of a signal has the opposite effect, namely increased signal/noise ratio.

As a result, three kinds of adaptations in acoustic signals could increase correct reception of signals by receivers. Where noise levels are high, as in ecological communities with a high diversity of species and for communication at extremely long ranges, birds could improve the detectability of their signals by limiting their repertoire and by employing repeated phrases or song patterns. In addition, an alerting signal increases the reliability of detecting and recognizing subsequent signals. Thus, repetition of phrases in a song and alerting notes are complementary techniques for achieving the same end: improved performance of receivers.

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