ECOLOGICAL SOURCES OF SELECTION ON AVIAN SOUNDS

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Considerable importance is placed on the identification and measurement of sources of natural selection, the one unifying process in the biological sciences. Usually, sources of selection can only be hypothesized; they can rarely be measured because the long time periods involved cannot be duplicated in the laboratory for experimental purposes.

This paper attempts to measure sources of selection on bird sounds that are derived from the acoustic properties of their habitats. Because all sounds do not propagate equally well in a given habitat, selection should favor the use of sounds that give the greatest broadcast area for a given source sound pressure level. Therefore, this study is concerned with signals used for communicating over relatively long distances. These include most passerine "song" notes, many passerine call notes, and contact notes used by a pair of conspecifics to remain in auditory contact when they may be too far apart to maintain visual contact.

In an environment without vegetation or boundaries such as the ground, and through a homogeneous, frictionless medium, sound diverges spherically from a source that is small relative to the sound's wavelength. Because of spherical divergence the intensity of the far sound field will drop at a rate of 6 dB per each doubling of distance, due to the inverse-square law (e.g., Peterson and Gross 1967).

Natural environments, of course, differ greatly from the ideal circumstances within which sound attenuation follows the inverse-square law. However, this theoretical attenuation rate provides a convenient base from which natural environments may be compared. In natural environments other factors either reduce sound energy, such as absorption by air, ground, and vegetation, or redirect sound energy, as by reflection or diffraction. Thus, absorption of sound energy and spherical divergence are directly proportional to the length of the sound propagation path, while the redirective forces are generally not proportional to the length of the sound propagation path.

The purpose of this paper is to describe the acoustics of natural environments and to determine whether the physical structure of bird sounds used in long-distance communication correlates with differences in habitat acoustics.

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Data were obtained from lowland tropical habitats in Panama and the Canal Zone. I separated the habitats studied into forest, edge, and grassland categories based on vegetative structure. These categories were chosen because, with rare exceptions, any bird species spends most of its time entirely within one category.

The forest habitat studied is classified as Tropical Monsoon Forest because there is a well-defined dry season (less than 60 mm of rainfall during January through March) (Bennett 1963). This habitat was defined in terms of tree-foliage strata following Bennett's categories 1 and 2. The forests had two tree-foliage strata, the lower stratum averaging about 20–40 feet in height. The lower stratum is variably open and closed, and the upper stratum (75–100 feet in height) is usually open but joined by vines. Because of low light intensity the floor vegetation is usually moderate and chiefly woody; root buttresses, lianas, and small palms are common (Allee 1926).

Edge habitat included a wide array of vegetative structures ranging from young second-growth stands of trees to scattered bushy growth interspersed with herbaceous plants. Second-growth stands with a single tree-foliage stratum not above 25 feet and occasional dense labyrinths of lianas are defined as edge.

Grass habitats were probably man made in the area studied and are maintained by annual burning during the dry season. Tests were made in tall grass (4–5 feet high) and in partially barren short-grass areas near Cocoli in the Canal Zone.

MATERIALS AND METHODS

Because of absorptive and redirective effects, sound attenuation should be derived from factors that are directly proportional to distance and factors that are of unpredictable magnitude over distance. The total attenuation is their sum. Ideally, it would be best to calculate the exact sound level at a given point in space due to a given sound source. In a real environment, as opposed to controlled conditions, the ability to perform such calculations is very limited. The actual geometry of the propagation path is too complex to be handled analytically. In addition, the acoustical impedance of the boundaries (i.e., the ground, trees, grasses, etc.) is unknown. Also, the microstructure of the atmosphere is unknown and probably changing.

One way that propagation tests can be made is to use a calibrated source of known acoustical characteristics. Knowing these it is possible to calculate the sound level at any point in space under the assumption of an infinite, homogeneous, lossless medium. Measured sound levels can then be compared with these predictions to determine "excess attenuation." The problem with this approach is that acoustical sources such as loudspeakers are not stable either in time or in frequency response.

I approximated a calibration by measuring the sound level from the speaker at a relatively close distance, choosing an unobstructed line-of-sight recording at 25 feet from the speaker as the reference sound level. If the source level varies from test to test it is taken into account in the data reduction. Subtraction of

sound levels in decibels is equivalent to taking energy ratios, so the frequency response characteristics of the source do not really enter into the calculations. The sound propagation tests were designed to sample the sound levels in a straight-line direction from the sound source horizontally to the ground. A standard procedure was used to produce data that may be used to compare the habitats.

Habitat sound propagation characteristics were measured using a pre-recorded playback test tape as the sound source. The test tape contained 20 sound frequencies at ⅓-octave intervals from 100 to 15,850 Hz. The test tape contained 15 seconds of pure tone sound at each of these frequencies followed by 15-second intervals of random noise bands, ⅓-octave wide, centered on the pure tone frequencies (excluding the 100-Hz tone). The pure tone frequencies were produced with a Hewlett-Packard sine wave oscillator, and the random noise bands were produced with a General Radio 1390-B Random Noise Generator and filtered to ⅓-octave bandwidths using a General Radio Band Pass Filter. These sounds were recorded at 0-dB level on the tape recorder modulometer using a Nagra 111B tape recorder at a tape speed of 15 inches per second. The playback level of the test tape subsequently showed all frequencies to be within ±1 dB.

Two criteria used in choosing test sites were uniformity of habitat (i.e., all grass or all edge, etc.) and flatness of terrain. A 300-foot wire line marked at 25-, 100-, and 200-foot distances was used to mark the speaker and microphone placements in all test sites. The test tape was played back at 15 inches per second on a Nagra 111B tape recorder, using the hi-fi setting, through a Nagra speaker. The tape recorder playback volume control was set at +15 dB, and the speaker volume setting was set at full volume output. I used full gain settings on the tape recorder and speaker to insure maximum equality of sound output level for all tests and to reduce the chance of accidentally changing the gain settings during a test. The test tape was recorded at 7½ inches per second, 25, 100, 200, and 300 feet from the speaker using another Nagra 111B tape recorder with the line input control set at +15 dB. I used a Sennheiser MKH104 omni-directional microphone, adapted to the Nagra's accessory socket input, for all recording. The microphone response was essentially flat (less than 1-dB deviation) for the frequencies tested. I used a handmade attenuator (1% carbon resistors, flat in the frequency range tested) between the microphone and the recorder to avoid overloading the tape recorder when recording close to the speaker. The attenuator allowed me to reduce the signal in any combination of 5-, 10-, or 20-dB settings. The attenuator resistance could be shunted at the longer recording distances and thus was retained in the recording channel even though not used.

Through most test sites, propagation measurements were run at 1 foot ("ground level") and at 5 feet. Several were also run at 10–20 feet above the ground at forest sites. At each test site two sets of data were obtained, four measurements along the ground (corresponding to the four recording distances, 25–300 feet), and four measurements at 5 feet.

The sound propagation test recordings were played back through a Nagra 111B tape recorder into a General Radio Type 1564 Sound and Vibration

Analyzer coupled to a General Radio Type 1521-B Graphic Level Recorder. The tape recorder playback level control dial was kept at the 0-dB setting. The signal was filtered using the analyzer's $\frac{1}{3}$-octave bandwidth centered on the appropriate sound propagation test frequency. The output signal amplitude was measured and recorded on paper by the level recorder using a chart speed of $7\frac{1}{2}$ inches per minute and a 3 inches per second writing speed.

The sound pressure levels (SPLs) in decibels for the test frequencies were obtained from the level recorder chart for the four recording distances. The decibel reference level throughout this paper is 0.0002 μbar.

The data at this stage show effects of the speaker response in addition to effects due to the environment and distance. This presents no difficulty for computing sound propagation values because I measured the *relative* drop in SPL over distance, not decibel levels in absolute terms. The comparison of SPLs at 100, 200, and 300 feet from the speaker were relative to the reading obtained at 25 feet (which was always recorded with a direct line of sight from speaker to microphone).

The data were reduced by subtracting the measured SPLs from the 6 dB per doubling of distance rate due to spherical divergence to obtain excess attenuation values. For example, if the test signal attenuated 14 dB from 25 to 100 feet, this represents an excess attenuation of $+2$ dB since the loss due to spherical divergence is 12 dB over this distance (there are two doublings of distance between 25 and 100 feet). Excess attenuation values represent anomalies in sound propagation produced by the environment and permit habitats to be compared. In this case, anomalies in sound propagation are the "natural" situation within which natural selection operates. Excess attenuation values presented here were calculated for the full test distance of 300 feet by summing the intermediate attenuation measurements. Differential attenuation due to humidity was not an important factor in the frequency range tested (less than 2×10^{-2} dB/ft air absorption for the highest frequencies tested; Kneser 1933).

Bird sounds were recorded with a Nagra 111B tape recorder at 15 inches per second tape speed using a Sennheiser MKH104 microphone mounted on a 36-inch parabolic reflector. The number of species analyzed was 177. I was able to record the common sound-producing bird species occurring in the Canal Zone lowland area, and other species were obtained from the Cornell University Laboratory of Ornithology's Library of Natural Sounds. All of my recordings are deposited in the Library of Natural Sounds.

The sounds were analyzed with a Kay Electric Company Type 6061-A Sonagraph using the FL-1, linear scale, and narrow filter band settings. I used a -2-dB or less recording amplifier setting to guard against spurious harmonics in the spectrograms (Greenewalt 1968). Data taken from spectrograms were frequency range and frequency emphasized for the fundamental or most intense harmonic (the procedure for determining frequency emphasized is described below), number of harmonics if present, and presence of amplitude or frequency modulation.[1]

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[1] A list of bird species considered and mean excess attenuation values may be obtained from the author on request.

RESULTS

Sound Propagation

The mean excess attenuation values (EAVs) for each frequency tested were calculated by summing the excess attenuation values for 300 feet and dividing by the number of 300-foot tests (N).[2] The raw data for the sound propagation tests have been presented elsewhere (Morton 1970).

It might be assumed that EA in most natural environments is directly related to sound frequency, with higher frequencies attenuating more rapidly than lower frequencies (Konishi 1970). This is because the ability of sound waves to travel around objects rather than reflect off them is related to the wavelength of the sound. The energy of the higher frequencies is lost through reflections off branches and leaves, etc., while only the earth and large root buttresses should reflect sizable amounts of energy at low frequencies. However, the habitats differed significantly in this respect.

Forest Habitat

Figure 1 shows excess attenuation data for pure tones at three elevations in the forest habitat. The EA does not follow the hypothesized frequency-dependent pattern. Instead, there is less EA from 1,585 to 2,500 Hz than for higher or lower frequencies with a large rise in EA (12 dB) above 2,500 Hz. This lower elevation pattern changed at the two higher elevations such that above 15 feet there was no pronounced lessening of EA in the 1,585–2,500-Hz range ($P < .05$, Student's t-test).

The results for ground-level random noise propagation in the forest habitat are presented in figure 2. The EA curves for pure tones and random noise are not significantly different. It appears on the basis of sound propagation qualities that a bird living near the ground in the forest habitat would attain a greater broadcast area if it used a sound in the 1,000–2,500-Hz range.

Edge and Grassland Habitats

Excess attenuation data for ground level, edge, and grassland habitats are presented graphically in figure 3. Edge-habitat EA is intermediate between forest and grassland for both pure tones and random noise bands, but the EAVs are not significantly different from grassland values at the .05 level. This is likely due to variance in the edge test sites whose structure varied greatly in "openness," causing high statistical variance in the lumped edge propagation test results. The edge habitat showed a broad plateau of similar EAVs from 500 to 2,500 Hz. Excess attenuation increased with increasing frequency above 2,000 Hz.

A comparison of random noise band propagation in grass and edge habitats at ground level is presented in figure 2. Again, as in pure tone attenuation, the
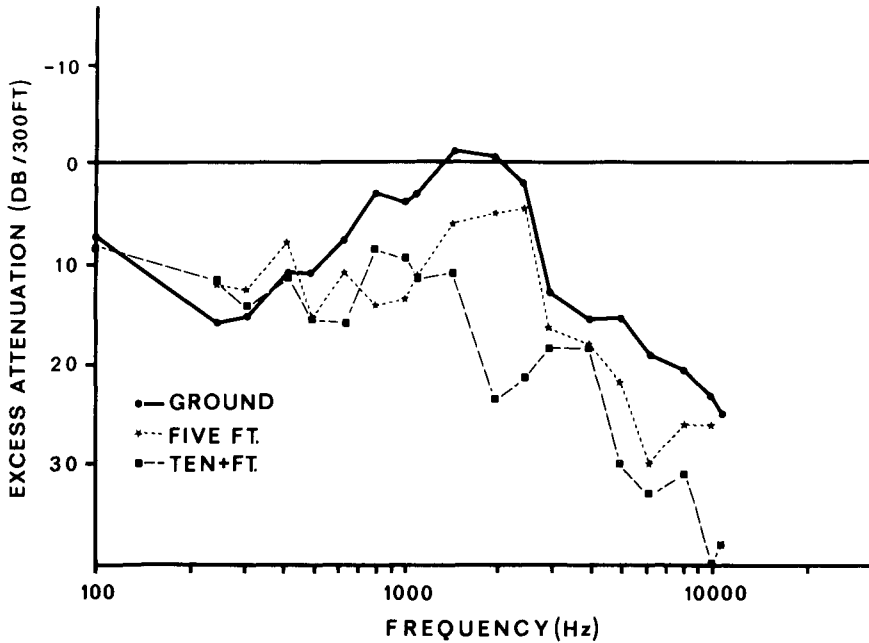
[2] See n. 1 above.

Fig. 1.—Curves showing excess attenuation in decibels per 300 feet plotted against sound frequency for pure tone sound propagation at ground, 5 feet, and 10–20-foot elevations in forest habitat. The solid line at 0-dB excess attenuation represents what the plot would look like if the frequencies were all attenuating at the rate of 6 dB per doubling of distance.

edge data is intermediate to forest and grass habitat sound propagation. The differences in edge and grass EA means approach significance in the frequency range from 800 to 1,585 Hz; the 1,000-Hz means are significantly different. There was no significant difference in EA between random noise and pure tones in either the grass or edge habitat.

Edge-habitat propagation tests were made at ground level and at 5 feet above ground over the same test sites. No difference in EAVs between the two heights was found in this habitat except for 310 Hz.

A Comparison of Excess Attenuation in the Three Habitats

At lower elevations, forest random noise and pure tone propagation differs significantly from edge and grassland in the frequency range from 1,585 to 2,500 Hz. Forest pure tone EA ranges from 10.8 to 13.9 dB less than edge EA in this frequency range. Forest EA is also 17.5–20.2 dB less than grass EA in this range. The mean EAVs for random noise are similar to those for the pure tones in each habitat and corroborate those results.

Several hypotheses explain the excess attenuation differences. The habitats differed in vegetative structure and density and in the homogeneity of the surrounding air. Daytime wind and temperature gradients and air turbulence
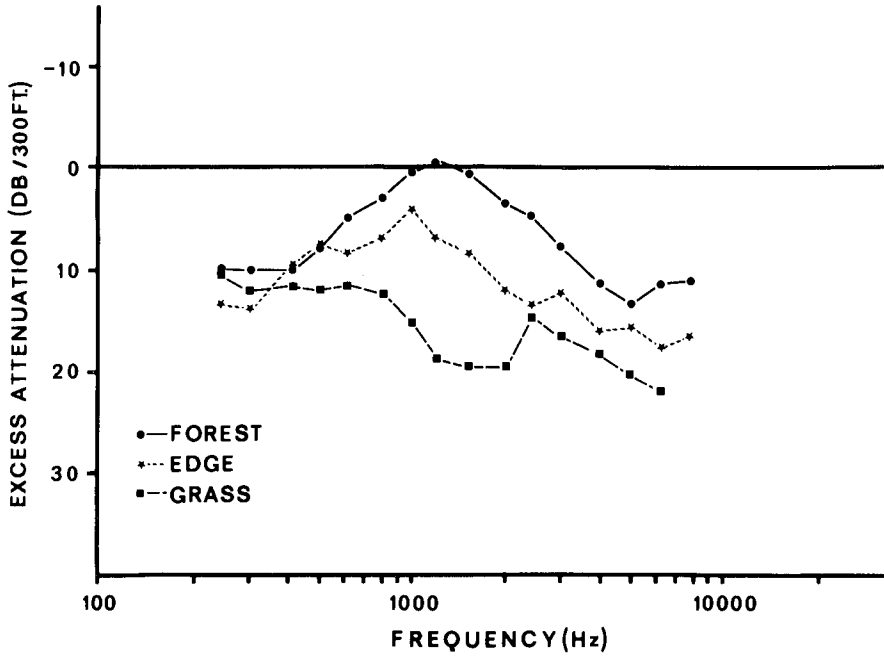
Fig. 2.—Excess attenuation levels for random noise band sound propagation at ground level in forest, edge, and grassland habitats. Axes as in fig. 1.
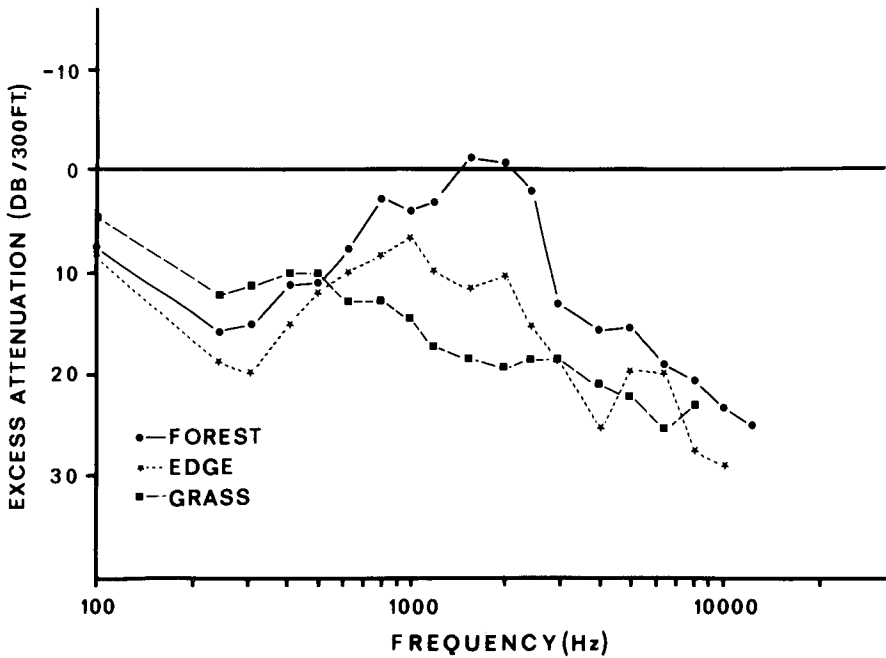

Fig. 3.—Excess attenuation levels for pure tone sound propagation at ground level in forest, edge, and grassland habitats. Axes as in fig. 1.

are predictably present in edge and grass habitats, but the air under the canopy in Panamanian forests is comparatively homogeneous (Allee 1926; Tatge 1965). Sound attenuation in the grass habitat, and to a lesser extent in edge, increased with increasing frequency. This is probably because the effects of these atmospheric wind speed gradients, temperature gradients, and turbulence on sound propagation vary directly with increasing sound frequency (Pridmore-Brown and Ingard 1955, 1956; Mokhtar and Marrous 1955).

Bird Sounds

The vocalizations of 177 species of neotropical birds were analyzed: 85 species occupied the lower- and upper-level forest habitat, 71 species the edge, and 21 species were grassland inhabitants.

I analyzed three components of the sounds: the frequency range, the extent of frequency modulation, and a measure of the sound energy distribution over time and frequency, which I term "frequency emphasized." The modulation component describes the nearly instantaneous energy distribution of sound whereas frequency emphasized indicates the frequency where most of the sound energy is centered. Frequency emphasized was determined by placing a clear plastic grid with horizontal lines at 500-Hz intervals over each spectrogram and estimating, to the nearest 500 Hz, the frequency emphasized in the whole sound, as indicated by the relative darkness of the spectrogram trace. The frequency emphasized is essentially the frequency "backbone" of the sound and is used to circumvent the complexity found in most bird sounds due to selection for specific distinctiveness. To characterize the extent of frequency modulation, each sound was classified as either pure tonelike, rapidly modulated, or a mixture of both these sound types. Sounds classified as pure tonelike ranged from "whistles" with little frequency change to sounds with considerable frequency change but still whistle-like in quality and producing spectrogram traces without sidebands. The rapidly modulated category pertained to rapid trills (pulsed sounds) and rapidly modulated (usually frequency modulated, but some containing amplitude modulation as well) sounds such as those described by Stein (1968). Signals of this type sound "buzzy" to the human ear and, if the modulation rate is above 200 Hz, are resolved as carrier frequency and side bands by the spectrograph.

Figure 4 presents data on the frequency-emphasized component. I found little individual variation within species in this component. The mean of all species for each habitat is indicated on the horizontal axis. The means of edge and grassland bird sounds were not significantly different ($t = .7111$, $P < .9$, 90 df). The means of lower-level-forest bird sounds and grassland bird sounds were significantly different ($t = 7.2335$, $P < .001$, 87 df), as were the means of lower-level-forest and edge bird sounds ($t = 6.0703$, $P < .001$, 137 df). Table 1 presents evidence that differences in frequency emphasized are not due to a particular taxonomic entity but are based on habitat differences. For example, oscines living in the lower forest have significantly lower frequencies emphasized than their counterparts living in edge ($P < .05$, by χ^2).
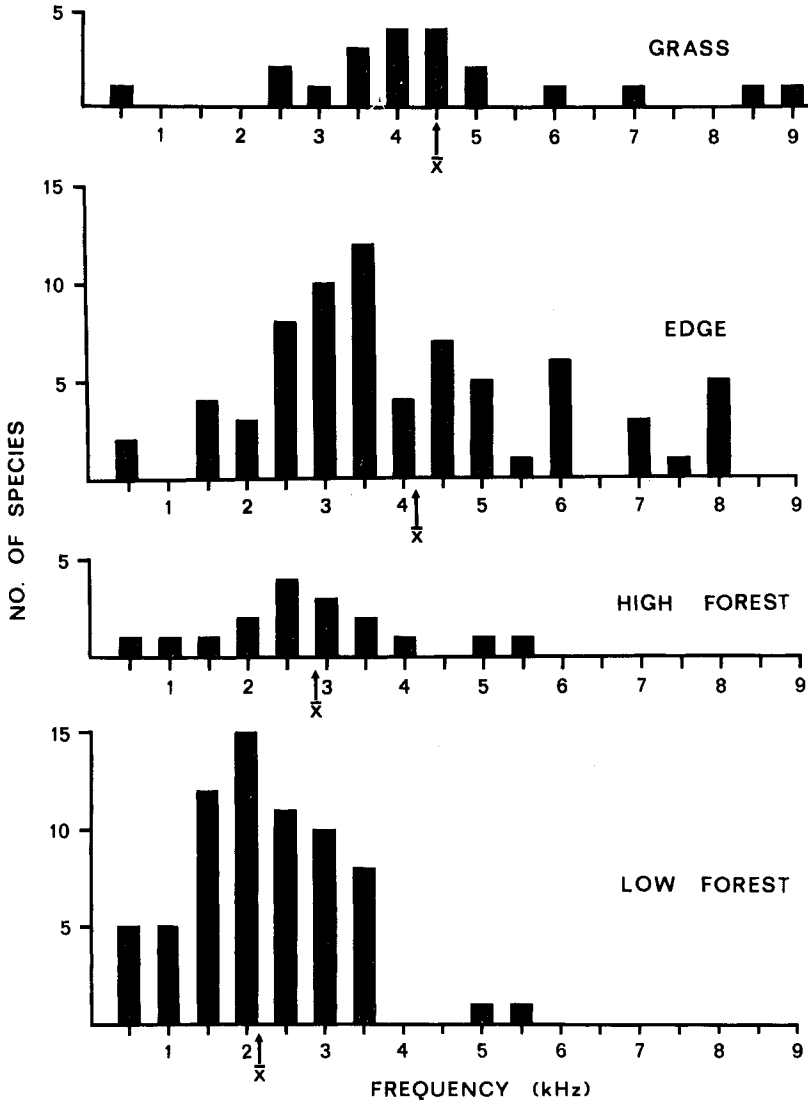
FIG. 4.—The histograms depict the frequency emphasized in the sound of bird species (to the nearest 500 Hz, see text) arranged according to the habitat in which the species occurred. The mean frequency emphasized ($\bar{X}$) is the sum of the frequency emphasized for all species in each habitat divided by the number of species in that habitat.

Sounds with rapid modulation were given mainly by birds restricted to grass and edge habitats (table 2). Lower-level-forest bird sounds are predominantly pure tonelike and contain less rapid modulation and less combination sound types than expected by χ^2 distribution. Upper-level-forest bird sounds are also more pure tonelike than expected, but rapid modulation occurrence matches that predicted by χ^2. Many edge bird sounds are combinations of pure tonelike

TABLE 1

MEAN FREQUENCY EMPHASIZED IN SOUNDS OF BIRD SPECIES
ARRANGED INTO THREE TAXONOMIC CATEGORIES (kHz)

Habitat	Nonpasserines	Nonoscine Passerines	Oscine Passerines
Upper forest	2.0 (6)	3.1 (7)	3.6 (4)
Lower forest	1.5 (17)	2.3 (32)	2.7 (19)
Edge..............	3.6 (9)	3.6 (28)	4.7 (34)
Grass	3.1 (6)	4.1 (9)	5.8 (6)

NOTE.—Number of species in parentheses.

and rapid modulation sound types. Grassland bird sounds have more rapid modulation than expected and less pure tonelike sounds.

Rapid modulation occurred in grassland bird sounds more than in edge bird sounds. In the edge habitat, those species having both sound types in their signals had them in nearly equal parts. Grassland species had the whole signal, or most of it, rapidly modulated. In forest bird sounds containing both sound types the pure tonelike part predominated.

DISCUSSION

For low-level-forest propagation tests (fig. 1) sound is attenuating at a rate less than or near 6 dB per doubling of distance within the frequency range 1,585–2,500 Hz. This indicates that sound is reaching the sampling points by indirect as well as direct pathways in the forest tests. The forest may be thought of as a large "room" with the canopy acting as a ceiling. The direct sound field probably predominates at 25 feet, especially in tests made above ground level, because there will be little chance for reflected sound to be received at this close distance. However, when the source and receiver are at ground level, the direct sound is highly attenuated with the ground as an absorbent boundary. At greater distances, 100 feet or more, reflected sound energy may predominate or make up a greater part of the sampled sound. The major difference in EA

TABLE 2

NUMBER OF SPECIES WHOSE SOUNDS WERE LARGELY PURE TONELIKE,
HIGHLY MODULATED, OR TRILLED, OR A COMBINATION,
ARRANGED ACCORDING TO HABITAT

| HABITAT | SOUND TYPE | | | |
	Pure Tonelike	Modulated	Both	Total
Low forest	59 (45.3)	1 (6.9)	8 (15.8)	68
Upper forest	14 (11.3)	2 (1.7)	1 (3.9)	17
Edge	38 (47.3)	7 (7.2)	26 (16.4)	71
Grass	7 (14)	8 (2.1)	6 (4.9)	21

NOTE.—Expected number of species in parentheses; χ^2, $P < .001$.

TABLE 3

ESTIMATED DISTANCE FROM SOUND SOURCE TO POINT WHERE SIGNAL LEVEL
EQUALS AMBIENT SOUND PRESSURE LEVEL (SEE TEXT)

Frequency (Hz)	Forest	Edge	Grass
500	61 (23)	70 (23)	49 (30)
1,000	76 (20)	113 (20)	74 (20)
1,585	106 (22)	...	...
2,000	113 (22)	81 (22)	62 (20)
2,500	119 (22)	...	...
3,000	50 (26.5)	...	...
4,000	37 (31)	32 (31)	60 (20)
8,000	20 (38)	23 (35)	56 (20)

NOTE.—Distance given in meters. Ambient noise level in decibels shown in parentheses.

between edge and forest occurred at these greater distances. The return of sound energy to the receiver near the ground is most likely the result of reflection from the canopy. Sound energy in the edge habitat would continue to attenuate at a higher rate because the energy spreading upward would not be reflected back to the sampling point in the absence of a canopy.

The distance a bird is able to communicate by sound depends on the attenuation rate of the sound used, the amplitude of the sound at the source, the level of masking ambient noise, and the auditory sensitivity of the individual receiving the sound. The data presented above do not contain all the information required for predicting communication distance. However, if we assume a series of pure tone frequencies each with a source level of 80 dB, we may approach the question: How far will each frequency propagate before equaling the ambient sound pressure level?

Table 3 presents this information for sounds broadcast through each habitat. Ambient sound levels for 0700 hours (a peak time for bird vocal activity) are taken from Morton (1970). The excess attenuation values taken from ground-level tests were divided by 300 to obtain excess attenuation in terms of decibels per foot. Then the following formula was solved for r_2: $T \cdot r_2 + 20 \log r_2 = Lw - Lp_2 - 0.5$, where r_2 = distance from the source, T = excess attenuation in decibels per foot, Lw is the initial sound power level (80 dB), and Lp_2 is the ambient sound pressure level. The calculation of these distances assumes that the excess attenuation is the same throughout the sound propagation path. The indicated distances are probably representative within the 91.4 meters (300 feet) that my propagation tests covered.

If the acoustic data presented here indicate sources of selection on the frequency of sounds used by forest species that live near the ground, we should expect that individuals using frequencies in the 1,585–2,500-Hz range for their long-distance communication signals would be favored by selection.

The mean frequency emphasized in forest bird sounds used in long distance communication is 2.2 ± 1.0010 kHz SD (fig. 4), within the frequency range predicted by the acoustic data.

Forest bird sounds are pure tonelike when compared with bird sounds from

other habitats (e.g., Willis 1966; Chappuis 1971). My analysis of spectrograms of the sounds of 68 species of forest birds shows this to be true (table 2). In addition to their pure tonelike quality, the forest bird sounds are relatively frequency constant. I calculated a mean frequency range for the sounds in each habitat by adding the frequency ranges of each species in a habitat and dividing by the total number of species in the habitat sample. The mean frequency range of lower-forest bird sounds was 1.48 ± 1.3939 kHz SD, which is significantly lower than upper-forest bird sounds (2.71 ± 5.5193 kHz), edge (3.69 ± 6.2508 kHz), or grassland bird sounds (3.45 ± 5.6505 kHz). The sound propagation data presented here indicate that the frequency-emphasized component of low-elevation-forest bird sounds results from selective forces produced by forest acoustics. But their pure tonelike quality and small frequency range remain unexplained by my data. Possibly the small frequency range of the forest sound "window" (1,585–2,500 Hz) is sufficient to result in these characteristics. Another possibility, discussed further below, is that the comparatively stable atmosphere in the forest *permits* selection to favor mechanisms to increase source amplitude. That is, if there is no selection pressure against producing pure tonelike sounds, these may be favored because this permits a bird to concentrate the sound energy into a narrow frequency range resulting in greater source amplitude than if the same energy was spread out over a wide frequency band. Or, signal reception may be more efficient for pure tonelike sounds against a background of wide band noise produced by rain or wind-rustled leaves.

There are data indicating that the sound window phenomenon may occur in other forest types than neotropical rainforest. Embleton's (1963) data on sound propagation in north-temperate deciduous and evergreen woods also showed that lower attenuation in the 1–3-kHz frequency range for cedar (*Thuja*), pine (*Pinus*), spruce (*Picea*) leaves may be driven as forced oscillators by the action of the sound field causing enhanced sound pressure levels for certain frequencies and distances from the source due to phase velocity changes. He found a drop in excess attenuation at 4 feet above the ground between 1,000 and 4,000 Hz lower attenuation in the 1–3-kHz frequency range for cedar (*Thuja*), pine and cedar woods and from 1 to 2 kHz in deciduous woods at 50–100 feet from the sound source. Embleton (1966) postulates that the trunks of forest trees may function to change attenuation of a sound field in predictable ways. The variables are tree density, trunk diameter, and the surface impedance of the trunks. Different growth forms or tree-trunk densities may push the range of optimum sound propagation up or down. Chappuis (1971) points out differences between bird sounds in forest and open habitats in equatorial Africa that parallel my findings.

Contrary to what one might intuitively expect, grasslands are a difficult environment for sound propagation. On windy days the wind speed is low at ground level and increases with increasing elevation due to ground friction. Temperature tends to decrease with increasing elevation. Turbulence also affects sound propagation in the open habitats more than in forest. These factors, regular though fluctuating, cause sound attenuation to increase with increasing frequency (Mokhtar and Morrous 1955; Pridmore-Brown and Ingard

1955, 1956). It is theoretically possible, under "ideal" conditions, that a pure tone signal, broadcast from ground level, would not be detectable over a short horizontal distance (say 60 feet or less), depending on the frequency of the signal and the steepness of the temperature gradient. According to Pridmore-Brown and Ingard (1955, 1956), some of the spherically diverging wavefront emanating from a sound source near the ground will be absorbed by the earth. The wavefront advancing parallel with the earth will be diffracted upward due to air temperature and wind gradients (upwind, not downwind). The term they used for the soundless area under this wave front is the "shadow zone." If a bird calls from as little as 10–20 feet above the ground it will erase most of the shadow-zone effects and increase broadcasting area.

In Panama about 25% of the grassland species characteristically sing in flight. Flight songs are more prevalent in species of temperate grasslands and tundra (Armstrong 1963, p. 221). Most other grassland species in Panama sing from high perches and take readily to man-made perches such as telephone lines. This is in contrast to many forest species which both forage and call from the ground.

In grasslands excess attenuation tends to increase with increasing frequency (fig. 3), and there is no significant difference between pure tone and random noise propagation. From these data one might predict that grassland birds would use low-frequency sounds but not necessarily with a pure tonelike quality.

However, figure 4 does not indicate any tendency toward the use of low-frequency sounds. The mean frequency emphasized for all species combined is 4.4 kHz ± 1.8948 SD. In terms of sound quality grassland species use modulated or trilled sounds more than edge or forest species (table 2).

I suggest that the preponderance of rapidly modulated sounds, in species occupying open habitats, may be due to selection pressures against the use of information transfer based largely on signal frequency. Shadow-zone influences and air turbulence distort sound frequencies: higher-frequency components are lost before the lower frequencies. Selection probably favors information coding based on the temporal components of sound signals, for in open environments as long as the sound is audible the temporal pattern will remain little changed and should provide a more efficient means of communication. The empirical data in table 2 support this hypothesis.

The edge habitat is intermediate in acoustics and in vegetative structure to the other habitats. The excess attenuation decreases slightly in the 1,585–2,500-Hz range where forest attenuation lowers markedly. Otherwise it is similar to grasslands in that attenuation increases directly with frequency. There is no difference between random noise band and pure tone attenuation. Edge differs from forest in that there is no narrow optimum frequency range for sound propagation. Edge differs from grassland in that low frequencies do not consistently propagate better than higher frequencies.

If no sound window effect is present in edge habitat the evolution of edge bird sounds may be more influenced by selection pressures favoring species distinctiveness or qualities reducing habituation. Certainly, the sounds in this habitat are relatively more variable in structure than forest bird sounds. Edge

contains more species having both rapidly modulated and pure tonelike elements in their sounds than the other habitats (table 2).

It is difficult or impossible to obtain direct experimental evidence to support a hypothesis dealing with selective forces because, in part, the element of time cannot be built into the experiment. However, one test of the hypothesis is to compare congeneric species of birds occupying different habitats.

In Panama, four sympatric species of *Hylophilus* vireos occur in different habitats: *H. flavipes* is found in edge areas with scattered low bushy growth (its habitat is the most open of the four species); *H. aurantiifrons* occurs in dense edge that approaches young forest in structure; *H. decurtatus* occurs in this habitat and in the forest canopy; and *H. ochraceiceps* is found near the ground in forests. Figure 5 illustrates the advertising phrases of each species. *Hylophilus ochraceiceps*'s call fits the predicted pure tonelike sound. This sound is often accompanied by lower-frequency "doy-doy" sounds (not illustrated). *Hylophilus flavipes* has a redundant call, a series of five to 40 similar, relatively low-frequency whistles that are delivered at a rate of 2.4 per second. The precise time spacing of the notes in the long call is in contrast to the other species and may enhance this species' communication efficiency in the open habitat it occupies. The sounds of *H. decurtatus* and *H. aurantiifrons* are relatively similar, which correlates with the similarity in edge and forest canopy sound propagation. The timing of the elements in *aurantiifrons*'s call is more stereotyped than the elements in *decurtatus* calls, perhaps reflecting the more open habitat of the former. The calls and habitat differences in the latter two tropical vireos are paralleled by the North American *Vireo griseus* and *V. olivaceous*.

The antbirds, *Myrmeciza exsul* and *M. longipes*, occupy different habitats, *exsul* being a terrestrial forest species and *longipes* a terrestrial edge species. Figure 6 represents spectrograms of the calls of both species. *Myrmeciza exsul*'s call is pure tonelike and relatively frequency constant while *M. longipes* has a rapid series of notes that gradually lower in frequency range and increase in the time between notes. The call differences in these species support the predictions from habitat acoustics discussed above.

At the bottom of figure 6, the song of the blue-black grosbeak (*Cyanocompsa cyanoides*) is illustrated. This species and the confamiliar slate-colored grosbeak (*Pitylus grossus*; not illustrated) occur in low forest elevations and have pure tonelike sounds with a narrow frequency range. Their sounds differ from most other fringillids (which, in the tropics, are mainly edge and grassland inhabitants) and have converged toward the sounds of forest birds in general.

Another sort of habitat acoustic correlation with sound structure was found in grassland birds that call only at certain times of day. Some species that used rather high-frequency calls that were pure tonelike called only in the early morning, probably before daylight temperature gradients developed. For instance, the rufous-tailed hummingbird, *Amazilia tzacatl*, sang only from approximately 0600 to approximately 0650, using a pure tonelike sound, while the fork-tailed emerald, *Chlorostilbon canivetii*, used a buzzy sound and called most of the day. The wedge-tailed ground-finch, *Emberizoides herbicola*, occurring in grassland on Cerro Campana, has a pure tonelike song and sings only for a short period before sunrise, while a small population in grassland
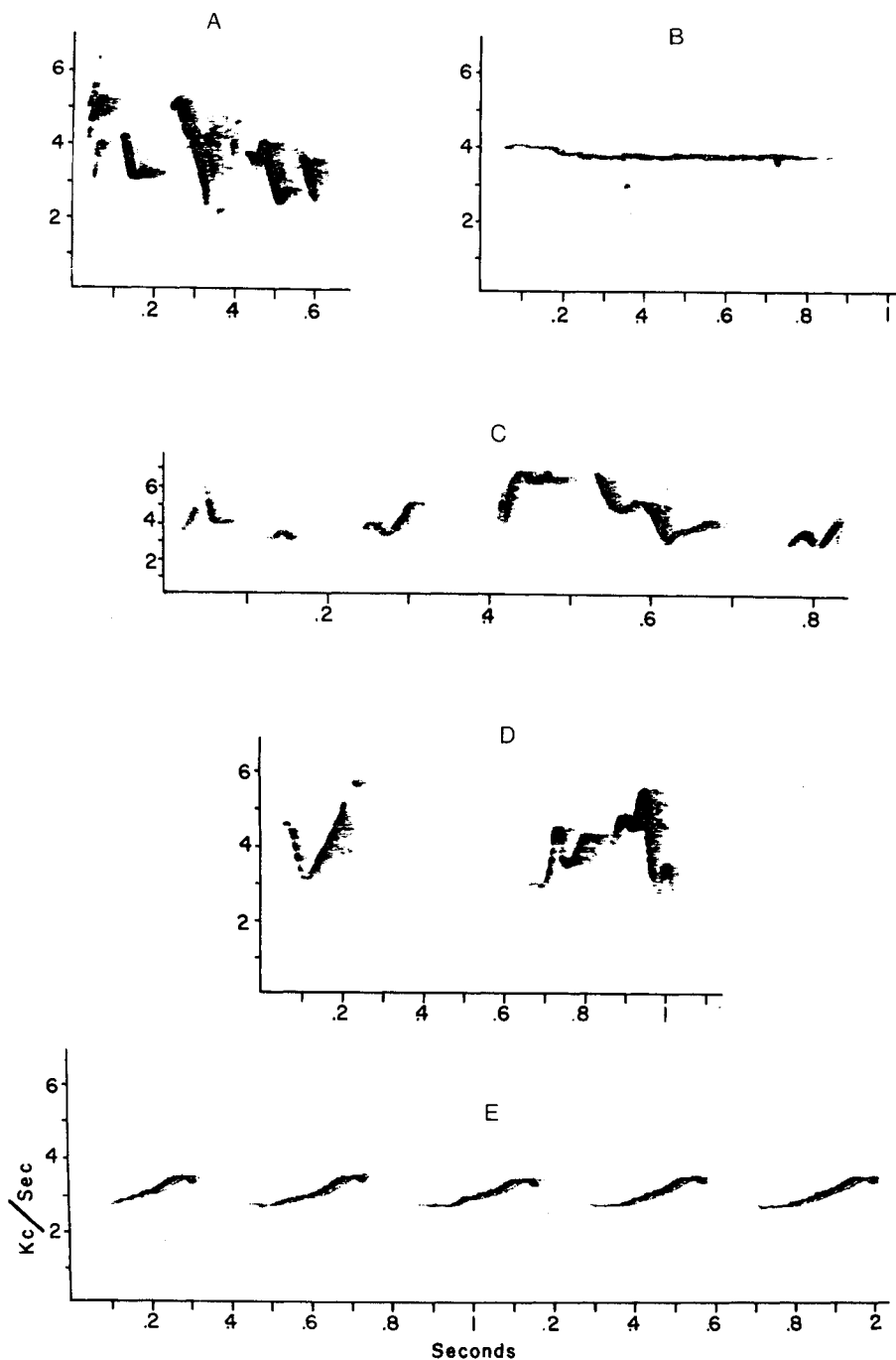
FIG. 5.—Sound spectrograms of the advertising phrases (song) of four sympatric species of *Hylophilus* vireos. The horizontal axis represents time in tenths of seconds, the vertical axis represents frequency in kHz. *A, H. aurantiifrons. B, H. ochraceiceps. C, H. decurtatus. D, H. minor* (now considered conspecific with *decurtatus*). *E, H. flavipes* (a portion of the total call). See text for a discussion of voice-habitat correlations.
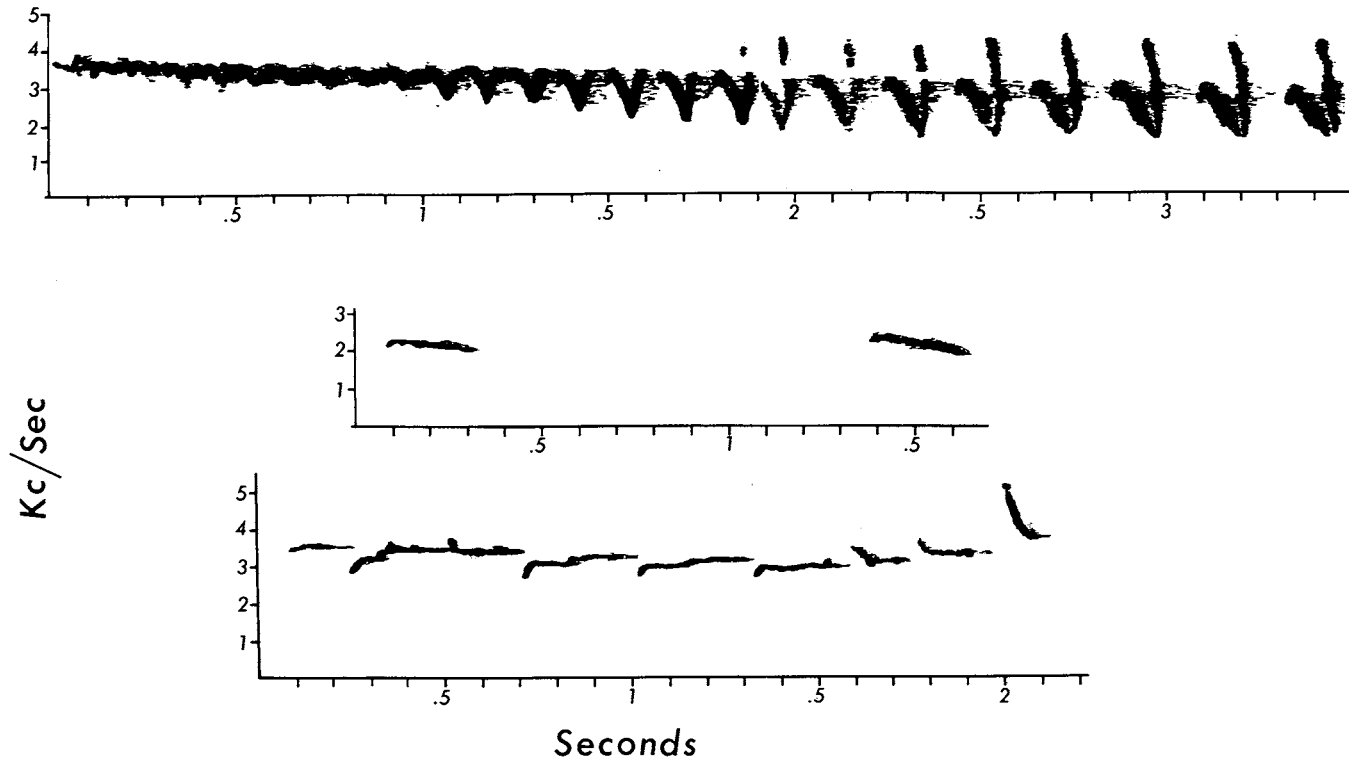
Kc/Sec

Seconds

Fig. 6.—Sound spectrograms of the calls of *Myrmeciza longipes* (top), *M. exsul* (center), and *Cyanocompsa cyanoides* (bottom). The horizontal axis represents time in tenths of seconds; the vertical axis represents frequency in kHz.

near Tocumon Airport sings sparingly throughout the day but has a buzzy song.

There are, then, trends in the sounds of congeneric species living in different habitats, trends within communities of birds sharing the same structural habitat, and temporal trends within the same habitat, that concur with predictions based on measurements of sound transmission reported here and on data from the acoustic literature which have rarely been applied to animal sounds.

If we are to understand the evolution of sound communication in animals there are, of course, many selective forces to identify and study. I propose that habitat acoustics produce selective forces favoring certain features of sound signals: pure tonelike sounds within a relatively narrow frequency range in forest birds living near the ground, highly modulated or trilled sounds in open habitat species. I view habitat acoustical characteristics as a framework within which other sources of selection such as sexual selection, selection for species distinctiveness, territory size, and pair bond length, to name a few, operate to mold sounds into the structures that we encounter.

SUMMARY

This study describes selection derived from habitat acoustics on the physical structure of avian sounds. Sound propagation tests were made in forest, edge, and grassland habitats in Panama to quantify pure tone and random noise band sound transmission levels. The sounds of bird species in each habitat were analyzed to determine the emphasized frequency, frequency range, and sound type (whether pure tonelike or highly modulated).

Forest habitats differ from grass and edge in that a narrow range of frequencies (1,585–2,500 Hz) has lower sound attenuation than lower or higher frequencies. Attenuation increases rapidly above 2,500 Hz. Bird sounds from species occurring at the lower forest levels were found to be predominantly pure tonelike with a frequency emphasized averaging 2,200 Hz, conforming to the predictions based on sound propagation tests.

The edge habitat is characterized by a wide range of frequencies having a generally similar attenuation rate. Pure tone and random noise band sounds did not differ in attenuation rates. The sounds of edge birds have high variance in the frequency-emphasized component, and more are composed of both modulated and pure tone elements to a greater extent than forest or grassland species. It is suggested that this variance is a reflection of a relative lack of selection pressure from habitat acoustics.

Grassland propagation tests showed a positive correlation between increasing frequency and increasing attenuation. It is hypothesized that information transfer may be based on temporal aspects of the signal since these are less distorted in temperature- and wind-speed-stratified open environments.

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