

REVERBERATIONS AND AMPLITUDE FLUCTUATIONS
IN THE PROPAGATION OF SOUND IN A FOREST:
IMPLICATIONS FOR ANIMAL
COMMUNICATION

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A few pioneering studies have attempted to identify features of the environment that affect transmission of sounds through the atmosphere and relate them to characteristics of the acoustic signals of animals in different environments. These studies have primarily considered the effects of attenuation on the maximum distances at which different sounds can be detected. Morton (1970, 1975) and Chappuis (1971) investigated attenuation of sound as a function of frequency and the general nature of the vegetation in the communication channel. Waser and Waser (1977), Linskens et al. (1976), Marten et al. (1977), and Marten and Marler (1977) have pursued this line of research; see reviews by Wiley and Richards (1978) and Michelsen (1978).

Studies of acoustic communication must also consider distortions of the structure of the sound under different conditions (Wiley and Richards 1978). Whenever information requires more complex coding than the presence or absence of sound at a particular frequency, any degradation of acoustic patterns, in addition to overall attenuation of acoustic energy, is deleterious to communication.

In this paper we focus on two of the most important variables affecting identification and localization of acoustic signals in a forest: amplitude fluctuations and reverberations. All researchers who have used pure tones to measure attenuation have noted amplitude fluctuations in the received signal (for instance, Morton 1970; Wiener and Keast 1959). These fluctuations, primarily a result of scattering from air turbulence, vary in strength with weather conditions, time of day, and carrier frequency (see Wiley and Richards 1978). To counteract this variability in amplitude, Morton averaged several measurements for each of his values of attenuation. Linskens et al. (1976), Marten et al. (1977), and Marten and Marler (1977) did not average measurements and consequently obtained considerable scatter in their determinations of attenuation. These random fluctuations affect the distance over which an animal can detect a sound. Furthermore, once

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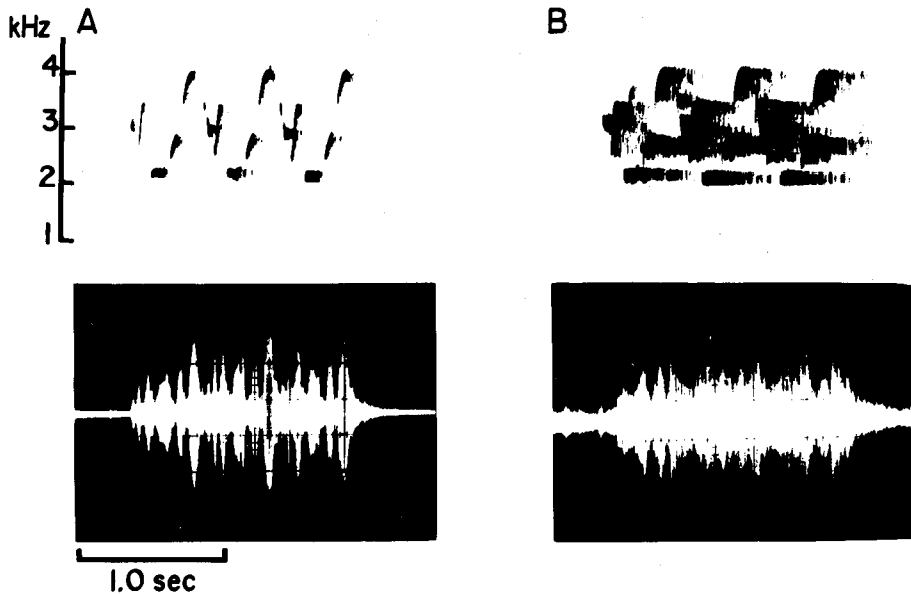


FIG. 1.—Spectrograms (above) and oscillograms (below) of recordings of the song of a Carolina wren: A, 10 m from the singing bird; B, 50 m from the bird.

the sound is detected the level of the fluctuations will determine the intelligibility of any information carried by amplitude modulation on the signal.

Reverberations are another common distortion of signals in forests. From studying spectrograms, it is difficult to obtain a quantitative measure of the intensity and duration of reverberations; yet it is clear that reverberations, which interfere with visual recognition of patterns on spectrograms, would interfere with acoustical recognition by animals (see fig. 1).

Because not all sounds propagate equally well in a given habitat, selection should favor the use of frequencies, intensities, and sound structures that can carry the information the required distance, not necessarily the longest distance. For instance, when predators are present it would be advantageous to have certain information (such as species identity and location) not propagate any farther than necessary for intraspecific communication.

This paper presents measurements of amplitude fluctuations and reverberation for artificially generated sounds in a deciduous forest and relates these effects to the strategies adopted by animals for effective communication.

METHODS

Study Area

Our transmission experiments were conducted in a mixed deciduous forest within the research area of the North Carolina Botanical Garden, 4 km southeast of the center of Chapel Hill, North Carolina. The dominant canopy trees in this

forest are post oak (*Quercus stellata*), white oak (*Q. alba*), and hickories (*Carya* spp.); the most prominent shrub is shortstalk arrowwood (*Viburnum rafinesquianum*). There are an average of 110 trees over 8 cm in diameter per hectare and 1,600 shrub stems per hectare. Average canopy height is 20 m (range 15–30 m), with 74% canopy cover and 29% ground cover (for more details on the vegetation see Wiley [1977]). The terrain is essentially flat near the sites for transmission studies.

Amplitude fluctuations

We investigated the effects of atmospheric heterogeneities on the reception of artificially generated sounds by broadcasting pure tones, recording them at several distances, and analyzing the received sounds by computer, oscilloscope, and real-time spectrum analyzer.

Pure tones were recorded on a magnetic tape from a Wavetek Model 30 function generator. In the field the tones were played back with a Uher 4000 Report L tape recorder, through either a Realistic MPA-20 20-watt amplifier or a Dynaco Mark III 50-watt amplifier and either an omnidirectional Poly-Planar P-20 loudspeaker or a highly directional Realistic Power Horn 12 speaker (see fig. 2 for the directional radiation patterns of the speakers). The speaker was mounted securely on a braced wooden pole (4 × 8 cm in cross section) at a standard height of 2 m. For some experiments the Wavetek generator was connected directly to the amplifier to eliminate any fluctuations from the Uher tape recorder. Tones at 2, 4, 6, 8, and 10 kHz were broadcast for 45 s each, with 15 s of silence between, at each distance of the receiver. Owing to the drop-off in the response of the horn speaker above 4 kHz and the limited power of the amplifiers, the higher frequencies were sometimes not loud enough for analysis at the longer distances. For these trials we added frequencies of 1.5 and 3 kHz.

Received sounds were recorded at 19 cm/s on a Nagra 4.2 tape recorder with an Altec omnidirectional dynamic microphone. A switchable four-section handmade T-attenuator in the microphone line reduced the level of input to the tape recorder at high sound levels; the gain of the recorder was always kept at maximum. The microphone was mounted 2 m above the ground on a camera tripod and aimed at the speaker. Recordings were made at 5, 10, 20, 40, 60, and 80 m distances.

The received sounds were analyzed in two ways. First, with a PDP 11/45 computer and an analog-to-digital (A/D) converter, we computed the standard deviation (root mean square or RMS) of the amplitude fluctuations as a measure of their intensity. Peak-to-peak values were also determined. The recorded sounds were played back on the Nagra recorder through a Krohn-Hite Model 3500 band-pass filter to eliminate noise. A handmade diode demodulator/filter then removed the audio carrier frequency and left only the fluctuations for analysis. The filter attenuated above 100 Hz, with a gentle slope of approximately 10 dB per octave. All traces of carrier ripple above 2 kHz (the lowest frequency in the experiment) were removed. This amplitude envelope, a fluctuating DC voltage, was fed into the A/D converter and sampled at 100 samples/s. The 12-bit A/D converter could only accommodate fluctuations below about 36 dB peak-to-peak.

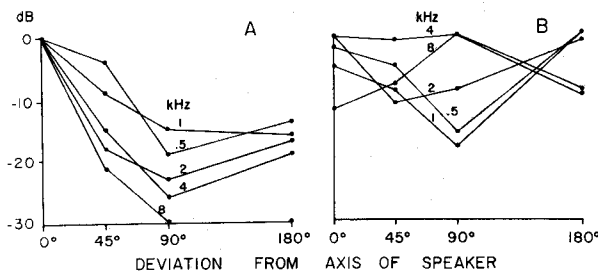


FIG. 2.—Directional radiation pattern of speakers. A, horn speaker (essentially unidirectional); B, Poly-Planar speaker (essentially omnidirectional). In each diagram, the direction of greatest intensity is normalized to 0 dB for each frequency; numbers indicate frequencies in kHz.

For an analysis of the frequency spectrum of the fluctuations, we employed a Spectral Dynamics 301C real-time spectrum analyzer and the same playback arrangement used with the computer. We analyzed frequency spectra of the amplitude fluctuations in each of the 45-s segments of the received signal. The output of the spectrum analyzer was displayed on a Tektronix 502A oscilloscope and photographed with a time exposure to obtain an ensemble of spectra for the entire 45 s segment. We employed an analysis range of 1-500 Hz, for which the spacing of filters was 1 Hz and the 3 dB filter bandwidth 1.5 Hz.

Reverberations

Pulses of sound from 500 Hz to 12 kHz were broadcast as described above. Square pulses of sine waves at different frequencies were generated with the Wavetek function generator triggered by a Grass SD9A stimulator. After trying various pulse widths and rates in preliminary experiments, we selected a pulse rate of 2/s and a width of 25 ms, similar to that found in the trills of various passerine birds. The pulses were filtered to remove transients before amplification. We broadcast these pulses from a speaker at a location approximately 100 m from the location used for the fluctuation measurements. The recording microphone was placed at either of two locations, 25 m south or 25 m east of the speaker. Both speaker and microphone were over 150 m from the nearest edge of the forest. We also made recordings 25 m from a speaker in an open field with grass approximately 0.5 m in height. We recorded the received pulses, as described above, with an omnidirectional microphone to eliminate effects of microphone directionality.

For analysis, we played back the recorded signals in the laboratory on a Tandberg Series 15 tape recorder, through the Krohn-Hite filter, into a Tektronix 502A oscilloscope. For each experiment, at each frequency, two representative samples of the received pulses were photographed from the face of the oscilloscope. The negatives were then projected and the amplitude envelopes of the pulses and the following reverberations traced on graph paper. Our measure of the amount of reverberation incorporated both duration and intensity as follows: The

area under the 200 ms following the pulse was divided by the area under the 25-ms pulse to obtain an index of reverberation. We chose a 200-ms period because it encompassed virtually all the reverberations in the experiments.

RESULTS

Amplitude Fluctuations

Fluctuations took the form of random amplitude variations superimposed on the tonal carrier frequency (fig. 3). The intensity of the amplitude fluctuations was strongly dependent on wind speed near the ground and the consequent turbulence. Atmospheric turbulence and wind tend to be greatest during midday when the heat of the sun produces temperature stratification (see Wiley and Richards 1978). Changes in atmospheric conditions from minute to minute caused corresponding changes in the intensity of the fluctuations.

At midday, with the conditions essentially stable from minute to minute and no air movement measurable with simple anemometers (only intermittent, slight movements of leaves in the understory), amplitude fluctuations increased in magnitude with increased carrier frequency and increased distance of the receiver from the transmitter (fig. 4A). This result confirms Chernov's (1960) derivations of the dependence of amplitude fluctuations on carrier frequency. In the early morning and evening, with the sun low and air turbulence minimal, amplitude fluctuations were very small and there was no measurable relationship between their magnitude and either frequency or distance (fig. 4B).

With even a slight wind (< 10 km/h, usually variable in strength), the fluctuations increased in magnitude, and the relation of magnitude to frequency and distance became difficult to measure. Peak-to-peak values of over 40 dB, beyond the analysis capabilities of the analog-to-digital converter, occurred within 45 s. These corresponded to RMS values greater than 5.5 dB (figs. 4C, 5). Changes in the wind conditions thus swamp the effects of carrier frequency and distance.

To determine the effect of the fluctuations on a receiver's ability to discriminate amplitude-modulated signals with particular modulation frequencies, it is necessary to know the spectrum of the fluctuations; in other words, the frequencies at which the fluctuations modulate the tonal signal. The spectra obtained at all distances, carrier frequencies, and wind conditions were remarkably similar. Spectral density dropped approximately exponentially to about 30 dB below peak at 50 Hz (fig. 6). Thus, amplitude fluctuations from atmospheric turbulence would primarily mask information encoded in rates of amplitude modulation below 20–50 Hz.

Reverberations

The occurrence of reverberations in sounds from distant sources in a forest is familiar from spectrograms or oscillograms (fig. 1). In our experiments reverberation depended on the carrier frequency of the sound pulses, the presence or absence of foliage, and the directionality of the speaker emitting the pulses.

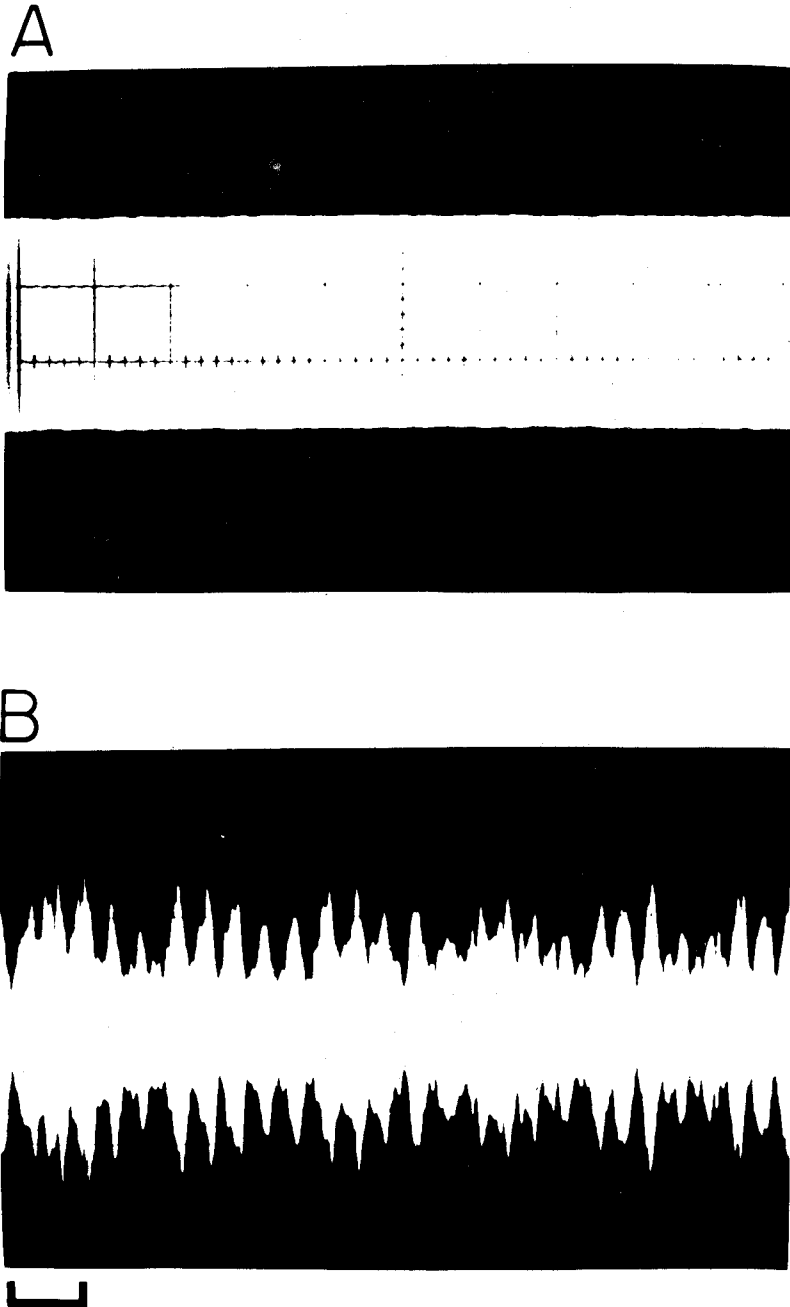


FIG. 3.—Oscillograms of amplitude fluctuations on a 2 kHz carrier frequency: A, broadcast signal; B, 60 m from source. Time scale = 1 s.

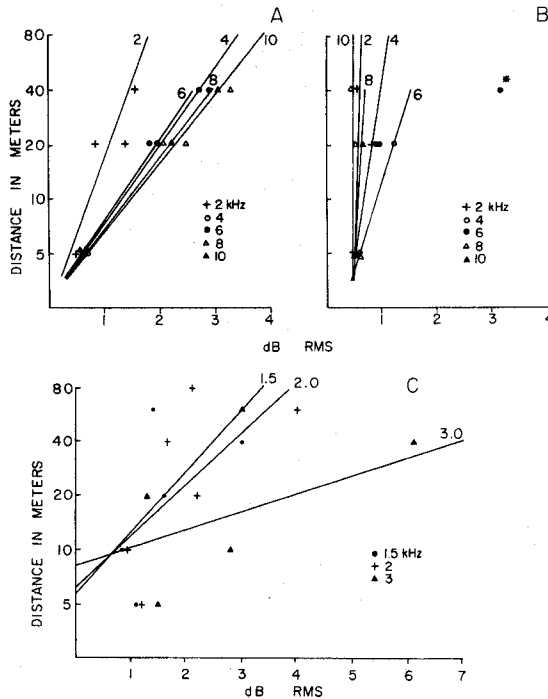


FIG. 4.—Representative amplitude fluctuations on tonal signals: A, mid-day, no wind; B, evening, no wind; C, mid-day, slight gusts of wind (<10 km/h). Numbers indicate frequencies in kHz. Asterisk indicates high value during gust of wind.

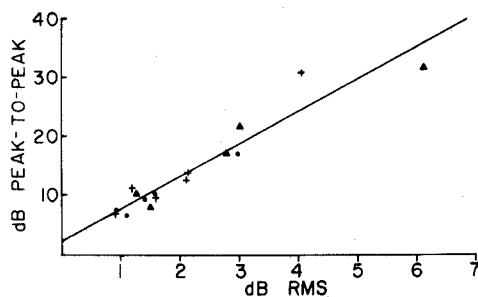


FIG. 5.—Comparison of RMS and peak-to-peak measurements of fluctuations (values from experiment in fig. 4C).

In the absence of foliage (March) the reverberation index decreased with the log of carrier frequency for the omnidirectional speaker ($r = -.36$, $P < .02$, $N = 46$) and for the horn speaker ($r = -.80$, $P < .01$, $N = 20$). The duration of reverberation was considerably longer for the lower frequencies (< 3 kHz; fig. 8), probably owing to the lower attenuation at these frequencies.

With full foliage (May, September, and October) the amount of reverberation at

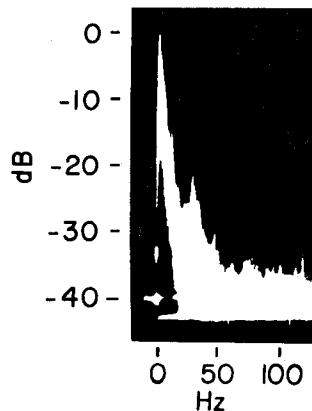


FIG. 6.—Representative spectrum of amplitude fluctuations on a tonal signal (2 kHz, 80 m).

frequencies under 5 kHz did not change greatly. At 5 kHz and above, however, there was a large increase in reverberation, which was more pronounced with the omnidirectional speaker. Comparing pairs of means of the reverberation index at each frequency with a Wilcoxon matched-pairs signed-ranks test (Siegel 1956) for the omnidirectional speaker, with and without foliage, we obtained $T = 5$ ($P < .01$, two-tailed, $N = 12$). For the horn speaker, with and without foliage, we obtained $T = 0$ ($P < .01$, two-tailed, $N = 11$; fig. 7).

As a consequence of the increase in reverberation at higher frequencies with full foliage, the intermediate frequencies had significantly less reverberation than either the low or high frequencies. To compare reverberations in bands of low (0.5 and 1 kHz), intermediate (3 and 4 kHz) and high (8 and 9 kHz) frequencies, we compared the ranks of the pooled reverberation indices for each band (see table 1).

Regardless of the presence or absence of foliage, reverberation indices were consistently lower for the more directional speaker. Comparing pairs of means of the reverberation index for the horn and omnidirectional speakers at each frequency with a Wilcoxon matched-pairs signed-ranks test, we obtained $T = 1$ ($P < .01$, $N = 11$) without foliage and $T = 0$ ($P < .01$, $N = 12$) with foliage.

Reverberations at low frequencies, especially at 500 Hz and 1 kHz, often took the form of discrete echoes, whereas the reverberations at higher frequencies decayed randomly (fig. 8).

In an open field with grass 0.5 m high there was no appreciable reverberation with either speaker (fig. 7).

DISCUSSION

Signal Transmission

The amount of information transmitted between a signaler and a receiver depends in part on the diversity of signals produced by the signaler and discrimi-

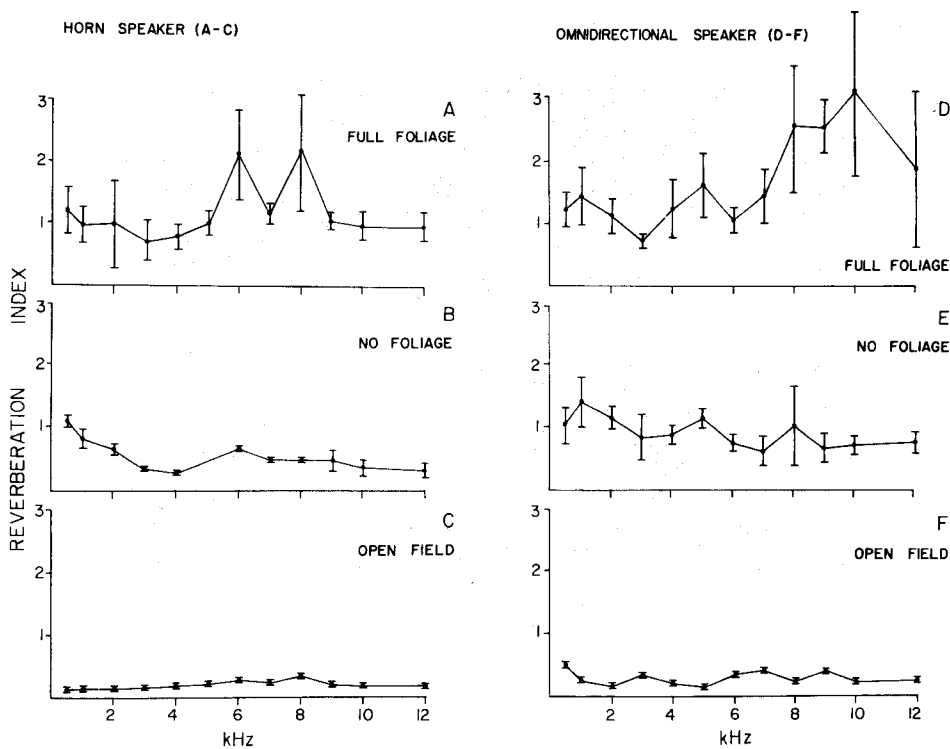


FIG. 7.—Reverberation indices (see text) vs. carrier frequency for reverberations after 25 ms sine wave pulses at 25 m from source. Vertical bars indicate one SD around each mean. Different N 's for each mean result from exclusion of samples with high background noise and from different numbers of experiments: A, $N = 4$, except for 8 and 10 kHz, for which $N = 6$; B–C, $N = 2$; D, $N = 6$, except for .5, 1, 2, 4, and 8 kHz, for which $N = 8$; E, $N = 4$, except for 5 kHz, for which $N = 2$; F, $N = 2$.

TABLE 1

COMPARISONS OF REVERBERATION INDICES FOR LOW (.5 and 1 kHz), INTERMEDIATE (3 and 4 kHz) AND HIGH (8 and 9 kHz) FREQUENCY BANDS FOR TRANSMISSION IN A FOREST WITH FOLIAGE

Frequency Bands Compared		U^*	N_1	N_2	P (2-tailed)
Omnidirectional speaker	Low vs. Intermediate	40	16	12	<.02
	Intermediate vs. High	10	12	16	<.002†
Horn speaker	Low vs. Intermediate	13	8	8	.05
	Intermediate vs. High	6	8	10	.002†

* Mann-Whitney U test (Siegel 1956).

† Intermediate frequencies have lower reverberation than either low or high frequencies.

nated by the receiver. Variations in signal structure that become degraded during transmission through the atmosphere will not allow the receiver to make the necessary discriminations.

Communication can employ three tactics to combat such degradation of signals during transmission: selecting times and locations in which the degradation of signals is minimized; coding signals in patterns that have minimal similarity to the patterns of other perturbations in the medium; and redundancy, serial or instantaneous correlations in the temporal or spatial organization of signals, which allow the receiver to predict the entire signal from a part of it or to average signals. Redundancy in acoustic signals could include stereotyped temporal sequences of sounds, often simple repetitions. Information is encoded in modulation, variations in the amplitude or frequency of signals. (See Marler [1968] and Stein [1968] for a discussion of the two types of modulation.) Amplitude fluctuations and reverberations degrade these two kinds of modulation in different ways.

What is the effect of amplitude fluctuations on the reception of a signal? The fluctuations will have no detectable effect on the carrier frequency. The random amplitude modulation slightly broadens the bandwidth for receivers with long analysis periods. For animals, the serious effect is on the amplitude patterning of the signal; the fluctuations impose a low-frequency, irregular amplitude modulation, which would interfere with the reception of amplitude modulation included in the signal by the transmitter. The energy in the fluctuations, concentrated below 50 Hz, causes the greatest interference with modulations below 50 Hz. Over long distances, when the signal level has attenuated almost to the background sound level, the fluctuations might easily exceed the modulation. It might be impossible to discriminate an unmodulated pure tone from a modulated tone at a great distance, even though it would be possible to detect the presence of a signal. Modulation rates greater than 50 Hz, predominantly perceived as variations in tonal quality by human ears (Green 1971; Gerber 1974), would not be masked by low-frequency fluctuations.

Reverberations, on the other hand, interfere with reception of rapid amplitude modulation in signals. In our studies reverberations reached the level of the background sound within 250 ms at all carrier frequencies. Most of the energy was concentrated in the first 20–50 ms following a 25-ms pulse. If pulsed signals are used, therefore, interference from reverberations will be most severe at interpulse intervals of 20–50 ms or less; for intervals shorter than about 20–50 ms a receiver will encounter increased difficulties in decoding variations in pulse width and interval. Signals composed of rapidly repeated pulses are common in birds (Marler 1960), insects (Alexander 1967), and amphibians (Blair 1963).

Reverberations impose limitations, in addition, on the rate of repetitive frequency modulation. To the extent that frequency modulation involves rapid recurrence of particular frequencies, reverberations will hinder the receiver's resolution of patterns of frequency modulation (fig. 1). Environments with numerous scattering surfaces might thus favor signals that avoided rapid, repetitive frequency modulation as well as rapid amplitude modulation.

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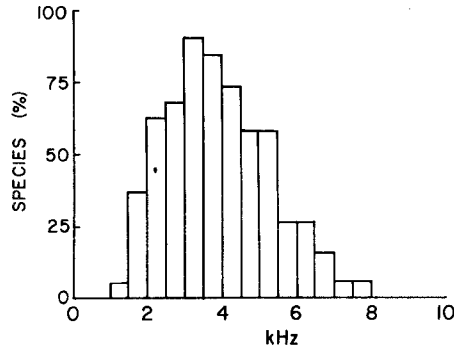


FIG. 9.—Frequencies in songs of passerine birds: abscissa shows the percentage of species that use frequencies in each 500 Hz band. $N = 19$ territorial species that breed in a North Carolina forest.

transients, such as frequency sweeps and sharp pulses that permit either binaural phase or time comparisons, arrive with substantial degradation. Accurate location of acoustic signals through a forest should present difficult problems for a receiver. Nevertheless, both man and primates can do remarkably well in judging the directions of sounds at a distance in forests (Eyring 1946; Waser 1977).

Our results show that reverberations in a forest occur particularly at high carrier frequencies (above 8 kHz) and to a lesser extent at low frequencies (below 2 kHz). Both intensity and duration of reverberations were least in the intermediate frequencies.

An examination of the recorded reverberations reveals a basic difference between reverberations at the lower frequencies and the higher frequencies. Discrete echoes follow low-frequency pulses; the echoes are sometimes nearly as intense as the original pulses (fig. 9). The time between the original pulse and the echoes (about 75 ms for a transmission range of 25 m) suggests reflection from the canopy. The echo might include both reflection from canopy foliage and reflection as a result of a difference in the acoustic impedances of the air volumes within the canopy and above it, analogous to the reflection of sound from the open end of an organ pipe (see Kinsler and Frey 1962). At high frequencies, on the other hand, the reverberations take the form of a lengthy period of decay after the pulse, without discrete echoes. At these frequencies the diameters of the leaves and trunks are of the same order of magnitude as a wavelength. Consequently, there are numerous sound reflectors; and the sound, as it scatters and rescatters in the environment, has a long decay time. The absence of canopy echoes might result from increased absorption of higher frequencies. In addition, any impedance mismatch between air volumes within and above the canopy would have less effect in reflecting shorter wavelengths than longer ones.

Adaptations for Vocal Communication

What strategies could animals adopt to minimize communication difficulties resulting from amplitude fluctuations, reverberations, and attenuation? As men-

tioned above there is some trade-off between strategies for avoidance of fluctuations or reverberations. Certain strategies, on the other hand, will tend to minimize both.

Frequency band.—For maximum range an animal should restrict its channel to intermediate or low frequencies. Atmospheric absorption, scattering, and ground attenuation combine to create a "sound window" with minimum attenuation at intermediate frequencies (about 1–4 kHz) for transmission near the ground. As height above the ground increases, the maximum for ground attenuation, and thus the lower slope of the "sound window," moves to lower frequencies (Morton 1975; Marten et al. 1977; Marten and Marler 1977; reviewed by Wiley and Richards 1978). The present study adds two further reasons that intermediate frequencies permit maximum range for acoustic communication. Reverberations are most severe outside the 2 to 7 kHz range, with prominent echoes below 2 kHz. In addition, amplitude fluctuations increase as frequency increases. At no time is a high frequency (above 8 kHz) advantageous for maximum distance.

The frequencies of bird songs are, in fact, concentrated in the optimal range for long-distance communication. Virtually all the territorial songs of passerine birds have the majority of their energy concentrated below 8 kHz. (See spectrograms in Robbins et al. [1966] and Greenewalt [1968].) Of the 19 territorial passerines that breed in the forest used for our experiments on sound transmission (Wiley 1977), 17 include frequencies between 3 and 4 kHz in their songs; almost none uses frequencies higher than 7 kHz or lower than 1.5 kHz (fig. 9; data from spectrograms in Robbins et al. 1966).

Experiments with song recognition in rufous-sided towhees (*Pipilo erythrophthalmus*) and Carolina wrens (*Thryothorus ludovicianus*) (Richards 1978) show that birds give strong aggressive responses to songs which have had the frequencies above 3 kHz removed by a filter, though much of the energy and structure in unfiltered songs is above 3 kHz. For willow warblers (*Phylloscopus trochilus*), song recognition does not require frequencies above 5.6 kHz (M. Schubert 1971). Since the higher frequencies attenuate first and are also most severely affected by both reverberations and fluctuations, it is reasonable that they should play a minor role in long-range species identification. The environmental pressures for songs concentrated below 8 kHz are apparently stronger than the selective pressures for divergence of the songs of different species to promote rapid species identification.

Over short distances (for instance, between mates or parents and young), on the other hand, both towhees and wrens, as well as many other passerines, make extensive use of sounds above 8 kHz. Clearly the high-frequency limit to long-distance territorial songs is not simply a result of the birds' hearing or vocal physiology; it is due rather to the poor transmission of information over long distances at higher frequencies, for a given amount of energy in the signal. By using higher frequencies for short-range calls, especially calls given in the vicinity of the nest (for instance, copulatory and begging calls) the bird minimizes the possibility of detection by predators or competitors.

Towhees significantly increase the minimum and dominant frequencies of their trills with increased trill rate. As a result, the frequencies used for faster trills are

TABLE 2
CORRELATIONS OF TRILL RATE WITH FREQUENCY CHARACTERISTICS OF
TRILLS IN SONGS OF TOWHEES ($n = 130$)

	Mean (kHz)	r^*	P (2-tailed)
Minimum frequency	2.83	.435	<.001
Dominant frequency	4.45	.220	<.05
Maximum frequency	5.85	.045	NS

* Linear regression coefficient.

nearer the mid-range optimum for lower reverberation. We measured sound spectrograms of the songs of rufous-sided towhees, a forest-edge species near the site of the transmission experiments. Towhee songs contain trills varying in rate from 4 to 40 syllables/s (Borror 1975). In 130 trills from 32 birds we correlated the repetition rate of syllables with the minimum, dominant, and maximum frequencies (table 2). Trill rate is significantly correlated with minimum and dominant frequencies in the trill. There is no change in the maximum frequency of the trills, though reverberation is severe at the higher frequencies. These frequencies, however, are not necessary for long-distance species recognition. Towhees thus avoid low frequencies in rapid trills, presumably in order to minimize reverberation.

Repetition rates at a given frequency.—Both Morton (1975) and Chappuis (1971) report that birds of open habitats in the tropics employ rapid frequency modulation more than do birds of undergrowth in forests. Nottebohm (1975) notes that rufous-collared sparrows (*Zonotrichia capensis*), with some exceptions, tend to have faster trill rates in open habitats than in wooded areas. Morton suggests that the reason for such differences lies in a distortion of sound frequencies, but not temporal patterns, by air turbulence and shadow zones in the open. In fact, amplitude fluctuations from turbulence do not change frequencies of propagating sound but do mask one sort of temporal pattern in sound, namely low rates of amplitude modulation. Instead, species in open habitats, in contrast to those in forests, can use rapid amplitude and repetitive frequency modulation because reverberation is much lower in the open than in forests. It is the absence of reverberation that permits rapid modulation. Because of greater reverberation in forests, forest birds should tend to use slow modulation rates in long-distance songs.

To investigate this prediction for birds of temperate forests, we measured sound spectrograms of long-range advertising songs of 44 passerine birds that breed in North Carolina (Robbins et al. 1966) and classified the predominant habitat of each species as forest, edge, park (scattered trees), or open. For each song we measured maximum repetition rate of the median frequency, either in repetitions of identical syllables, within a syllable, or between different syllables, and classified the rates as $< 10/s$ or $\geq 10/s$. Six birds of edge habitats were not included in the analysis since they often alternate between habitats. Tabulation of this data revealed that the forest birds are more likely to avoid high repetition rates than the

TABLE 3

ASSOCIATION OF HABITAT WITH MAXIMUM REPETITION RATES OF
FREQUENCIES IN SONGS OF PASSERINE BIRDS ($n = 38$ species)

Habitat	Maximum Repetition Rate	
	<10/s	≥10/s
Forest	10	13
Open and park	2	13

NOTE.— $G = 4.125$, $P < .05$ (Sokal and Rohlf 1969)

birds of open or park habitats (table 3), although there are many exceptions. For some forest species rapid repetition rates might serve primarily for communication at close range. Some forest birds, on the other hand, avoid rapid repetition, probably in order to minimize interference from reverberations.

The songs of Carolina wrens provide an example of acoustic structure that would minimize interference from reverberations. Although singing Carolina wrens produce notes in a rapid tempo, they tend to avoid rapid repetitions at any one frequency (fig. 1). In a sample of Carolina wren songs from near Chapel Hill ($n = 12$), the shortest time between two notes with the same structure (0.18 s, SD = 0.16) greatly exceeds the shortest time between any two successive notes (0.04 s, SD = 0.02). In addition, frequency sweeps tend to be separated by one or more narrow-band tones. Because of frequency discrimination by bird and mammal ears, a narrow-band note preceding an FM sweep would only mask that small section of the sweep at the same frequency. In general, if notes follow in rapid succession their frequencies should not overlap in order to avoid degradation by reverberation.

Frequency modulation for encoding information transmitted over long distances.—Because amplitude fluctuations and reverberations affect primarily the amplitude patterning of the signal, and not the carrier frequency, the use of frequency modulation to encode information would have advantages for long-range communication. The use of amplitude modulation to encode information would normally require enough redundancy, usually repetition, to counteract the effects of random fluctuations and reverberations. Frequency-modulated tonal signals have the additional advantage in long-range communication of permitting greater power per Hz bandwidth, which would increase the signal/noise ratio for receivers with frequency-discriminating receptors, like vertebrate ears. Many animals that employ long-range acoustic signals either emphasize frequency modulation over relatively wide frequency ranges or incorporate considerable redundancy in intensity modulation, often by exact repetition of sound pulses or by a combination of the two (Wiley and Richards 1978). At least for some passerine birds, playback experiments have demonstrated that amplitude patterns have little importance for song recognition (M. Schubert 1971; G. Schubert 1971).

Directionality.—The directionality of both the source and the receiver influences the effects of scattering on attenuation, reverberations, and the ease of

TABLE 4

EFFECTS OF DIRECTIONALITY OF SOURCE AND RECEIVER ON
COMMUNICATION IN A SCATTERING ENVIRONMENT

Directionality of Source	Directionality of Receiver
Decreases reverberation	Decreases reverberation
Increases locatability	Increases locatability of source
Permits limitation to receivers in known directions, but not wide broadcast	Increases signal/ noise ratio for beamed signals when source and receiver are properly aimed (extends range of detection)
Focuses sound energy (tends to extend range of detection on axis)	
Increases attenuation per m on axis (tends to decrease range of detection on axis)	

locating the source by the receiver. Because most sound sources are inherently more directional for higher frequencies than lower frequencies, narrowly beamed broadcasting would probably prove possible only for wavelengths appreciably shorter than the dimensions of the source. Although it is more difficult to produce narrowly beamed broadcasts at lower frequencies, the difficulty would possibly be offset by the lower attenuation and reverberation at these frequencies. Optimal designs for long-range communication in environments with many scattering surfaces, like forests, might require some compromises in the choice of directionality of the source and receiver (table 4).

Our reverberation experiments clearly demonstrate the effect of the directionality of the source. There is considerably more reverberation with an omnidirectional speaker; scattering occurs from surfaces in all directions from the sound source. The high directionality of the horn speaker reduced reverberations. In a location lacking scattering surfaces, an open field, reverberations were minimal with both types of sound source. Thus, to avoid reverberations in a forest it would be advantageous to use a narrowly beamed signal.

Narrowly beamed broadcasting would also permit a signaler to limit its signals to a specific receiver, but would prove disadvantageous if the signaler did not know the approximate location of potential receivers or needed to communicate in many directions at once. Passerine birds often sing for a time in each of several directions from a single perch.

A narrowly beamed source would increase the signal intensity within the sound beam and thus might increase the range of detection when the source was aimed at the receiver. On the other hand, a more widely beamed source might suffer less overall attenuation from scattering (see Wiley and Richards 1978). The directional characteristics of vocalizations by animals have just now begun to be studied quantitatively (Witkin 1977).

The directionality of the receiver, not investigated in this study, will also influence communication in scattering environments. Little is known about the directional characteristics of animal hearing. A directional receiver, by aiming toward the source, could exclude some of the background noise and thus increase

the signal-to-noise ratio of the received sound. This effect, however, would be reduced in a scattering environment, in which both the signal and the background noise would arrive from many directions.

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

SUMMARY

Effective communication requires that the receiver not only detect the presence of a signal but also discriminate significant variations in signals. Consequently, both attenuation and degradation of the structure of acoustic signals during transmission will limit the range of communication. In this study we document two primary sources of degradation of acoustic signals during propagation through natural environments, irregular amplitude fluctuations and reverberations.

Amplitude fluctuations arise especially from atmospheric turbulence, while reverberations also result from scattering surfaces, such as vegetation. Both primarily mask information coded in amplitude modulation of the signal and repetitive frequency modulation, like the trills in the songs of many passerine birds.

Irregular amplitude fluctuations primarily mask low frequencies of amplitude modulation in signals. Atmospheric turbulence from wind is the primary determinant of the intensity of irregular amplitude fluctuations, although amplitude fluctuations also increase with carrier frequency and range. In contrast, reverberations depend primarily on carrier frequency and range. Reverberations are least at intermediate frequencies (2–8 kHz). At lower frequencies reverberations in sound transmission near the ground often take the form of discrete echoes, probably from canopy foliage or from the change in acoustic impedance between air in the canopy and overlying air masses. At higher frequencies reverberations usually consist of a steady decay in acoustic energy. Consequently, in contrast to irregular amplitude fluctuations, reverberations primarily mask high rates of amplitude modulation and repetitive frequency modulation in acoustic signals.

Intermediate frequencies (2–8 kHz) are most suitable for long-range acoustic communication, because irregular amplitude fluctuations, reverberations, and attenuation increase with carrier frequency, while reverberations and attenuation from ground interference increase at low frequencies. The great majority of animals that engage in long-range acoustic communication use this middle range of frequencies. Perhaps because of the increase in reverberations at low carrier frequencies, the songs of rufous-sided towhees show a correlation between trill rate and the minimum frequency in trills.

To minimize the effects of amplitude fluctuations and reverberations on long-range acoustic communication, signals should encode information either in frequency modulation or in repetitive amplitude modulation that allow enough redundancy or signal averaging to permit recognition of signals by receivers. Because reverberations are more severe in environments with many scattering

surfaces, long-range acoustic communication in forests, as opposed to open environments, should avoid rapid amplitude modulation or repetitive frequency modulation. Among North Carolina passerine birds, species that breed in forests tend to avoid rapid repetition rates at any given frequency in their long-distance songs.

The directionality of both the broadcast and reception of acoustic signals will influence the effects of scattering on reverberations and attenuation of acoustic signals. In scattering environments, the optimal directionality of sound production and reception will require compromises.

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