

Reliability of sound attenuation in Florida scrub habitat and behavioral implications

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(Received 20 May 2002; revised 24 January 2003; accepted 11 February 2003)

Attenuation over distance in natural habitat is often difficult to predict when measured without respect to sound frequency. The physical-acoustic structure of Florida scrub habitat is described and both attenuation and reliability of attenuation are measured as a function of sound frequency, over several distances, speaker elevations, and microphone elevations. The spatial context of sound propagation in Florida scrub habitat is discussed and a model designed to describe contributions to overall attenuation from individual factors is presented. Sound frequencies below ~ 3.5 kHz attenuate more reliably than higher sound frequencies, suggesting that animals should pay greatest attention to relatively low sound frequencies when they assess attenuation or estimate sound-pressure level. © 2003 Acoustical Society of America. [DOI: 10.1121/1.1564817]

PACS numbers: 43.80.Ev, 43.80.Lb [WA]

I. INTRODUCTION

Attenuation over distance in natural habitat is often difficult to predict when measured without respect to sound frequency (e.g., Morton, 1975; Wiley and Richards, 1982). Nevertheless, playback experiments with amplified or attenuated stimuli have demonstrated that eastern towhees, *Pipilo erythrophthalmus* (Emberizidae, Passeriformes) in Florida are able to assess attenuation with surprisingly little error (Nelson, 2000; Nelson and Stoddard, 1998). More specifically, this small bird appears to estimate source sound-pressure level (SPL) using at least one correlated sound frequency or temporal variable and assess auditory distance using the difference between perceived (incident) and source SPL. One explanation for the towhee's ability to assess attenuation may be that subjects are able to process sound frequencies that attenuate reliably separately from those that do not. In fact, it has long been recognized that attenuation is frequency dependent and a recent experiment has demonstrated that towhees use SPL as an auditory distance cue only when they hear relatively low sound frequencies (below 3.5 kHz; Nelson, 2002).

Physical objects typically reflect (scatter) incident sound waves, and the magnitude of this sound reflection decreases as sound wavelength approaches and exceeds object diameter/ 2π , corresponding with the transition between Rayleigh and diffractive (Mie) scattering (Bowman *et al.*, 1987; Bradbury and Vehrencamp, 1998; Pye and Langbauer, Jr., 1998). Sound frequency can be derived directly from sound wavelength (frequency= c /wavelength, where c =speed of sound in air) and, as a result, a direct relationship exists between sound frequency and magnitude of sound reflection. Thus, if a broadband sound is reflected by a single object, or by many objects of similar size, then one should expect to observe an increase in sound reflection magnitude above a relatively narrow range of sound frequencies. For example, 1.5-cm objects should begin to reflect sound frequencies

above about 3.65 kHz [$(34\,400\text{ cm}/1.5\text{ cm})/2\pi \approx 3.65\text{ kHz}$].

Sound reflections with greater magnitude should interfere with sound transmission to a greater extent than reflections with lower magnitude. In addition, an increase in interference should, on average, result in greater attenuation over distance. Thus, an increase in sound reflection magnitude over relatively high sound frequencies should, on average, result in increased attenuation over these same relatively high sound frequencies. For example, if 1.5-cm objects begin to reflect sound frequencies above about ~ 3.65 kHz, then increased attenuation might also be expected above ~ 3.65 kHz. In fact, frequency-dependent attenuation has been described in numerous previous investigations and differential scattering has been recognized as an important process that can produce frequency-dependent attenuation (Wiley and Richards, 1982).

Florida scrub habitat has a relatively simple physical-acoustic structure. For example: (1) these vegetation associations are dominated by only a few xerophilous plant species (Abrahamson *et al.*, 1984); (2) leaves are abundant in relation to other potential reflective surfaces (e.g., stems and branches); (3) leaves are located within a relatively dense, 1–2-m-high matrix above the ground; (4) this matrix of leaves lies above a flat and relatively homogeneous sandy soil; and (5) leaves are structurally rigid (sclerophyllous), revolute and linear. Given these habitat characteristics, leaves of dominant Florida scrub plant species should function as an important source of interference during sound transmission.

In this study, I collect leaves in Florida scrub habitat and predict that leaf diameter will be distributed narrowly. I then obtain sound attenuation measurements over several sites, days, speaker elevations, and microphone elevations and predict that sound frequencies will attenuate less reliably as sound wavelength (wavelength= c /frequency) approaches and exceeds the diameter of the most abundant leaf size observed [i.e., as wavelength approaches and exceeds (c /leaf size)/ 2π]. Finally, I present a model in which I estimate the relative contributions to overall attenuation from atmo-

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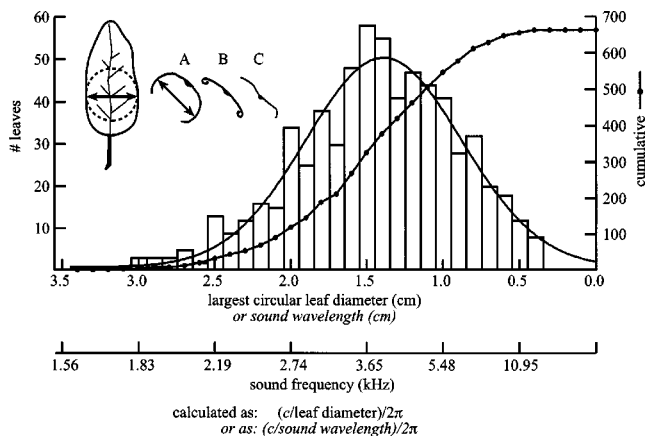


FIG. 1. Nonaccumulating and cumulative distributions of largest circular leaf diameter calculated from 663 leaves collected along sixteen 100-m transects (0.1-cm bins). Inset is an illustration of how largest circular leaf diameter was measured. The distribution is dominated by three species: *Quercus inopina* (46%; cross section depicted as inset A); *Q. geminata* (20%; inset B); and *Q. chapmanii* (12%; inset C). Reciprocal bottom axis predicts the sound frequency at which sound should begin to reflect with substantial magnitude as a function of largest circular leaf diameter [frequency = $(c/\text{leaf diameter})/2\pi$; c = speed of sound].

spheric absorption, ground reflections, and interference from vegetation.

II. EXPERIMENT 1. PHYSICAL-ACOUSTIC HABITAT STRUCTURE

A. Methods

I collected a single leaf every meter along 16 100-m linear transects. I chose sites with variable plant density, species distribution, and time since fire (natural or prescribed) and all sites were located within either a scrubby flatwoods or sand pine scrub vegetation association (Abrahamson *et al.*, 1984). Leaves, not lying on the ground, nearest each 1-m mark on the 100-m measuring tape were chosen, but no leaf was collected if the nearest leaf was closer to the previous or next 1-m mark. Leaves were selected at an elevation above the ground that was determined by the elevation of the 100-m measuring tape stretched above each transect and then allowed to rest naturally within the vegetation. I collected palmetto (*Serenoa repens* and *Sabal etonia*) fronds if they were nearest to each 1-m mark, but did not include these fronds in my analysis.

Leaves were placed in a plastic bag during collection and scanned into a computer (300 dots per inch resolution) within 3 h of collection. Leaves were placed flat along their widest side so that they lay stable on the scanner's bed but were not compressed prior to scanning. Leaf shape did not appear to change prior to scanning.

Leaf images were analyzed digitally by overlaying the largest diameter circle that fit completely within the outside edges of each leaf (inset in Fig. 1). Thus, largest circular leaf diameter is defined as twice the length of radius that can be rotated 360° from a single point without extending beyond the edge of a leaf displayed as a two-dimensional object on its widest side (Fig. 1, inset). Largest circular leaf diameter, as just defined, encompasses what appears to be the most relevant dimension in analyses of several simple shapes (e.g.,

a disk, thin strip, cylinder, sphere, etc., Bowman *et al.*, 1987, see below) and, as a result, this measurement is assumed to represent the most relevant dimension in this analysis.

Variation in leaf shape and orientation decreases the effective size of a leaf depending on the leaf's exact three-dimensional shape. For example, a flat 0.1-cm-thick leaf with a largest circular diameter of 1.5 cm should reflect sound as if it had a largest circular diameter of between 0.1 and 1.5 cm depending on direction of sound incidence upon the leaf. In other words, the function between leaf orientation and magnitude of sound reflection is comparable to what is observed when direction of sound incidence is varied relative to the orientation of, for example, a thin rigid strip (Bowman *et al.*, 1987). As a result, an accounting of variation in leaf shape and orientation should, on average, skew a nonaccumulating distribution of leaf diameter towards a smaller average value, increase the number of small leaves in a cumulative distribution, and accentuate the inflection point of the cumulative distribution. This shift towards a smaller effective leaf diameter is expected to magnify the relationships I describe and, as a result, I do not attempt to account for variation in leaf shape or orientation.

B. Results

Largest circular leaf diameter measurements are distributed normally (mean \pm s.d. = 1.46 ± 0.54 ; $N = 663$, Fig. 1) with 68% of values falling between 0.92 and 2.0 cm. The distribution has a mode near 1.5 cm and is described well by a Gaussian function despite having a slightly positive skew (0.61) and negative kurtosis (-1.04 ; Fig. 1). The distribution is dominated by leaves of *Quercus inopina* [Fig. 1(A); $46 \pm 5\%$ mean \pm s.d., s.d. calculated across the 16 transects], *Q. geminata* [Fig. 1(B); $20 \pm 8.4\%$], and *Q. chapmanii* [Fig. 1(C); $12 \pm 3.8\%$]. The remaining 22% of leaves collected and analyzed were collected from *Lyonia* spp., *Vaccinium* spp., *Befaria racemosa*, *Palafoxia feayi*, and a few other less abundant species. After adjusting for palmetto (*Serenoa repens* and *Sabal etonia*) fronds which were excluded from this analysis, these percentages correspond well with estimates of percent cover obtained previously for sand pine scrub (oak understory phase) and scrubby flatwood (*inopina* phase) vegetation associations (Abrahamson *et al.*, 1984).

III. EXPERIMENT 2. RELIABILITY OF SOUND ATTENUATION

A. Methods

I obtained sound attenuation measurements over five sites in 1998 and over five additional sites in 1999. I obtained recordings at each site on at least 2 different days in May and June between 0600–0800. Recordings were obtained when no birds were near the microphones, and all recordings included in my analyses were preceded and followed by ambient sound with a spectrum level at least 6 dB below spectra of experimental recordings (1.6–8 kHz; see Results).

In both 1998 and in 1999 I recorded at least 6 s of Gaussian noise (Brüel & Kjaer WB 1314, -24 -dB/octave passband filter 1.6–10 kHz) played from a single 1-in. dome

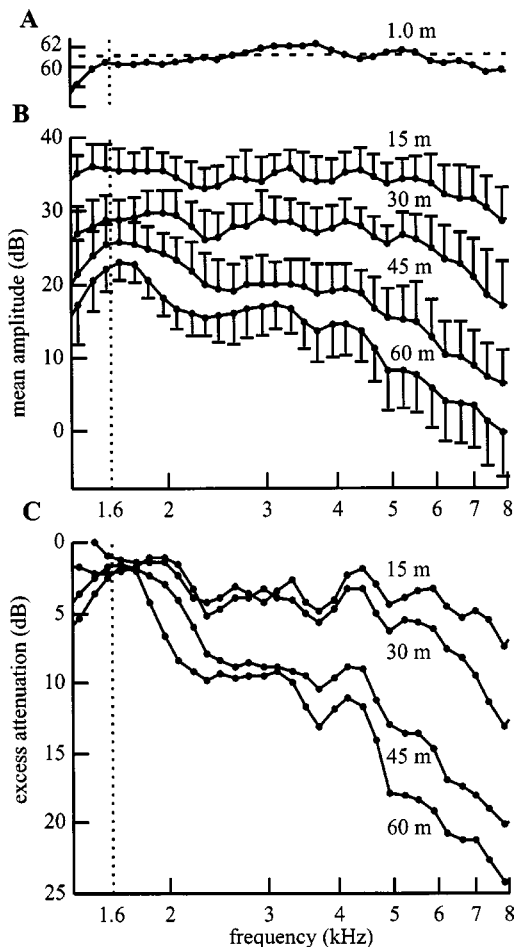


FIG. 2. Attenuation as a function of sound frequency and distance between speaker and microphone positions in 1998 (Fig. 2). (A) Spectrum level (dB, $re: 20 \mu Pa$) of Gaussian noise measured under free-field conditions at a distance of 1 m used to assess sound attenuation in 1998 (the average noise level in 1999 was 4 dB greater, 1.6–8 kHz). Values are averages within 1/12th-octave bands. (B) Mean level of Gaussian noise recordings obtained over 15-, 30-, 45-, and 60-m distances calculated across all recordings obtained with the speaker and microphone placed 1.5 or 2.0 m above the ground ($N=20$ over each distance, error bars=1 s.d.); (C) excess attenuation calculated as: source spectrum-level—mean level of recording—attenuation expected from spherical spreading. The vertical dashed line marks the location of the 1.6 kHz high-pass filter.

speaker (MB Quart QTC 25.01 driven by a Soundstream D200 amplifier, Bescor 14-V, battery and 0.5 farad capacitor) using two calibrated omnidirectional measuring microphones (Brüel & Kjaer 4189), two microphone preamplifiers (Brüel & Kjaer 2671), and a digital audiotape recorder (HHB PortaDAT, 16-bit, 44.1 kHz). Noise was played from the speaker at 94 dB in 1998 [rms at 1 m; 61 ± 1.5 -dB spectrum level between 2–8 kHz, Fig. 2(A)], and at 98 dB in 1999 (rms at 1 m). Source output levels at a distance of 1 m were obtained in an open field with both the speaker and microphone placed 2 m above two stacked acoustic foam panels positioned on the ground between the speaker and the microphone (cutting wedge $48 \times 48 \times 3$ in., $122 \times 122 \times 7.6$ cm, Systems Development Group). Output from the noise-generating system was verified several times each year and only minor ($< \pm 1$ -dB) adjustments were required throughout the 2-year period to maintain a consistent output level (± 1 dB between 1.6 and 8 kHz) under these free-field conditions [Fig. 2(A)].

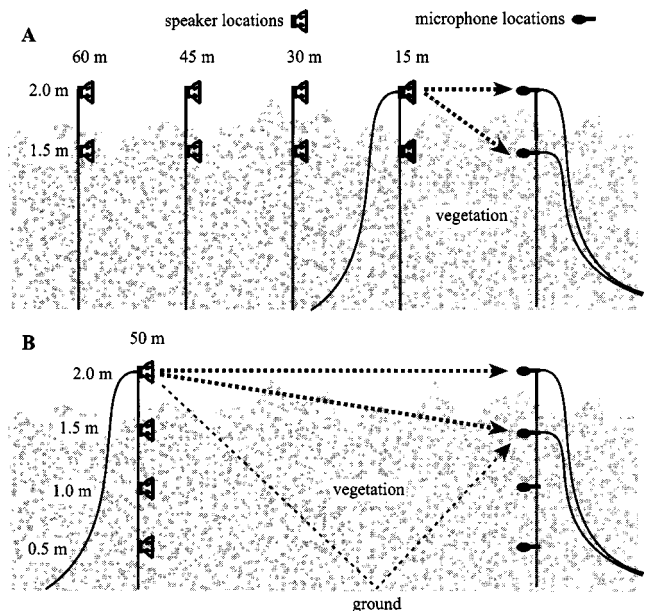


FIG. 3. Distances and elevations of the speaker and microphones used to measure attenuation in 1998 (A) and in 1999 (B). On average, the 2.0-m elevation placed the speaker and a microphone just above surrounding vegetation. In contrast, the 1.5-m elevation usually placed the speaker and a microphone just within surrounding vegetation and the 1.0- and 0.5-m elevations usually placed the speaker and microphone within surrounding vegetation (see the text). The third dashed line in (B) depicts a reflection from the ground.

In 1998, I recorded Gaussian noise with speaker and microphone elevations of 1.5 or 2.0 m [Fig. 3(A)]. I chose these elevations because an elevation of 2 m placed the speaker and microphone, on average, just above surrounding vegetation while an elevation of 1.5 m placed the speaker and microphone, on average, within the maximum elevation (1–2 m) of surrounding vegetation (Abrahamson *et al.*, 1984). For example, from an elevation of 2 m, and over a distance of 60 m, I could usually see a small, 5-cm-diameter brightly colored object (speaker) that was also placed at an elevation of 2 m. In contrast, I could rarely see this same object from an elevation of 1.5 m. These elevations were also chosen because towhees often forage on the ground, but typically perch at an elevation between 1.5 and 2.0 m when vocalizing (personal observation) or when interacting with real or perceived rival conspecifics (Nelson and Stoddard, 1998; Nelson, 2000). During this same year the speaker and microphones were separated by distances of 15, 30, 45, and 60 m [Fig. 3(A)]. Towhees often communicate over 15–60 m (see Discussion) and these four distances were chosen because they span the distances from which stimuli were played to towhee subjects in sound localization experiments (Nelson and Stoddard, 1998; Nelson, 2000).

In 1999, I recorded Gaussian noise with the speaker and microphones positioned at additional elevations of 0.5, 1.0 m [Fig. 3(B)]. These two lower elevations were included to better describe elevation as a source of variation and because towhees often perch at these lower elevations when not vocalizing or interacting with real or perceived rival conspecifics. A single distance of 50 m was used as both a regular

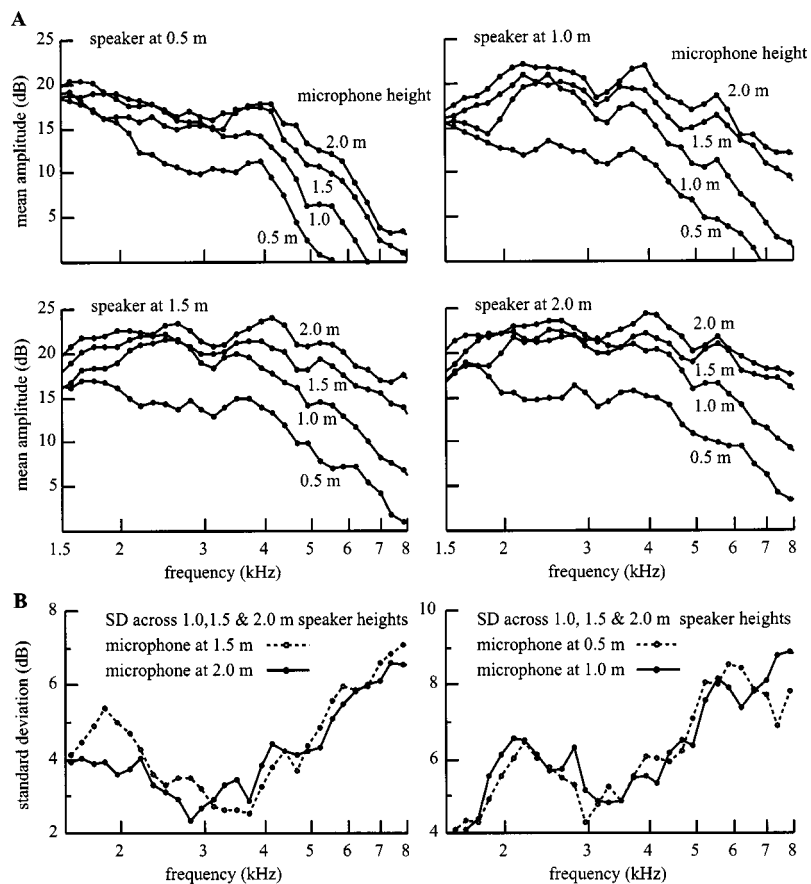


FIG. 4. Attenuation as a function of sound frequency, speaker height, and microphone height above the ground in 1999 (Fig. 2). (A) Mean level of Gaussian noise recordings, averaged within 1/12th-octave bands obtained over a single 50-m distance in 1999. Each plot illustrates mean values obtained with a microphone elevation of 0.5, 1.0, 1.5, and 2.0 m when noise was played from one of the four speaker elevations (0.5, 1.0, 1.5, or 2.0 m, $N=10$ for each condition). (B) Standard deviation (s.d.) calculated across the 1.0-, 1.5-, and 2.0-m speaker elevations for recordings obtained at each microphone elevation (0.5, 1.0, 1.5, and 2.0 m, $N=30$ for each microphone elevation) as well as across sites sampled and between days. Measurements of s.d. demonstrate that sound frequencies below ~ 3.5 kHz attenuate more reliably in comparison with sound frequencies above ~ 3.5 kHz.

(standard) and intermediate distance between the 45- and 60-m distances tested in 1998.

Outputs from the two microphones were recorded simultaneously on separate channels of the stereo recorder (HHB PortaDAT, 16-bit, 44.1 kHz). In 1999, simultaneous recordings were obtained from the 2.0- and 1.5-m elevations and then from the 1.0- and 0.5-m elevations (or vice versa). Gaussian noise recordings on each stereo channel were transferred to a microcomputer (Digigram PCXPocket A/D 44.1 kHz, 16-bit, SPDIF digital interface) and scaled to a proper absolute SPL using reference 1-kHz, 94-dB calibration tones (Brüel & Kjaer 4321) recorded just before and after each recording period. Power spectral densities (PSD) were produced with a Hanning window and 2048-point FFT over 5.99 s (129×2048 point) noise selections (Igor Pro). Magnitudes for each 43.07-Hz linear bin were then averaged within 1/12th-octave bands.

Attenuation and variation in attenuation (s.d.) are both difficult to assess as a function of sound frequency for reasons described below. However, attenuation and variation in attenuation (s.d.) should be positively correlated above ~ 3.5 kHz if both attenuation and s.d. are produced by interference from vegetation (experiment 1). I used line-fit procedures (Igor Pro) to evaluate these correlations as a function of sound frequency below 3.3 kHz and above 3.5 kHz. In all cases, s.d. was calculated over 50 m and across the 1.0-, 1.5-, and 2.0-m speaker elevations.

In a second related analysis I used iterative line-fit procedures to calculate the frequency range over which the maximum correlation coefficient could be obtained. In all

cases this variable frequency range included sound frequencies above 5 kHz but was allowed to include any sound frequency between 2 to 5 kHz if doing so resulted in a larger correlation coefficient. I interpret the lowest frequency included in this iterative analysis as the frequency at which the correlation between attenuation and s.d. begins to change from relatively weak (<0.5) or negative to relatively strong and positive.

Finally, I measured ambient noise level at each microphone elevation (0.5, 1.0, 1.5, and 2.0 m) prior to and after each Gaussian noise recording ($N=20$ for 0.5-, 1.0-, 1.5-, and 2.0-m microphone elevations). Ambient noise level was measured as a function of sound frequency using methods described above over 9.98 s (215×2048 point) waveform selections.

B. Results

Sound attenuation and excess attenuation (i.e., attenuation in addition to that expected from spherical spreading of sound from a single point source) increased with recording distance (Fig. 2). Excess attenuation also increased markedly between the 30- and 45-m recording distances (Fig. 2). Finally, attenuation decreased with speaker and microphone elevation [Fig. 4(A), $N=10$ each elevation] and increased substantially when either the speaker or a microphone was placed at an elevation of 0.5 m.

Attenuation varies as a function of sound frequency (ANOVA $P < 0.01$), although statistical contrasts cannot be drawn because, as predicted, there is significant variation in

variance as a function of sound frequency (i.e., the data are heteroscedastic; Levene's test, $P < 0.05$). *Post hoc* tests for unequal variance (e.g., Dunnett's pairwise comparison with a control) are also inappropriate because there is no control against which attenuation over each distance might be compared. Finally, there seems to be little justification for transforming these data both because the relationship between s.d. and mean attenuation appears to depend on speaker and microphone elevation and because a relationship between mean attenuation and s.d. can be defined only over relatively high sound frequencies (above ~ 3.5 kHz; see below).

Variation in sound attenuation (s.d.) increases above 3–4 kHz under the following conditions: (1) when calculated across the 1.0-, 1.5-, and 2.0-m speaker elevations; (2) when limited to recordings obtained at each microphone elevation [Fig. 4(B), $N = 10$]; (3) when calculated across recordings obtained at all microphone elevations ($N = 40$, not illustrated); and (4) when assessed across all speaker elevations (including the 0.5-m speaker elevation), although overall variation observed in this last analysis is greater due to the large increase in attenuation that is observed when either the speaker or the microphone is placed at an elevation of 0.5 m (not illustrated). Variation in sound attenuation (s.d.) also increases between approximately 2 and 3 kHz, although much of this variation appears to be produced by ground reflections (experiment 3 and Discussion).

Attenuation levels observed over 45 m in 1998 correspond well with attenuation levels obtained over 50 m in 1999 after adjusting for variation in source spectrum level (94 dB vs 98 dB rms) and the 5-m difference in sound propagation distance. In addition, spectra obtained over 50 m in 1999 correspond well with spectra obtained over 15, 30, 45, and 60 m in 1998. As a result, attenuation trends observed as a function of speaker and microphone elevation in 1999 do not appear to occur only over a 50-m propagation distance.

The Levenberg–Marquardt best-fit algorithm (Igor Pro) reports relatively small chi-square values (1.70 ± 0.64 ; mean \pm s.d.; Fig. 4) for power functions describing attenuation over 50 m, whereas larger chi-square values are reported for line fits (2.52 ± 0.93). Thus, attenuation is frequency dependent and appears to be described best over 50 m using a power function in which attenuation is approximately equal to sound frequency (in kHz) raised to a power between 1 and 2 (f^1 to f^2 , where f is frequency in kHz). Residuals reveal that a spectral ripple is imposed on amplitude spectra and that peaks and notches occur at relatively constant frequency intervals above ~ 3 kHz regardless of speaker or microphone elevation (Fig. 5).

Positive linear correlations were observed between attenuation and variation in attenuation (s.d.) above ~ 3.5 kHz in all tests (Table I, Fig. 6). In contrast, relatively weak or negative correlations were observed over sound frequencies below ~ 3.3 kHz. Correlations above 3.5 kHz become stronger as speaker elevation decreases from 2.0 to 0.5 m. In addition, slope values (b) calculated above 3.5 kHz decrease as speaker elevation decreases from 2.0 to 0.5 m (Table I, Fig. 6).

Iterative line fits revealed that stronger positive correlations between attenuation and variation in attenuation (s.d.)

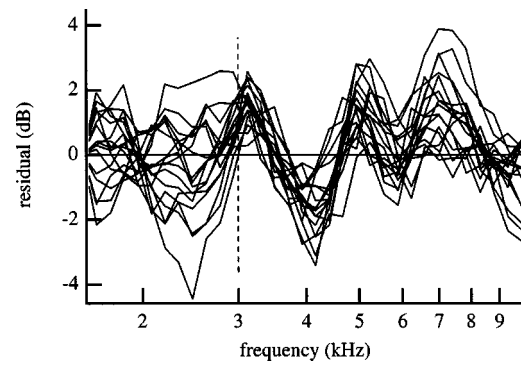


FIG. 5. Residuals from power functions fit to attenuation curves obtained in 1999 over 50 m and across each speaker and microphone elevation. Residuals reveal that a spectral ripple is imposed on amplitude spectra and that peaks and notches in this ripple occur at relatively constant frequency intervals above ~ 3 kHz regardless of speaker or microphone elevation.

could often be obtained by including sound frequency points just below or above 3.5 kHz (Table I, Fig. 6). The lowest frequency measurement included to obtain a larger correlation coefficient decreases with microphone elevation and decreases markedly when the microphone is at 0.5 m. On average, and across the 1.0-, 1.5-, and 2.0-m microphone elevations, the lowest frequency measurement included to obtain a maximum correlation coefficient was 3.612 ± 0.30 kHz (mean \pm s.d.; Table I).

Ambient sound levels attenuate rapidly over distance above ~ 4 kHz (Fig. 7). In addition, ambient sound levels decrease between ~ 1.5 and 2.5 kHz and rise again below ~ 1.5 kHz (not illustrated). Ambient sound levels are lower at the 0.5- and 1.0-m microphone elevations than at the 1.5- and 2.0-m microphone elevations.

TABLE I. Relationship between attenuation and variation in attenuation (s.d.). Correlation coefficients (r) are calculated for each speaker and microphone elevation across sound frequencies either below 3.3 kHz or above 3.5 kHz. Slopes (b) are also reported for sound frequencies above 3.5 kHz. In the last column I report the lowest frequency (kHz) that could be included to obtain a larger correlation coefficient over higher sound frequencies (Fig. 6).

Elevation speaker, mic.	r		b	Lowest kHz to obtain larger r
	<3.3 kHz	>3.5 kHz	>3.5 kHz	
0.5, 0.5	0.345	0.734	0.136	2.473
1.0, 0.5	0.305	0.697	0.170	2.473
1.5, 0.5	0.274	0.726	0.221	2.473
2.0, 0.5	0.482	0.689	0.239	2.334
0.5, 1.0	0.305	0.943	0.206	2.941
1.0, 1.0	-0.621	0.926	0.259	3.498
1.5, 1.0	-0.747	0.938	0.332	3.301
2.0, 1.0	-0.801	0.919	0.315	3.705
0.5, 1.5	-0.905	0.961	0.241	3.926
1.0, 1.5	0.267	0.898	0.424	3.498
1.5, 1.5	-0.529	0.907	0.537	3.498
2.0, 1.5	-0.691	0.759	0.639	3.705
0.5, 2.0	-0.805	0.938	0.197	3.926
1.0, 2.0	-0.015	0.894	0.343	3.498
1.5, 2.0	-0.313	0.822	0.444	3.926
2.0, 2.0	-0.278	0.765	0.466	3.926

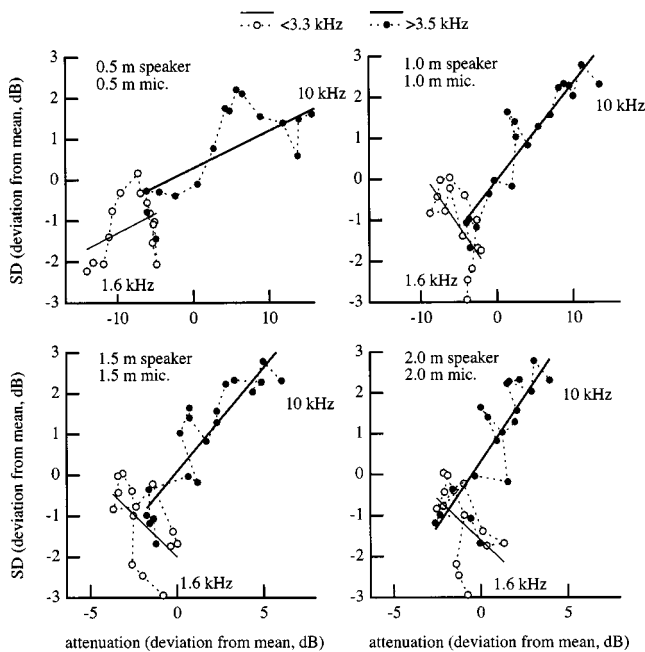


FIG. 6. Relationship between attenuation and reliability of attenuation (s.d.) as a function of sound frequency. A positive relationship exists for sound frequencies above approximately 3.5 kHz. In contrast, a relatively weak or negative relationship exists for sound frequencies below approximately 3.3 kHz. Correlation coefficients are reported in Table I.

IV. EXPERIMENT 3. CONTRIBUTIONS TO ATTENUATION

A. Methods

Attenuation in Florida scrub habitat appears to be due to three primary factors: (1) atmospheric absorption; (2) interference from vegetation; and (3) interference from ground reflections. I present a simple model of sound transmission in Florida scrub habitat and use the results of this model to estimate the contributions to both attenuation and variation in attenuation from each individual factor.

Wiley and Richards (1982) suggested that attenuation

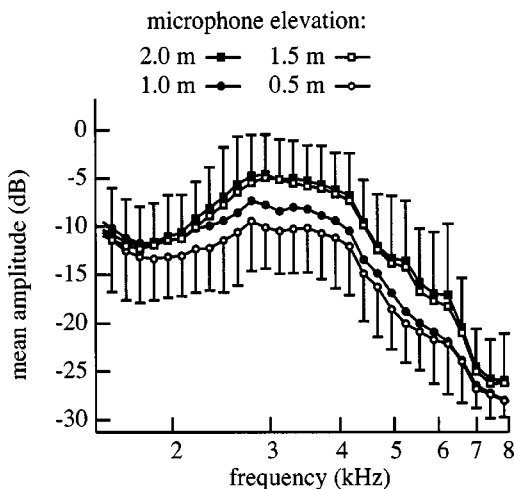


FIG. 7. Ambient noise levels measured at 0.5-, 1.0-, 1.5-, and 2.0-m microphone elevations in 1999 ($N=20$, 9.98 s. samples). Error bars (1 s.d.) are plotted only for the 0.5- and 2.0-m elevations; however, error measured at 1 m is similar to error measured at 0.5 m and error measured at 1.5 m is similar to error measured at 2 m.

(dB) should be approximately equal to sound frequency raised to a power of between 1 and 2. Power coefficients between 1 and 1.3 appear to approximate attenuation when the speaker and microphone are located above vegetation, while larger coefficients (1.3 to 1.7) appear to approximate attenuation when the speaker or microphone are located within vegetation (experiment 2). I therefore approximate attenuation (in dB) due to atmospheric absorption as sound frequency (kHz) raised to a power between 1 and 1.3 [Fig. 8(A)] and attenuation due to both atmospheric absorption and interference from vegetation as sound frequency (in kHz) raised to a power between 1 and 1.7 [Fig. 8(A)].

Ground reflections are often difficult to predict in natural habitats due to soil heterogeneities (Martens *et al.*, 1985; e.g., Wiley and Richards, 1982). However, the soils where I obtained attenuation measurements can be described as sandy, well drained (1.8 to >3 m), and relatively homogeneous (Abrahamson *et al.*, 1984). Sandy soils are acoustically “hard” because reflection coefficients have relatively large real parts (0.7–1.0) and relatively small imaginary parts (0.0–0.2, Bolen and Bass, 1981; Martens *et al.*, 1985). As a result, ground reflections should arrive at microphone positions with both substantial magnitude and minimum phase shift [Fig. 3(B)].

I calculate the delay time (Dt) of reflections from the ground

$$Dt = \left(\left(\sqrt{S^2 + \left(d \cdot \frac{S}{S+M} \right)^2} + \sqrt{M^2 + \left(d \cdot \frac{M}{M+S} \right)^2} \right) - d \right) \div c, \quad (1)$$

where S is speaker elevation, M is microphone elevation, d is the distance from the speaker to the microphone (50 m), and c is the speed of sound in air (340 m/s).

Sound propagating down to the ground should experience substantial frequency-dependent attenuation from vegetation. Furthermore, sound that is reflected back upwards from the ground should experience additional attenuation if both the speaker and microphone are positioned within or above the vegetation (Fig. 3). As a result, I attenuate ground reflections using a relatively large reflection coefficient (0.7) and power coefficient (2)

$$A = 0.7 \cdot 10^{-f^2/20}, \quad (2)$$

where f is sound frequency (kHz). I then calculate amplitude as a function of sound frequency at a (nondirectional) receiver’s location by summing both direct and reflected sound waves

$$W(t) = \cos(2 \cdot \pi \cdot Hz \cdot t) + A \cdot \cos(2 \cdot \pi \cdot Hz \cdot (t + Dt)), \quad (3)$$

$$dB = 20 \cdot \log(\text{rms}(W(t))), \quad (4)$$

where A is the amplitude of the ground reflection [Eq. (2)], t is time (s), Dt is the delay time of the ground reflection [s; Eq. (1)], $W(t)$ is a waveform, and rms is a function computing root mean square (rms) amplitude over the waveform defined by $W(t)$.

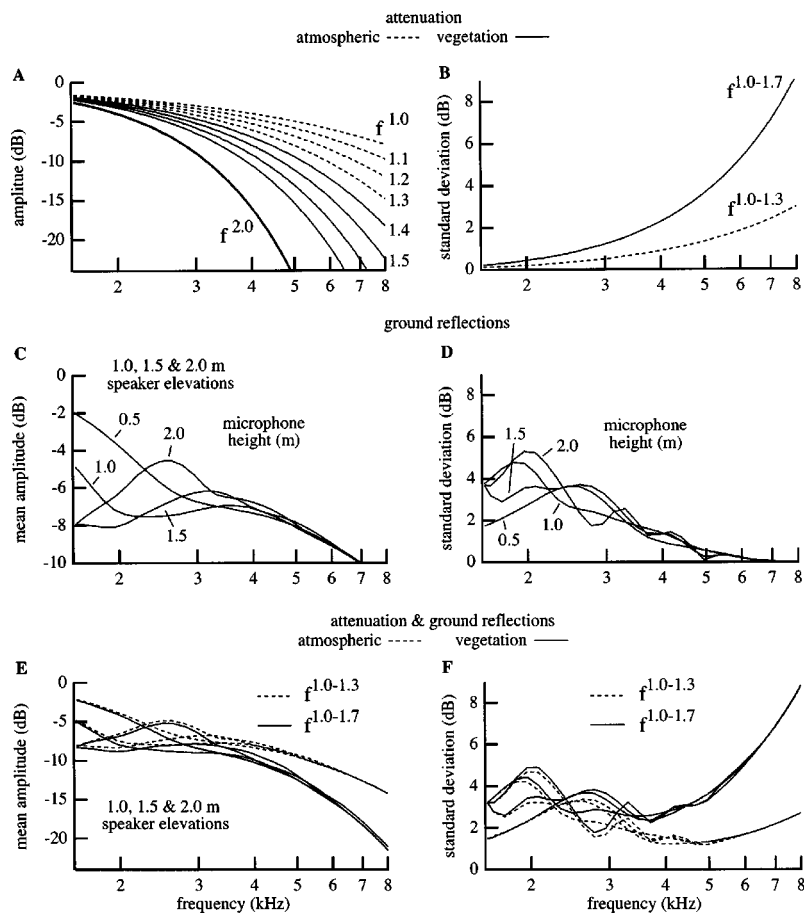


FIG. 8. Estimated contributions to overall attenuation from atmospheric absorption, interference from vegetation, and interference from ground reflections. (A) Attenuation derived from power functions ($f^{1.0}$ to $f^{1.7}$) where f is sound frequency in kHz. (B) Variation in attenuation (calculated across power coefficients) describing attenuation due to atmospheric absorption ($f^{1.0}$ to $f^{1.3}$) and interference from vegetation ($f^{1.4}$ to $f^{1.7}$). (C) Attenuation due to ground reflections at each microphone elevation; calculated as an average across speaker elevations. (D) Variation in attenuation due to ground reflections; calculated across speaker elevations. (E) Attenuation curves derived both from power functions and ground reflections. (F) Variation in attenuation due to atmospheric absorption ($f^{1.0}$ to $f^{1.3}$), interference from vegetation ($f^{1.4}$ to $f^{1.7}$), and ground reflections; calculated across speaker elevations.

For comparison with empirical data I calculated attenuation and variation in attenuation (s.d.) over 50 m and across the same 0.5-, 1.0-, 1.5-, and 2.0-m speaker and microphone elevations evaluated during 1999 in experiment 2. I calculated attenuation for individual sound frequencies in this model for clarity but verified results in a second comparable model that employed Fourier analyses of Gaussian noise waveforms that were similarly attenuated (filtered), delayed, and summed (results not presented).

B. Results

Variation in attenuation (s.d.) increases with sound frequency when attenuation is described by a power function [Fig. 8(A)] and when the power coefficient describing attenuation is varied between 1.0 and 1.3 [Fig. 8(B); s.d. = $0.11 * f^{1.6}$, where f is frequency in kHz]. Thus, s.d. might be expected to increase with sound frequency even when there is minimum variation in attenuation due to atmospheric absorption. s.d. increases more rapidly with sound frequency when the power coefficient describing attenuation is varied between 1.0 and 1.7 [Fig. 8(B); s.d. = $0.186 * f^{1.88}$]; a range of coefficient values that would appear to more closely approximate attenuation through vegetation [Fig. 4(B)].

Ground reflections undergo substantial frequency-dependent attenuation in this model and, as a result, these reflections appear to produce interference primarily over relatively low sound frequencies [Fig. 8(C)]. In addition, interference appears to depend on both speaker and microphone elevation [Fig. 8(D)]. In fact, the combined effects of

attenuation and ground interference [Figs. 8(E) and (F)] are not vastly different from empirical measurements obtained in experiment 2 (Fig. 4). Finally, results lend support to the hypothesis that the relationship observed between attenuation and variation in attenuation (s.d., Fig. 6) might be due primarily to ground reflections below ~ 3 kHz and by atmospheric absorption and interference from vegetation above ~ 3.5 kHz (Fig. 9).

V. DISCUSSION

A. Physical-acoustic structure of the habitat

Natural outside environments are complex, and numerous factors can lead to both increased attenuation and de-

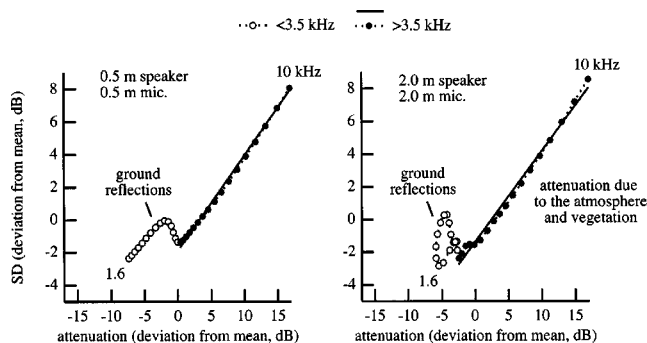


FIG. 9. Relationship between attenuation and variation in attenuation (s.d.) observed in the output of the model (Fig. 8). The relationship is complex and dependent on both speaker and microphone elevation below ~ 3.5 kHz but becomes both positive and linear above ~ 3.5 kHz.

creased reliability of attenuation. For example, the variable and frequency-dependent nature of atmospheric absorption might alone often produce substantial variation in attenuation over relatively high sound frequencies [Fig. 8(B)]. Nevertheless, vegetation is likely to be an important factor in determining how sound attenuates in Florida scrub habitat (experiment 1).

Leaves in Florida scrub habitat can be described as having a relatively narrow size distribution with a peak near 1.5 cm (Fig. 1), which led to the following three predictions: (1) sound frequencies above ~ 3.5 kHz (3–4 kHz) should attenuate rapidly with distance and attenuate with greater variation in attenuation over distance in comparison with lower sound frequencies because sound frequencies above ~ 3.5 kHz are likely to face strong interference from numerous leaves with a largest circular diameter larger than 1.5 cm; (2) a moderate amount of attenuation should occur between ~ 2.75 and 3 kHz as a result of interference from a moderate number of leaves with diameter between 1.5 and 2 cm; and (3) a negligible amount of attenuation should occur below ~ 2.75 kHz as a result of negligible interference from a relatively low number of leaves with a circular diameter larger than 2 cm. These predictions are illustrated graphically in Fig. 1 by reciprocal bottom axes.

Sound is not normally transmitted along a single direct pathway between a signaler and a receiver but is, instead, dispersed upon production and then (in most cases) resolved by directional hearing mechanisms during reception. As a result, the role that sound propagation plays during communication is likely to be substantial in comparison with the role that is normally attributed by analyses of monaural sound recordings. For example, monaural sound recordings may often need to be interpreted with caution because we do not yet fully understand the mechanisms by which animals resolve direct sound from reverberant sound. In addition, while neither birds nor humans localize sound reflections (lagging stimuli) that arrive within a few milliseconds of direct sound (e.g., Blauert, 1997; Litovsky *et al.*, 1999; Dent and Dooling, 2003), it has been demonstrated that humans pay attention to these reflections when discriminating sound level (Freyman *et al.*, 1998).

With these cautions in mind, attenuation measurements might often be interpreted most clearly in relation to the physical-acoustic structures of the habitats in which measurements are obtained. I suggest that sound frequencies below ~ 3.5 kHz are likely to attenuate more reliably than higher sound frequencies because these lower sound frequencies encounter a lower level of interference from leaves lying along the direct pathway between a speaker (signaler) and microphone (listener). In contrast, sound frequencies above ~ 3.5 kHz attenuate less reliably because they are more likely to experience a variable level of interference during propagation.

Previous investigators often emphasize how natural environments can “degrade” temporally modulated vocalizations during transmission. I do not investigate temporal changes that sound might undergo after transmission through Florida scrub habitat and, as a result, I do not describe how Florida scrub habitat might degrade temporally modulated

vocalizations. Leaves are expected to reflect sound frequencies above ~ 3.5 kHz with greater magnitude in comparison with lower sound frequencies and, as a result, one might expect to observe increased degradation above ~ 3.5 kHz. On the other hand, leaves are scattered diffusely throughout Florida scrub habitat and this interpretation must, again, be viewed with caution until we learn more about mechanisms for hearing in natural environments.

B. Attenuation due to ground reflections

Ground reflections can sum together with direct sound and produce pronounced spectral peaks and notches in sound recordings (Bradbury and Vehrencamp, 1998; Roberts *et al.*, 1979; Wiley and Richards, 1982). This is especially true when recordings are obtained with a single omnidirectional microphone that is sensitive to both direct and reflected sound. Ground reflections are important because, when they exist, attenuation at any single sound frequency can depend to a large extent on several factors including the height of a sound source (signaler), height of a receiver (listener), and the distance between a sound source and a receiver (Fig. 3). Ground reflections are important in this study because sound frequencies below ~ 3.5 kHz are not expected to reflect from leaves, and are therefore expected to reflect from the ground and sum together with direct sound with substantial magnitude.

Spectral peaks and notches are evident below ~ 5 kHz in field recordings obtained where scrub vegetation had been cleared or burned within the last year. These peaks and notches can be attributed to ground reflections because they vary predictably with changes in both the elevation of the speaker or microphone and with the distance over which the speaker and microphones are separated (unpublished data). However, when otherwise identical recordings are obtained over vegetation (i.e., over at a site where vegetation has not been cleared or burned within the previous year), peaks and notches are most evident below ~ 3 kHz (unpublished data). As a consequence, variation in attenuation observed between ~ 2 and 2.5 kHz would appear to occur primarily as result of increased interference due to ground reflections (Fig. 4).

Animals may experience similar ambiguity (i.e., variation in attenuation) when unable to resolve indirect sound reflections separately from direct sound. However, directional hearing may allow subjects to avoid some of this variation if reflections can be suppressed or otherwise distinguished from direct sound. For example, if the auditory system can suppress sound reflections (lagging stimuli) that arrive within a few milliseconds of direct sound (e.g., Blauert, 1997; Litovsky *et al.*, 1999; Dent and Dooling, 2003), then it remains possible that ground reflections will not interfere with mechanisms for assessing the SPL of direct sound. In fact, some of these reflections may improve assessment of attenuation if reflections can contribute to an animal’s overall assessment of SPL (e.g., Freyman *et al.*, 1998).

C. Frequency-dependent attenuation

Ground reflections can produce variable attenuation patterns over relatively low sound frequencies (< 3 kHz) but are

not expected to produce variable attenuation patterns over relatively high sound frequencies (Wiley and Richards, 1982). Instead, it would appear that attenuation over relatively high sound frequencies is best approximated as sound frequency (kHz) raised to a power of between 1 and 2 in many habitats including Florida scrub (Wiley and Richards, 1982, experiment 2).

That attenuation increases as a function of sound frequency has long been recognized. However, that variation in attenuation should also increase with sound frequency has received less attention. In this study, I demonstrate that variation in attenuation increases above ~ 3.5 kHz (experiment 2). Furthermore, I suggest that variation in attenuation above ~ 3.5 kHz may be due simply to variation in the function describing attenuation with respect to sound frequency (experiment 3).

Spectra obtained in both 1998 and in 1999 undulate with sound frequency, and the ripple that results from this undulation is most pronounced between 3 and 5 kHz (Figs. 4 and 5). This ripple does not appear to be due to ground reflections because peaks and notches in this ripple are pronounced only over relatively high sound frequencies ($> \sim 3$ kHz) and occur at roughly constant frequency intervals regardless of speaker and microphone elevation (Figs. 4 and 5). In addition, this ripple exists in recordings obtained using different equipment (unpublished data) and as thus does not appear to be an artifact. Spectral ripples are normally observed in reflected sound when wavelength exceeds object diameter/ π (Bowman *et al.*, 1987; Bradbury and Vehrencamp, 1998; Pye and Langbauer, Jr., 1998). Thus, one potential explanation for this ripple may be that sound is reflecting from numerous similarly sized objects during propagation. In fact, while this interpretation remains hypothetical, measurements of leaf diameter are narrowly distributed and leaves are expected to begin reflecting sound above approximately 3 kHz (Fig. 1).

D. Factors contributing to attenuation

Numerous factors can contribute to increased attenuation. Similarly, these same factors can often contribute to increased variation in attenuation (i.e., decreased reliability of attenuation). Nevertheless, individual contributions are often difficult to discern in empirical measurements. As a result, I present a relatively simple model intended to estimate the relative contributions to both attenuation and variation in attenuation from atmospheric absorption, interference from vegetation, and interference from ground reflections (experiment 3).

Attenuation due to atmospheric absorption is ubiquitous and will often limit the distance over which relatively high sound frequency vocalizations will propagate. On the other hand, variation in attenuation due to atmospheric absorption does not appear to decrease reliability of attenuation substantially as long as the function describing atmospheric absorption is not highly variable [Fig. 8(B)]. In contrast, attenuation due to increased interference from vegetation would appear to both increase attenuation and introduce substantial variation in attenuation over relatively high sound frequencies [Fig. 8(B)]. In fact, the use of a variable power coefficient to

describe attenuation in this model, as opposed to a linear function, appears to produce relatively strong variation in attenuation primarily above ~ 3 –4 kHz [Fig. 8(B)].

Ground reflections appear to be common in many habitats and may introduce substantial variation in attenuation over relatively low sound frequencies (e.g., Roberts *et al.*, 1979; Wiley and Richards, 1982). Variation in attenuation due to speaker elevation in this model does not appear to differ markedly from empirical measurements [Figs. 4(B) and 8(D)]. Nevertheless, nonsandy soils can often introduce phase shifts in ground reflections (e.g., Bolen and Bass, 1981; Martens *et al.*, 1985) and it should be recognized that such phase shifts can often produce highly variable attenuation patterns over relatively low sound frequencies.

Finally, it should be noted that additional factors are expected to contribute to both attenuation and variation in attenuation. For example, Wiley and Richards (1982) suggested that atmospheric turbulence can alone result in strong attenuation of relatively high sound frequencies. In fact, much of the frequency-dependent attenuation I attribute to atmospheric absorption and interference from vegetation might also be attributed to increased atmospheric turbulence.

E. Effects of signaler and listener elevation above the ground

Previous investigators have demonstrated that both a signaler's and listener's elevation above the ground can have substantial influences on characteristics of sound propagation (e.g., Dabelsteen *et al.*, 1993; Holland *et al.*, 1998; Mathevon *et al.*, 1996). In fact, these studies demonstrate that a change in speaker or microphone elevation can, in many ways, resemble a change in horizontal distance. A listener presumably often knows its own elevation and location within local habitat and, as a result, a listener might often be able to account for these factors when assessing attenuation. In contrast, listeners may rarely be able to assess the elevation of a distant signaler. Thus, while a greater amount of overall variation in attenuation is observed as a function of microphone elevation in comparison with variation assessed as a function of speaker elevation (Dabelsteen *et al.*, 1993), the results of this latter analysis may be of greater biological interest.

The attenuation levels that I observed as a function of microphone elevation in 1999 suggest that eastern towhees in Florida scrub habitat should move to an elevation of at least ~ 1 m to avoid a high level of excess attenuation [Fig. 4(A)]. In addition, results suggest that subjects should move to an elevation above ~ 1 m to avoid increased variation in attenuation [Fig. 4(B)]. Towhees may benefit additionally by perching above a 2-m elevation but can often do so in Florida scrub habitat only if willing to fly a considerable distance to one of a few relatively tall trees typically located within a towhee territory.

Towhees spend a substantial amount of time on or near the ground but nearly always move to an elevation between 1 and 2 m when interacting actively with real or perceived conspecific rivals that are located within or near their territory boundaries (Nelson and Stoddard, 1998; Nelson, 2000,

and personal observations). In addition, towhees often move to an elevation between 1 and 2 m just before vocalizing even if they return to the ground shortly after vocalizing (personal observations). These movements are likely to produce substantial variation in attenuation above ~ 3.5 kHz but are less likely to produce substantial variation in attenuation below ~ 3.5 kHz.

F. Implication for sound frequency windows

Morton (1975) described a sound frequency “window” for long distance communication in a forested habitat (see below) and argued that vocalizations may propagate farthest when produced within this range of sound frequencies. Sound frequency windows have subsequently been identified across a surprisingly broad range of habitats and, in most cases, these windows appear to be bounded by increased attenuation due to ground effects over relatively low sound frequencies and by increased attenuation due to atmospheric absorbance and interference from vegetation over relatively high sound frequencies (e.g., Marten and Marler, 1977a; Brenowitz, 1982; Marten and Marler, 1977b). For example, in a Panamanian forest both Morton (1975) and Marten and Marler (1977a) identified a sound frequency window between ~ 0.5 and 2.5 kHz (depending on interpretation). Similarly, Marten and Marler (1977b) defined a sound frequency window between ~ 1 and 3 kHz in several temperate habitats and Brenowitz (1982) defined a window between ~ 2.5 and 4 kHz in an open field. Roberts *et al.* (1979) suggested that many of these sound frequency windows might be explained by ground reflections (see Discussion above); however, it remains interesting that sound frequency windows have been identified in such variable habitats.

Attenuation increases with sound frequency in Florida scrub habitat and ground reflections introduce variable attenuation patterns below $\sim 2\text{--}3$ kHz. As a result, a sound window for long-distance communication often appears to exist between approximately 2.5 and 4.5 kHz in Florida scrub habitat.

Towhee calls are highly variable in acoustic structure but span a range of sound frequencies between ~ 1.8 and 4.5 kHz (Nelson, 2000). As a result, one might expect calls to propagate over relatively long distances. However, calls are also produced with variable source SPL ($\sim 70\text{--}84$ dB, *re*: $20\ \mu\text{Pa}$; Nelson, 2000) and estimates of propagation distance are, ultimately, dependent both on ambient noise levels (Fig. 6) and mechanisms for hearing in noise (Dent *et al.*, 1997). As a result, it remains difficult to estimate how far any single towhee call might propagate before it can no longer be detected or discriminated. For example, a 3.3-kHz signal (selected arbitrarily) might be produced with a source spectrum level of 45 dB (equivalent to a 75-dB rms SPL; *re*: $20\ \mu\text{Pa}$; Nelson 2000) and be emitted from a height of 1.5 m. This signal might then attenuate ~ 46 dB over 50 m and arrive at a receiver’s position with a spectrum level that is approximately 1 dB below ambient noise level at least $\sim 84\%$ of the time. However, this same signal can also be expected to arrive with an amplitude that is approximately 8 dB above ambient noise level $\sim 16\%$ of the time. Binaural release from

masking might decrease threshold by an additional 9 dB (Dent *et al.*, 1997) and, thus, this same 45-dB signal might sometimes be detected over an additional ~ 150 m depending on environmental conditions and the physiological mechanisms that listeners may employ for hearing in noisy environments (assuming ~ 7.5 -dB attenuation per doubling of distance). In summary, this variation is substantial and does not incorporate additional variation in active space that is expected to occur as a function of sound frequency or as a result of variation in source SPL (Nelson, 2000).

These results suggest that a bird like the eastern towhee may rarely be able to predict how far any single vocalization will propagate before it can no longer be detected or discriminated. However, much of this variation results from difficulty in quantifying when a vocalization falls below threshold and does not result from variation in attenuation. Thus, these results say little about variation in attenuation. In fact, sound frequencies below ~ 3.5 kHz may often attenuate reliably even if the active space of any single sound frequency or vocalization cannot be easily predicted.

G. Generality of results and behavioral implications

There are two main tasks to understanding ecological systems. The first task is to understand how individual processes operate and the second task is to understand how individual processes operate together. Florida scrub habitat has a relatively homogeneous physical-acoustic structure and, as a consequence, the results I present may be particularly robust. In fact, even a relatively simple model of sound propagation appears to produce similar results (experiment 3). On the other hand, the processes that contribute to attenuation in Florida scrub habitat are not specific to this habitat but are known to influence how sound propagates in numerous other habitats. For example, ground reflections, atmospheric absorbance, and interference from vegetation are all processes that are expected to produce attenuation in other habitats.

Eastern towhees use SPL as an auditory distance cue when they hear sound frequencies below 3.5 kHz but use another auditory distance cue when they hear sound frequencies above 3.5 kHz (Nelson, 2002). These results suggest that neural circuits used for judging attenuation might receive inputs primarily from low-frequency neural pathways (e.g., Irvine, 1992; Takahashi *et al.*, 1984). Alternatively, these circuits might select against high-frequency inputs during development if high frequencies do not normally attenuate reliably.

Use of SPL as an auditory distance cue can demonstrate that an animal is able to assess attenuation. However, if attenuation is reliable then variation in SPL might also convey additional information. For example, if distance can be judged using a visual cue or second auditory cue, then an ability to compensate for attenuation might allow an animal to assess source SPL. In fact, experiments have suggested that birds vary SPL when learning to sing (Brumm and Hultsch, 2001) and when vocalizing as adults (e.g., Brumm and Todt, 2002; Nelson, 2000; Cynx *et al.*, 1998; Manabe *et al.*, 1998).

ACKNOWLEDGMENTS

I thank Roderick Suthers, Sumit Dhar, Erica Goss, Ellen Ketterson, Bill Rowland, Troy Smith, and Philip Stoddard for helpful comments. Support was provided, in part, by NSF Grant No. BIR-9413220 to the Center for the Integrative Study of Animal Behavior at Indiana University and NIH Grant No. NS-29467 to Roderick Suthers. Archbold Biological Station provided access to research facilities.

- Abrahamson, W. G., Johnson, A. F., Layne, J. N., and Peroni, P. A. (1984). "Vegetation of the Archbold Biological Station, Florida: An example of the southern Lake Wales Ridge," *Florida Sci.* **47**, 209–250.
- Blauert, J. (1997). *Spatial Hearing: The Psychophysics of Human Sound Localization, revised edition* (The MIT Press, Cambridge, MA).
- Bolen, L. N., and Bass, H. E. (1981). "Effects of ground cover on the propagation of sound through the atmosphere," *J. Acoust. Soc. Am.* **69**, 950–954.
- Bowman, J. J., Senior, T. B. A., and Uslenghi, P. L. E. (1987). *Electromagnetic and Acoustic Scattering by Simple Shapes* (Hemisphere, New York).
- Bradbury, J. W. and Vehrencamp, S. L. (1998). *Principles of Animal Communication* (Sinauer Associates, Sunderland, MA).
- Brenowitz, E. A. (1982). "Long-range communication of species identity by song in the red-winged blackbird," *Behav. Ecol. Sociobiol.* **10**, 29–38.
- Brumm, H., and Hultsch, H. (2001). "Pattern amplitude is related to pattern imitation during the song development of nightingales," *Anim. Behav.* **61**, 747–754.
- Brumm, H., and Todt, D. (2002). "Noise-dependent song amplitude regulation in a territorial songbird," *Anim. Behav.* **63**, 891–897.
- Cynx, J., Lewis, R., Tavel, B., and Tse, H. (1998). "Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*," *Anim. Behav.* **56**, 107–113.
- Dabelsteen, T., Larsen, O. N., and Pedersen, S. B. (1993). "Habitat-induced degradation of sound signals: Quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song," *J. Acoust. Soc. Am.* **93**, 2206–2220.
- Dent, M. L., and Dooling, R. (2003). "Investigations of the precedence effect in budgerigars: Effects of stimulus type, intensity, duration, and location," *J. Acoust. Soc. Am.* **113**, 2146–2158.
- Dent, M. L., and Dooling, R. J. (2003). "Investigations of the precedence effect in budgerigars: Perceived location of auditory images," *J. Acoust. Soc. Am.* **113**, 2159–2170.
- Dent, M. L., Larsen, O. N., and Dooling, R. J. (1997). "Free-field binaural unmasking in budgerigars (*Melopsittacus undulatus*)," *Behav. Neurosci.* **111**, 590–598.
- Freyman, R. L., McCall, D. D., and Clifton, R. K. (1998). "Intensity discrimination for precedence effect stimuli," *J. Acoust. Soc. Am.* **103**, 2031–2041.
- Holland, J., Dabelsteen, T., and Larsen Ole, N. (1998). "Degradation of wren *Troglodytes troglodytes* song: Implications for information transfer and ranging," *J. Acoust. Soc. Am.* **103**, 2154.
- Irvine, D. R. F. (1992). "Physiology of the auditory brainstem," in *The Mammalian Auditory Pathway: Neurophysiology*, edited by A. N. Popper and R. R. Fay (Springer, New York), pp. 153–231.
- Litovsky, R. Y., Colburn, H. S., Yost, W. A., and Guzman, S. J. (1999). "The precedence effect," *J. Acoust. Soc. Am.* **106**, 1633–1654.
- Manabe, K., Sadr, E. I., and Dooling, R. J. (1998). "Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect," *J. Acoust. Soc. Am.* **103**, 1190–1198.
- Marten, K., and Marler, P. (1977a). "Sound transmission and its significance for animal vocalization. I. Temperate habitats," *Behav. Ecol. Sociobiol.* **2**, 271–290.
- Marten, K., and Marler, P. (1977b). "Sound transmission and its significance for animal vocalization. II. Tropical forest habitats," *Behav. Ecol. Sociobiol.* **2**, 291–2302.
- Martens, M. J. K., van der Heijden, L. A. M., Walthaus, H. H. J., and van Rens, W. J. J. M. (1985). "Classification of soils based on acoustic impedance, air flow resistivity and other physical parameters," *J. Acoust. Soc. Am.* **78**, 970–980.
- Mathevon, N., Aubin, T., and Dabelsteen, T. (1996). "Song degradation during propagation: Importance of song post for the wren *Troglodytes troglodytes*," *Ethology* **102**, 397–412.
- Morton, E. S. (1975). "Ecological sources of selection on avian sounds," *Am. Nat.* **109**, 17–34.
- Nelson, B. S. (2000). "Avian dependence on sound-pressure level as an auditory distance cue," *Anim. Behav.* **59**, 57–67.
- Nelson, B. S. (2002). "Duplex auditory distance assessment in a small passerine bird (*Pipilo erythrophthalmus*)," *Behav. Ecol. Sociobiol.* **53**, 42–50.
- Nelson, B. S., and Stoddard, P. K. (1998). "Accuracy of auditory distance and azimuth perception by a passerine bird in natural habitat," *Anim. Behav.* **56**, 467–477.
- Pye, J. D., and Langbauer, Jr., W. R. (1998). "Ultrasound and infrasound," in *Animal Acoustic Communication: Sound Analysis and Research Methods*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer, Berlin).
- Roberts, J., Kacelnik, A., and Hunter, M. J. (1979). "A model of sound interference in relation to acoustic communication," *Anim. Behav.* **27**, 1271–1273.
- Takahashi, T. T., Moiseff, A., and Konishi, M. (1984). "Time and intensity cues are processed independently in the auditory system of the owl," *J. Neurosci.* **4**, 1781–1786.
- Wiley, R. H., and Richards, D. G. (1982). "Adaptations for acoustic communication in birds: Sound transmission and signal detection," in *Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller (Academic, New York), pp. 132–163.