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# Sound Transmission and Its Significance for Animal Vocalization

## II. Tropical Forest Habitats

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**Summary.** 1. Attenuation of white noise and pure tones from 350 Hz to 10 kHz was measured at three secondary forest sites in Panama at different stages of maturity. Graphs of excess attenuation (E.A.) versus frequency were obtained near ground level, and at heights of 1, 2, 5, 10, and 12 m in each habitat.

2. The pattern of E.A. vs. frequency was similar for all habitats. For all heights other than ground level and 1 m the lower the frequency the better the sound carried. Sounds below 2 kHz were attenuated by a ground effect if the source was 1 m or less from the ground. Consequently there was a minimum of E.A. in all three habitats between 500 Hz and 2 kHz at ground level and 1 m.

3. Relevance of the data to assessment of the role of environmental variables in the natural selection of vocalization for long-distance transmission is discussed. Two facts mitigating against Morton's sound "window" as an explanation for lower frequencies in songs of forest as opposed to open country birds are presence of similar "windows" in both habitats and restriction of windows to a zone close to the ground in most habitats.

## Introduction

Research on sound transmission in open and forested temperate habitats yielded results somewhat at variance with the pioneering studies of Morton on sound attenuation in tropical habitats (Morton, 1970, 1975; Marten and Marler, 1977). The differences affected inferences about selection pressures bearing on animal vocalization adapted for long-distance transmission. Since somewhat

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different methods were used in our studies and in those of Morton, identical equipment to that used in our temperate studies was taken to Panama in an effort to repeat Morton's studies with our techniques. Under his guidance, we were able to approximate some of his original sites for testing sound attenuation in tropical forest habitats at different stages of maturity.

## Materials and Methods

Three variables were manipulated in these studies: sound frequency, height of the sound source, and the habitat in which the sound was broadcast. The methods have been detailed previously (Marten and Marler, 1977). Briefly, pre-recorded tapes of white noise and of 24 pure tones ranging from 350 Hz to 10 kHz were played from a loudspeaker at heights ranging from ground level through 1, 2, 5, 10, and 12 m. Attenuation was measured between one microphone 2.5 m from the loudspeaker, and another 100 m away over level ground. Intensity of each tone was measured ten times over a period of 30 s directly by a sound level meter. In the case of white noise tests 4 s stereo recordings were analyzed in the laboratory with a General Radio 1910-A wave analyzer. Data are presented in terms of 'excess attenuation (E.A.)', beyond that expected according to spherical spreading by the inverse square law (32 dB/100 m). Tests with pure tones yielded similar results to those with white noise, although the latter were less variable. To reduce the volume of data reported, results presented in this paper are derived from the white noise tests, while pure tone data are stressed in the report on temperate studies (Marten and Marler, 1977).

Tests were conducted in three tropical lowland secondary forest sites at different stages of maturity on the Pacific slope of the Panama Canal Zone, in July 1974, in the rainy season. The sites are described in order of decreasing maturity and increasing vegetation density at the source heights tested.

The most mature site, Madden Forest was on the east side of Madden Forest Road, 400 m north of Las Cruses Trail, and several hundred meters from the 'forest habitat sites' of Morton (1970, 1975). He defined it as 'Tropical Monsoon Forest', following Bennet, because there is a well-defined dry season (less than 60 mm of rainfall during January–March). There are two tree-foliage strata, the lower one averaging about 7–12 m in height. The lower stratum is variably open and closed, and the upper one (25–35 m in height) is usually open but joined by vines. Because of low light intensity the vegetation on the forest floor is usually moderate and chiefly woody; root buttresses, lianas, and small palms are common.

The less mature site, Fort Kobbe Forest, was 1 km west of the small arms range to the northwest of the Fort Kobbe Airstrip. There were fewer large trees than in Madden Forest, and undergrowth was thicker. As in Madden Forest, sound transmission at the 12 m height was through the lower portion of the canopy.

The least mature site, Farfan Edge, was one third of the way from Fort Kobbe to Farfan Beach near a power station bunker, to the left off Hurwitz Road. This site was 1 km east of the radio telephone antenna within several hundred meters of one of Morton's 'edge habitat sites'. As defined by Morton, this "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'." It was so dense that it took almost an hour to traverse the 100 m course. Note that the term 'forest edge' implies only the habitat that tends to surround areas of more mature forest. The transition is gradual, with no sudden boundary between trees of different heights. It is typically a dense, relatively young secondary growth, with a scarcity of mature trees.

Sites were chosen to be as level as possible. Although vegetation density was not measured, our impression was that vegetation density increased from Madden to Fort Kobbe to Farfan at all heights below 10 m. At 10 and 12 m transmission appeared to be above most of the vegetation at Farfan Edge. Because of disruption of the program by numerous rainstorms, different times of day were not systematically sampled. Replicate experiments were conducted in each habitat at the same site with the same equipment on different days at approximately the same time.

## Results

### *A Comparison of Pure Tone and White Noise Data*

A typical result of a test at Madden Forest at a source height of 2 m is shown in Figure 1. Excess attenuation (E.A.) is on the vertical axis and sound frequency on the horizontal axis. The 'pure tone' graph connects the means of the ten measurements during the 30 s run at each frequency. The vertical bars indicate the ranges in each of these 30 s samples. Since pure tones were tested consecutively an entire run at a given height samples attenuation conditions over a period of about 30 min. By comparison, a white noise test sampled attenuation conditions over a period of a few seconds, yielding less variable results and smoother curves. The two kinds of test give basically similar results, with the pure tone data fluctuating around those for white noise. The pure tone tests reveal variation in excess attenuation as great as 15 to 20 dB over the 30 s sampling period. The issue of temporal variation in attenuation, potentially important for animals communicating by sound (Morton, 1975), will be considered later. Only data from the white noise tests will be presented here. The average results for pure tone and white noise tests were similar, with absolute differences for a given frequency averaging 1.9 dB/100 m.

### *Variations in Attenuation within and between Sites*

For each source height at each site, 4 replicated white noise tests were run, except at Madden Forest where only three replicates were conducted. Results

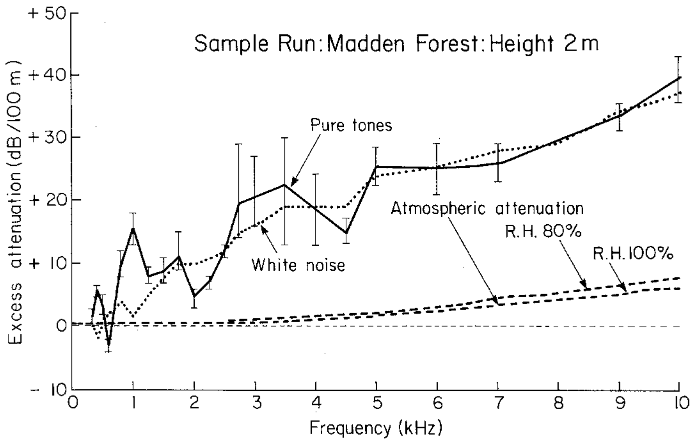

**Fig. 1.** An example of excess attenuation (E.A.) versus frequency for a single experimental test at Madden Forest, at a height of 2 m (the two top curves). Pure tone and white noise data from the same site are represented. The pure tone curve connects the means of each 30 s sample. The vertical bars indicate the ranges of the 10 tests run in each 30 s period. The white noise curve, as read from the wave analyzer charts (cf. Marten and Marler, 1977, Fig. 2) represents conditions over a much shorter, 4 s period. The two bottom curves show theoretical atmospheric absorption in still air (reading the vertical axis as attenuation in db/100 m rather than as E.A.) at relative humidities of 80% and 100%. This covers the range of humidities encountered in all experiments (for references see Griffin, 1971)

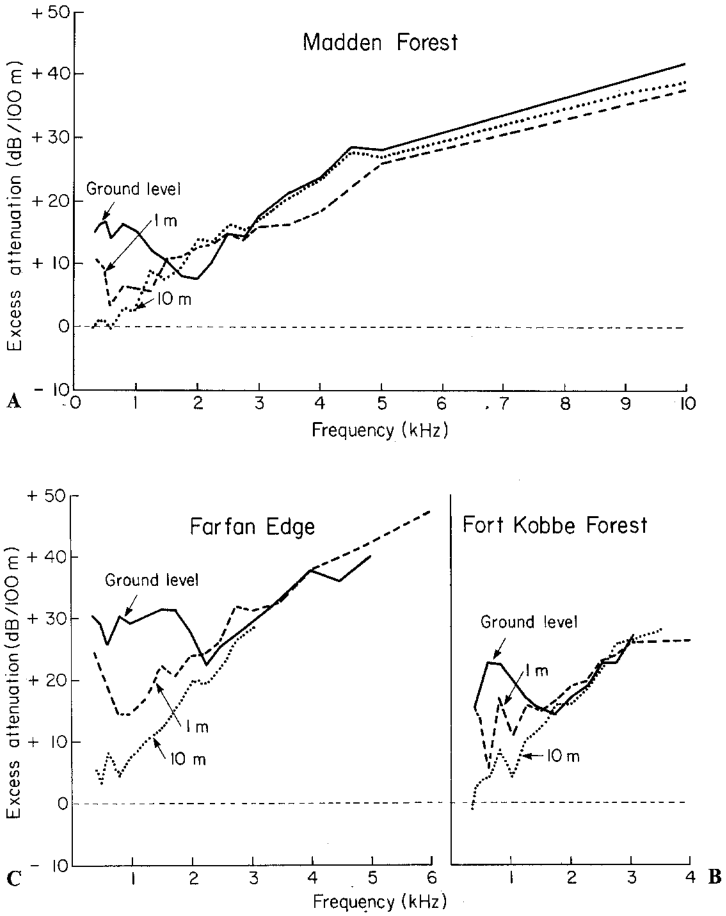

**Fig. 2.** Averaged data from white noise tests at 3 heights and 3 sites. The ground effect is evident at 1 m and ground level. At 10 m there is a monotonic increase of E.A. as is typical of heights above 2 m

of these replicate tests, averaged for each height and fequency, are presented in Figures 2 and 3. Figure 2 presents only data for three heights, ground level, 1 m and 10 m, serving to represent the major trends. As shown in Figure 3, for all heights above 1 m at Madden Forest, E.A. tended to increase monotonically with frequency. The same was true for the lower source heights with all frequencies above 2 kHz. Linear regressions were calculated for the monotonically increasing portion of all graphs, from the beginning of the monotonic increase up to 5 kHz. These are presented in Figure 4, and show different absolute values of E.A. and different slopes for the three sites. F-ratio tests were conducted for the significance of differences between regression lines, and most of them, even within a site, proved to be significantly different at the 0.05 level. At source heights of ground level and 1 m, at all three sites, there was increased attenuation with frequencies below about 2 kHz (Fig 2). Frequencies

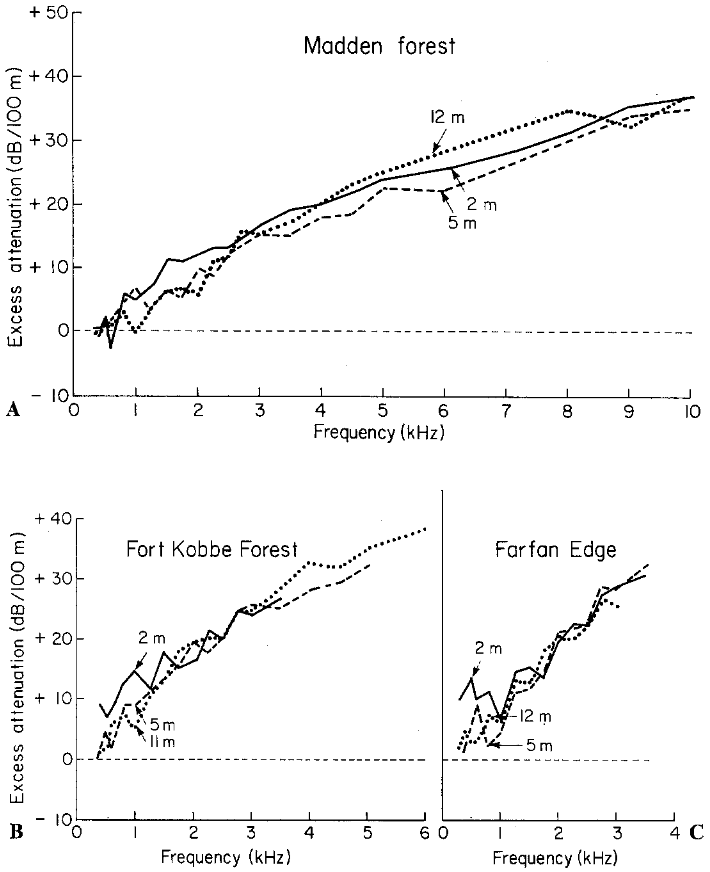

**Fig. 3.** Averaged data from noise tests at heights of 2 m, 5 m, and 12 m for the 3 habitats studied. All show a monotonic increase of excess attenuation with increasing frequency with the exception of the 2 and 5 m tests at Farfan Edge where there is an indication of an 'elevated' ground effect over dense vegetation

just above this zone of attenuated low-pitched sound constitute the sound 'window' found by Morton near these same sites (Fig. 5).

The entire set of graphs in Figures 2 and 3 were subjected to Bartlett's test for homogeneity of variances (Sokal and Rohlf, 1969) and proved to be homoscedastic with an average standard deviation of 2.1 dB/100 m.

It will be noted that data for attenuation of high frequencies are absent from many of the curves in Figures 2 and 3. This resulted from a combination of a high rate of attenuation and jamming by insect sounds, especially strong above 3 kHz at Fort Kobbe and Farfan Edge.

If a frequency window is defined as a band of frequencies with minimal excess attenuation, bounded above and below by more highly attenuating frequencies (Fig. 5), then examination of Figures 2 and 3 reveals such 'windows' at ground level and 1 m at all three of the sites tested. The window is more

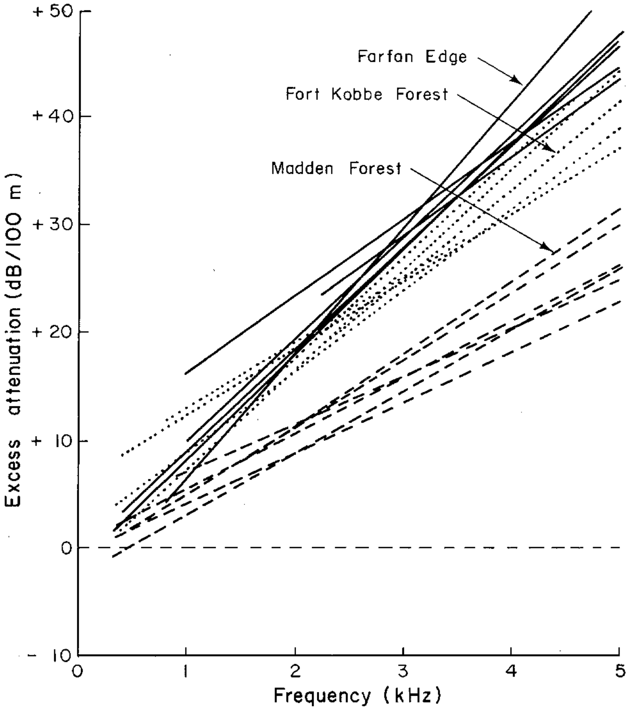

**Fig. 4.** Linear regressions of data on excess attenuation versus frequency for each height tested, in the 3 habitats sampled. The regressions are derived from the monotonically increasing portion of graphs for E.A. in Figures 2 and 3

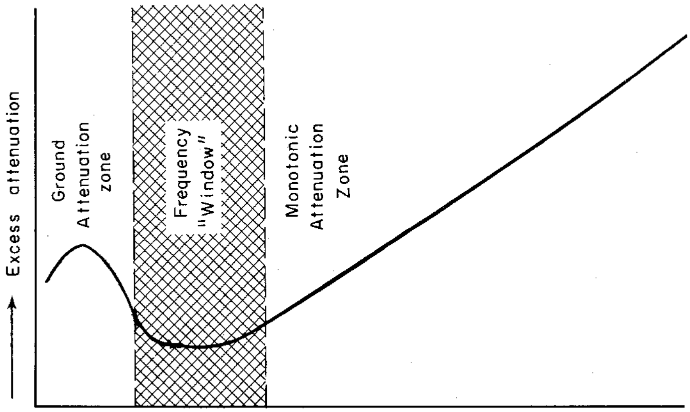

**Fig. 5.** An idealized diagram of Morton's frequency 'window' bounded below by the ground attenuation zone of frequencies and above by the monotonic attenuation zone

marked and at a higher frequency at ground level than at 1 m (cf. Ingard, 1951, 1953). Since such 'windows' are lacking with source heights above 1 m it may be preferable to call them ground effect 'windows'. They are well marked at the Madden and Fort Kobbe Forest sites, where they agree in shape with those obtained by Morton (1970, 1975). However, the values of E.A. at the best frequency obtained by us are rather higher than those of Morton. Whereas his data indicate about 0 dB/275 feet of E.A. at Madden Forest for the best frequency in the ground effect window, we obtained values of 8 dB/100 m at Madden Forest and 14 dB/100 at Fort Kobbe Forest.

Farfan Edge behaves somewhat differently than the other two sites, having as marked a ground effect window at 1 m as at ground level, with persistence of a window up to 5 m. As in the case of the other two sites, however, the window disappears at 10 and 12 m source heights.

## Discussion

### *Transmission Range as an Adaptive Feature of Animal Vocalization*

Within the set of vocal sounds used by an animal in its social behavior some are typically loud and others soft. Illustrations could be drawn from primates (e.g., Marler, 1973, 1974; Green, 1975; Waser and Waser, in press), carnivores, or birds (e.g., Baeumer, 1962; Konishi, 1963; Collias, 1963; Marler and Mundinger, 1975). It must be admitted that there is still little reliable information on the entire vocal repertoires of vertebrates, and even less on the intensity with which they are produced (Mayfield, 1966; Busnel and Gramet, 1956; Morton, 1970). Nevertheless it is obvious that, by design, some vocal signals within a species repertoire travel further than others. Similarly a comparison between audiograms and frequency emphasis in different avian vocalizations reveals that while the main energy of some bird vocalizations is concentrated in frequencies to which the ear of the species is most sensitive, other calls are clearly pitched outside this range (Konishi, 1970). Effective transmission range to potential communicants is an important adaptive feature of vocal signals, likely to vary in harmony with such factors as the nature and position of the intended recipient, and the information transmitted, sometimes favoring a limited range, at other times favoring the maximal broadcast range. The following discussion concentrates on this latter circumstance.

Among vocalizations thought to incorporate design features for maximizing transmission range are those involved in long-distance social spacing, such as territorial birdsongs and loud calls of forest-dwelling primates. Adult males are prone to assume the burden of maintaining the larger-scale-components of social spacing, including territoriality, and the louder components within a species repertoire are often those adult males employ in such spacing. To the extent that there is sexual dimorphism in sound-producing equipment this often seems to favor the production of louder sounds by adult males, whether it takes the form of greater size and heavier musculature or accessory resonators, as for example, in apes and monkeys (Marler and Tenaza, in press; Gautier, 1971). Thus one may reasonably assert that certain animal vocalizations are under selective pressure for maximization of the range over which they are audible to others. What light do experimental studies of the transmission of artificial sounds throw on the nature of such selective influences?

### *Vocal Design Features for Long Distance Transmission*

Significant evolutionary choices with a potential influence on the distance at which a vocal sound might be heard by another individual include where to call, what kind of sound to employ, and when best to vocalize, both in the long term and on a moment-to-moment basis.

Present data offer indications as to where best to vocalize in the terrestrial habitats tested, to maximize sound transmission. There is a great increase of sound attenuation when the source is closer than 1 m to the ground (cf. Morton, 1970, 1975; Marten and Marler, 1977). The increase is greatest with those low frequency sounds which otherwise, when produced further from the ground, are much the best for long distance transmission. This effect is clearly seen in all three of the tropical environments tested in this study (e.g., Fig. 2) although less obvious in Morton's data. It also occurs in temperate forest and grassland habitats (Marten and Marler, 1977) and over tilled ground (Aylor, 1971).

There can be no doubt that the simple expedient of getting more than 1 m above ground level for vocalizing is the most effective step most animals can take to increase the effective range of a vocalization, especially if it is a low-pitched sound. This precaution, taken by many arboreal or volant animals before vocalizing has the effect of removing them from the ground effect 'window'. For them this alleviates any special constraints the 'window' might impose on the best frequency for long-range sound transmission to be replaced by the general rule that the lower the frequency the better. Some tropical forest birds, however, remain on the ground to vocalize (Morton). It should also be borne in mind that while a vocalizer may take such precautions, the intended receiver could be at ground level. If competition for ground foods were at issue, for example, there could be selective value in using sounds most likely to reach a ground level intruder even if the call is given from a higher elevation.

Although variation in sound transmission with height above 1 m is slight compared to variation with source heights close to the ground, (e.g., Fig. 2 and 3), more comprehensive analysis of sound attenuation in temperate habitats revealed a small increase in sound attenuation as the canopy of a deciduous forest in leaf was penetrated (see Marten and Marler, Fig. 4B). Thus the ideal height for long distance sound transmission in a forest should be more than 1 m above ground level and somewhere below the canopy, a prediction nicely verified by the studies of Waser and Waser (in press) on transmission of monkey calls in tropical rain forest in Africa.

With regard to the *kind* of sound best adapted for long-distance transmission, loudness is of course an issue, within the limits set by morphology of the sound-producing equipment. The louder the sound the further it will travel. If the sound-producing equipment is designed so as to present an evolutionary choice between concentrating a given energy level in a narrow frequency band, or spreading the same energy through a broader range of frequencies, the former will be preferred for long-distance transmission (cf. Morton, 1975).

Such a choice seems to be present in production of loud calls of adult male *Cercopithecus* monkeys. Gautier (1971) has shown experimentally that the unusually hypertrophied extra-laryngeal sac of a male *Cercopithecus neglectus* seems to concentrate energy in the fundamental frequency of the loud call (at about 150 Hz) at the expense of energy in higher harmonics. It may be that the laryngeal sacs of apes serve a similar function, in producing those sounds in which the sacs are involved such as the long-distance pant-hooting of chimpanzees (Marler and Hobbet, 1975; Marler and Tenaza, in press).

The situation will differ if energy can be spread across a broad frequency range without sacrifice of intensity at any one frequency, as may be the case with some avian vocalizations. Chappuis (1971) has indicated certain congeneric bird species pairs with one member a forest dweller, and the other living in grassland in which the forest representative uses a narrower range of frequencies in its song. Lacking measurements of the absolute intensity of such songs, it is not known whether narrowing of the frequency band achieves a greater intensity at those frequencies. Morton (1970, 1975) has noted similar contrasts between forest and grassland birdsongs.

Both authors have drawn attention to another difference between songs of birds in open and forested tropical habitats, namely a lowering of the frequency at which most energy is represented in the forest. This reduction is especially marked in songs of birds that Morton describes as living at lower elevations in the rain forest. He interprets this trend as resulting from exploitation of a frequency 'window' in the forest which is absent in open habitats. Our data have led us to a different position on this question.

Sound 'windows' or ground effect 'windows' as we prefer to call them, do indeed occur as Morton (1970, 1975) originally described them. However, we have indicated two facts that mitigate against such 'windows' as an explanation for the lower frequency of forest birdsongs. Frequency 'windows' exist in open as well as forest habitats, and they are restricted in most habitats to a zone close to the ground.

According to Aylor (1971) who studied the effects of vegetation and ground surfaces on sound attenuation, the relative increase of attenuation of low frequency sounds in a variety of environments both open and forested, is indeed attributable to a ground effect. Curves of excess attenuation versus frequency presented by Aylor for both open and wooded environments demonstrate that this ground attenuation effect is frequency dependent, involving especially low frequency sounds. The role of texture was demonstrated by Aylor (1971) by a comparison of E.A. over the same ploughed and smoothed field before and after disking, the latter serving to lower the frequency of maximal attenuation by about 400 Hz at 1 m (see review in Embleton, et al., 1976).

Addition of the attenuation by the ground of frequencies below about 2 kHz to the monotonic increase of attenuation at higher frequencies creates the frequency 'window' diagrammed in Figure 5.

Morton's (1975) tests of attenuation in open habitats were done over both short and tall grass, the latter 4–5 feet high. The absence of a frequency 'window' in these data may be attributable to effects on ground attenuation of the long grass. Aylor (1971) conducted tests in a densely planted corn field, and found very little low frequency attenuation. Apparently the corn reduced or eliminated ground attenuation so that the frequency 'window' disappeared. At least one of the grassland environments tested by Morton, with tall grass, may have affected sound transmission in a similar way.

Probably short-grass savannah and meadow habitats in the tropics have sound attenuation preperties much like those we found in temperate regions (Marten and Marler, 1977). It remains an issue of interest to explore possible relationships between song features and habitat structure in birds that typically inhabit tall grass and dense reedbeds where, to judge from the cornfield analogy, low frequency sounds are little attenuated, and high frequencies, beginning above about 2 kHz, are very highly attenuated (cf. Aylor, 1971).

### *Relevance of Short-Term Variations in Micro-meteorological Conditions*

Considerable temporal variation was found in the sound transmission characteristics at a given site in both temperate and tropical habitats. On one hand were variations with the time of day. Attenuation was as much as 20 dB/100 m more at midday than at dawn or dusk at the same site, source height and frequency, especially in open habitats (Quine and Marler, in preparation).

There is a remarkable degree of moment-to-moment variation in sound attenuation, sometimes through ranges as great as 15–20 dB (e.g., Fig. 1). This variation approaches in magnitude the differences in excess attenuation between different frequencies, source heights and sites. The parameters that must be described to fully understand variations in the propagation of sound through a given segment of the atmosphere include temperature and the vertical temperature gradient, wind speed and the vertical wind gradient, and humidity (Wiener and Keast, 1959). Measurements of relative humidity and temperature, taken in each of our tests, indicate a range from 78 to 98% relative humidity. The two lower curves in Figure 1, for frequency-dependent attenuation at two levels of relative humidity indicate that the variations recorded cannot account for moment-to-moment variations, nor for changes in excess attenuation from height to height and site to site, although they do contribute to the observed monotonic increase of E.A. with frequency.

The variability is more likely to be attributable to temperature and wind gradients and the associated air movements. Temperatures at shoulder height, measured during some tests, appeared to remain stable. No attempt was made to measure gradients. Although days with strong, steady winds were avoided for tests, air movement is probably an important determinant of moment-to-moment fluctuations of E.A. (Wiener and Keast, 1959). One would expect variability of vertical temperature and wind gradients to differ from habitat to habitat even in cases where the average attenuation characteristics are similar. If a closed forest is less susceptible to such variations than more open habitats (Morton, 1975), this could have profound consequences for sound transmission by animals living there. More frequent vocalization under variable conditions might increase the chances of some coinciding with optimal transmission conditions. Clearly the nature and causes of short-term variations in sound attenuation and any frequency-related effects they may have (Wiley and Richards, in press) are worth study as possible explanations for the broader range of frequencies found in the song of open country birds (Chappuis, 1971; Morton, 1970, 1975). Relative stability of the attenuation characteristics of forest environments whether close to the ground or well above it, may permit exploitation of some potential advantages of tonal sounds for long-distance signalling (Morton, 1975). These might include the concentration of energy in narrow frequency bands, and the coding of species-specific, individual and other information in tone sequences and patterns of energy distribution across the frequency spectrum (Marler, 1969). Further studies of the stability of the sound attenuation characteristics of different environments may thus help to explain the contrast in frequency structure of open country and forest birdsongs.

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## References

Aylor, D.: Noise reduction by vegetation and ground. J. acoust. Soc. Amer. **51**, 197–205 (1971)

Baeumer, E.: Lebensart des Haushuhns, dritter Teil – über seine Laute und allgemeine Ergänzungen. Z. Tierpsychol. **19**, 394–416 (1962)

Busnel, R.G., Gramet, P.: Recherches préliminaires sur le comportement acoustique de *Quelea quelea quelea* Latham en captivité. Bull. I.F.A.N. **18**, 280–326 (1956)

Chappuis, C.: Un exemple de l'influence du milieu sur les emissions vocales des oiseaux: l'evolution des chants en foret equitoriale. Terre et Vie **25**, 183–202 (1971)

Collias, N.E.: A spectrographic analysis of the vocal repertoire of the African Village Weaverbird. Condor **65**, 517–527 (1963)

Embleton, T.F.W., Piercy, J.E., Olson, N.: Outdoor sound propagation over ground of finite impedance. J. acoust. Soc. Amer. **59**, 267–277 (1976)

Gautier, J.P.: Etude morphologique et fonctionelle des annexes estralaryngees des cercopithecinae; liason avec les cris d'espacement. Biologica Gabonica **7**, 229–267 (1971)

Green, S.: Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study. In: Primate behavior, Vol. 4 (ed. L.A. Rosenblum), pp. 1–102. New York: Academic Press 1975

Griffin, D.R.: The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Anim. Behav. **19**, 55–61 (1971)

Ingard, U.: On the reflection of a spherical sound wave from an infinite plane. J. acoust. Soc. Amer. **23**, 329–335 (1951)

Ingard, U.: A review of the influence of meteorological conditions on sound propagation. J. acoust. Soc. Amer. **25**, 405–411 (1953)

Konishi, M.: The role of auditory feedback in the vocal behavior of the domestic fowl. Z. Tierpsychol. **20**, 349–367 (1963)

Konishi, M.: Comparative neurophysiological studies of hearing and vocalizations in songbirds. Z. vergl. Physiol. **66**, 257–272 (1970)

Marler, P.: Tonal quality of bird sounds. In: Bird vocalizations (ed. R.A. Hinde), pp. 5–18. Cambridge: Cambridge University Press 1969

Marler, P.: A comparison of vocalizations of red-tailed monkeys and blue monkeys, *Cercopithecus ascanius* and *C. mitis,* in Uganda. Z. Tierpsychol. **33**, 223–247 (1973)

Marler, P.: Animal communication. In: Non-verbal communication. Advances in the study of communication and affect, Vol. 1 (eds. L. Krames, P. Pliner, T. Alloway), pp. 25–50. New York: Plenum Press 1974

Marler, P., Hobbet, L.: Individuality in a long-range vocalization of wild chimpanzees. Z. Tierpsychol. **38**, 97–109 (1975)

Marler, P., Mundinger, P.: Vocalizations, social organization and breeding biology of the twite, *Acanthus flavirostris.* Ibis **117**, 1–17 (1975)

Marler, P., Tenaza, R.: Signalling behavior of wild apes, with special reference to vocalization. In: How animals communicate (ed. T. Sebeok), Bloomington: Indiana University Press (in press) (1977)

Marten, K., Marler, P.: Sound transmission and its significance for animal vocalization. I. Temperate habitat s. Behav. Ecol. Sociobiol. **2**, 271–290 (1977)

Mayfield, H.: Hearing loss and birdsong. Living Bird, 167–175 (1966)

Morton, E.S.: Ecological sources of selection on avian sound. Ph.D. diss. Yale University (1970)

Morton, E.S.: Ecological sources of selection on avian sounds. Amer. Natur. **108**, 17–34 (1975)

Sokal, R.F., Rohlf, F.J.: Biometry: The principles and practice of statistics in biological research. San Francisco: Freeman 1969

Waser, P., Waser, M.S.: Experimental studies of primate vocalization: Specializations for long distance propagation. Z. Tierpsychol. (in press) (1977)

Wiener, F.M., Keast, D.N.: Experimental study of propagation of sound over ground. J. acoust. Soc. Amer. **31**, 724–733 (1959)

Wiley, R.H., Richards, D.G.: Physical constraints on acoustic communication in the atmosphere. (in press)