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Is there a "sound window" for primate communication?

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Summary. It has long been asserted that habitat acoustics can determine the frequency band best-adapted for long-range communication, but the generality and validity of measurements claiming to demonstrate a "window" of best frequencies have recently been questioned. We report the discovery of a prominent sound window in Kenyan rain forest in a study that is free of methodological difficulties. Our results allow us to calculate the range advantage attained by an animal vocalizing within the sound window, and show that sound windows can be a potent factor for the evolution of primate communication.

Introduction

Many primates produce distinctive loud calls with energy confined to a single narrow low-frequency channel ranging from 125 to 500 Hz (Gautier and Gautier 1977; Marler 1973; Oates and Trocco 1982; Waser 1982). These vocalizations, usually conspicuous gobbles, whoops, roars, or tonal booms, are produced by the adult males of a large number of forest dwelling species. In order to produce loud low-pitched sounds many species have evolved hypertrophied vocal resonating sacs (Gautier 1971), and at least some species have developed heightened perceptual capabilities to detect low-frequency sounds (Brown and Waser, in press).

These specializations for loud call production and perception are generally thought to reflect strong selection for a specific set of acoustic features "designed" to promote long-distance propagation. However, acoustical surveys in a number of habitats have yielded mixed results: some investigators report evidence of a sound window – a frequency channel in which signals are very favorably propagated, sometimes better than expected from the inverse square law (Aylor 1971; Bowman 1979; Marten and Marler 1977; Marten et al. 1977; Morton 1977; Waser and Waser 1977; but see Embleton 1963; Eyring 1946; Piercy et al. 1977; Wiener and Keast 1959). A serious challenge to the idea that sound windows exist, and thus that habitat acoustics produce significant selective effects on vocalizations, is the possibility that reported windows are artifactual (Michelsen 1978; Roberts et al. 1979). "The crucial question is whether observations of sound windows in some studies but not others is due to real differences between the habitats investigated, or to the differences between the apparatus and experimental design of the investigations" (Michelsen 1978, p. 362).

In earlier studies window-like results could have been spuriously produced by broadcast speakers with directionality characteristics that varied with frequency. The speaker could beam some sound frequencies, but not others, along the axis of measurement. Tests could inadvertently have been conducted downwind or across asymmetric microclimatic gradients (Michelsen 1978). Furthermore, direct and ground-reflected sound waves interact to form points of constructive and destructive interference at locations dependent on frequency and on speaker and microphone height. If boundary interference is a major contributor to attenuation, and if sound pressure levels at two locations are subtracted to measure attenuation, the value obtained could depend more on the relative microphone positions than on the actual attenuation between speaker and microphones (Michelsen 1978; Roberts et al. 1979; Wiley and Richards 1978, 1982). All of these factors could make the habitat appear to promote sound propagation at some frequencies and oppose it at others, hence creating the illusion of a sound window. The unequivocal demonstration of a sound window requires several conditions to be met: the speaker's directional radiation patterns must be measured, the output of the speaker must be calibrated, microclimatic variables must be controlled for, and most important, the signal must be measured at several distances from the source (Michelsen 1978).

Materials and methods

Our Kenya rain forest measurements meet these requirements. We broadcast pure tones between 63 Hz and 4000 Hz with a Uher Report-L recorder and Nagra DH speaker in the Kakamega Forest Reserve, western Kenya. Signals were rerecorded with a Nagra IV-S recorder and AKG omnidirectional microphones. The signals were broadcast and rerecorded at an elevation of 7–8 m for propagation distances of 12.5, 25, 50, and 100 m. We broadcast 6 test series from a single point, two series in each of three directions. Measurements at the same site with the same microphone varied ±1.3 dB between tests ($n = 250$) (Brown and Waser, in press).

We measured the pressure level of our signals, the radiation pattern of our speaker, and calibrated our microphones in an anechoic room. We measured sound pressure level (SPL) re 20 µPa at a distance of 2 m from the speaker with an Ivie IE-30A sound level meter with third-octave filters. We empirically determined that our calibration measurements of signals 200 Hz and above were conducted in the far-field (i.e., SPL obeyed the inverse square law), but we noted near-field effects for signals at 63 Hz and 125 Hz. By measuring the rate of SPL dropoff in the anechoic room just within the near field, we estimated its contribution to be an extra 1 dB at 125 Hz, 3 dB at 63 Hz, and decreased our source SPL estimates accordingly. These values are in good agreement with the theoretically expected near field contribution at 2 m: 1.7 and 3.1 dB, respectively (Skudrzyk 1971).

To estimate attenuation we measured modal sound pressure level in third-octave bands for each 20 s rerecorded signal using the Ivie spectrum analyzer. Thus we were able to calculate excess attenuation, the difference between observed sound pressure levels at each frequency and expected values given the speaker's actual output and the 6 dB loss per doubling of distance due to the inverse square law.

Results

Our data indicate that signals around 200 Hz in frequency propagate as well or better than expected by the inverse square law, while both lower and higher frequencies are more rapidly attenuated (Fig. 1). 200 Hz was the best frequency for sound transmission at all measured distances. Microphone location and speaker-microphone separation indeed influenced measured attenuation values in complex ways, so that the cautionary statements of Michelsen and others (Michelsen 1978; Roberts et al. 1979; Wiley and Richards 1982) are well founded, but the window remains prominent despite these effects.

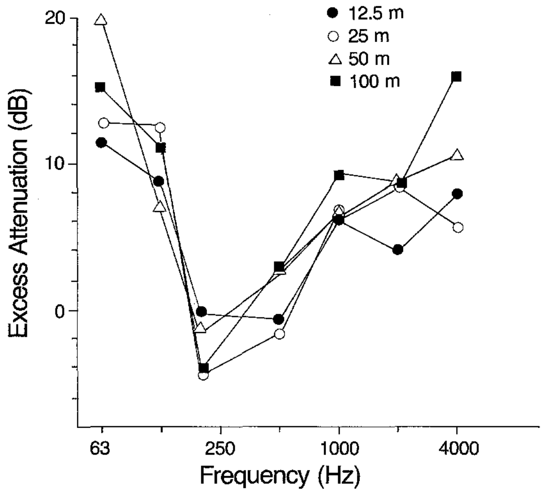

Fig. 1. Excess attenuation measured as described in text between speaker and microphones at 12.5 m, 25 m, 50 m, and 100 m distance and at 7–8 m height in Kakamega forest, Kenya. Standard deviations vary from 1.1 to 5.8 dB with most between 3 and 4 dB

Discussion

Because we are comparing the sound pressure level of the propagated signal with the speaker's actual output, and because the window is stable with distance, it cannot be explained as an artifact of microphone placement. Our tests control for microclimate and habitat asymmetries; the window is equally clear in broadcasts in opposite directions. Moreover, our speaker's directionality increases monotonically with frequency, so that no effect of source directionality on attenuation could produce the observed pattern.

In neotropical forests, sound windows have been reported only within a few m of the ground (Marten et al. 1977; Marten and Marler 1977). However, tests in a Ugandan forest (Waser and Waser 1977) that included frequencies lower than those broadcast by Marten et al. are consistent with a trend observable in their data: the best frequency for sound transmission decreases and the window becomes more "open" with increasing elevation (Fig. 2). Our Kakamega data calculated in the common, though incorrect way [using the near microphone response (12.5 m) as a reference level for the far microphone response (100 m)] neatly fit this same trend (Fig. 2).

Comparison of Figs. 1 and 2 indicates that, far from being an artifact of methodology, the sound window's magnitude may be underestimated if it is measured between "near" and "distant" microphones. Perhaps (as Michelsen suspected) speaker directionality has had significant effects in previous tests, particularly at the near microphone. This

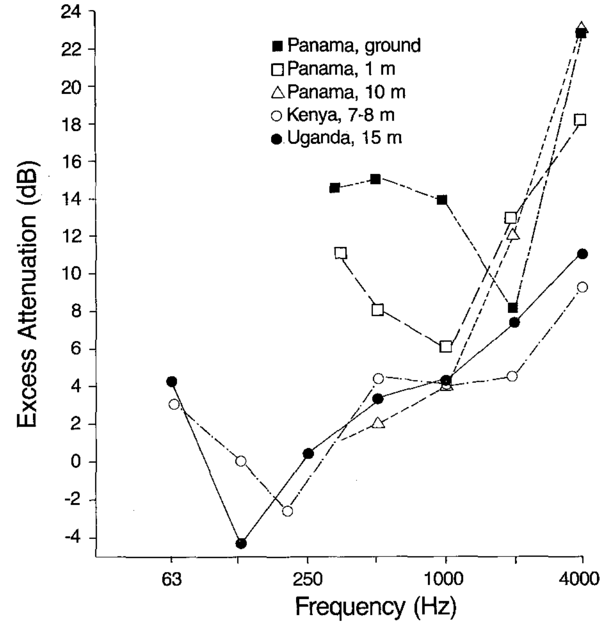

Fig. 2. Excess attenuation in tropical forests as a function of speaker and microphone heights, calculated by comparing SPL between "near" and "distant" microphones. Panama data are replotted from Marten et al. (1977); Uganda data from Waser and Waser (1977); Kenya data from these tests. Marten et al. did not broadcast signals below 350 Hz. Excess attenuation was measured between 2.5 m and 102.5 m (Panama), 5 m and 100 m (Uganda), and 12.5 m and 100 m (Kenya)

finding, in conjunction with the results of previous habitat acoustic measurements, indicates that sound windows are not a rare phenomenon.

Given that signals of a few hundred Hz really propagate best from elevated locations in tropical forests, how much would animals gain by broadcasting through the sound window? Studies using only two recording distances have not been able to address this question, since depending on the source of attenuation, signal amplitude need not decrease linearly or even monotonically with distance (Michelsen 1978; Roberts et al. 1979; Wiley and Richards 1982). In our tests excess attenuation grows proportionally to the logarithm of distance, a finding that indicates that scattering is its major source, and we can use this result to extrapolate the distance at which the signal/noise ratio for a broadcast tone would equal 1. Though the ability of monkeys to detect signals in habitat noise is presently unknown, this value permits us to make a first approximation of the "active space" (Marler and Marten 1977; Brenowitz 1982; Brown and Schwagmeyer, in press) of vocalizations of similar frequency and amplitude. For signals matching the amplitude of primate loud calls, active space is strikingly influenced by the sound window (Table 1). Most loud primate vocalizations (barks, alarm calls, screams) are pitched above 1000 Hz and would transmit at best a few hundred m. However, if the caller can maintain the same amplitude and decrease the call's frequency to 200 Hz, the active space exceeds 2 km, an order of magnitude increase in vocal range.

Table 1. Ambient sound pressure level, rates of excess attenuation, and estimated active space for tones (80 dB SPL at 2 m) broadcast 7–8 m above ground in Kakamega forest. Ambient sound pressure level measured as described in Brown and Waser (in press). Rate of excess attenuation per doubling of distance calculated assuming it increases linearly with the log of distance and dividing excess attenuation between 2 and 100 m by $5\frac{1}{2}$ doublings of distance. Active space is the distance at which signal/noise ratio equals 1 for an 80 dB tone at 2 m, a level approximating that of loud monkey calls (Waser and Waser 1977)

Frequency (Hz)	Ambient SPL (dB)	EA (dB/doubling of distance)	Active space (m)
63	49	2.8	50
125	31	2.0	140
200	27	−0.7	2050
500	25	0.5	700
1000	28	1.7	220
2000	32	1.6	160
4000	34	2.9	70

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