could relate to the observation that the signal duration of these ectotherms is affected by temperature (Zeigler & Stewart 1977), and that the small size of stoneflies allows them to exist in a variety of proximate thermal microhabitats along a stream bank. In *P. drymo*, signal length has been observed to vary by over 15% for a 1-°C rise or fall in temperature (Zeigler & Stewart 1977). This effect could be even more pronounced when the black-body effect of a male positioned in the sunlight versus a shaded female is considered, since many stonefly adults are dark in colour.

The signals of these two stonefly species can be successfully computer-simulated, and for each species there are definable female recognition 'windows' for particular variations in male calls. Continued work with other species and more signal variations should reveal the relative importance of each call parameter. Also, such studies will more clearly define overlap (or lack thereof) in female recognition among the calls of related species.

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Environmental Bioacoustics: Evaluation of a Commonly-used Experimental Design

It has been suggested (e.g. Morton 1975) that the structure of acoustic signals has evolved under selection to increase transmission distance by decreasing frequency-dependent attenuation (see also Ryan & Brenowitz 1985). This hypothesis is often tested by broadcasting the signal through the environment and determining its rate of attenuation. The rate of attenuation is then compared among habitats in which the species is resident and non-resident, or it is compared with that of signals used in short-range communication (Gish & Morton 1981; Brenowitz 1982; Ryan 1985). Michelson (1978) advised caution when applying this approach because it does not measure or control for several important variables: (1) speakers will often beam frequencies differently from the animal; (2) the outcome of the constructive and destructive interference interaction of sound waves will vary with only slight differences in distance from the source; and (3) microclimatic and vegetational effects will vary within the same habitats. All of these variables could result in sound attenuation being non-linear and unpredictable.

In this study, I compare the amount of attenuation of a tape-recorded mating call of the frog *Physalaemus pustulosus*, broadcast by a speaker, to the amount of attenuation of the same call, broadcast by the frog, under identical conditions. This allows me to evaluate the validity of the technique in which the animal's signal used for long range communication is artificially broadcast and its rate of attenuation is determined. This is, to my knowledge, the first measure of attenuation rates of naturally-produced animal acoustic signals, as well as the first test of this commonly-used experimental design in environmental bioacoustics.

The frog call consists of two components, a whine and a chuck (Ryan 1985). The whine is a frequency sweep consisting of a dominant frequency that begins at 900 Hz and sweeps to 400 Hz in circa 400 ms. The chuck is circa 26 ms and is harmonically structured with a fundamental frequency of 200–270 Hz. Most of its energy is concentrated around 2500 Hz. The whine is necessary and sufficient for species recognition, and the chuck is important to females choosing mates at relatively short distances (e.g. 10 cm; Ryan 1980, 1983a, b; Rand & Ryan 1981; Ryan et al. 1982). Ryan (1985) showed that the whine attenuates less than the chuck. These results are consistent with the hypothesis that the species recognition component has been designed for transmission over longer distances relative to the chuck component, which appears to function at close range.

Experiments were conducted in a large, open field at ground level (the height of the sender and receiver in this communication system) in Gamboa, Panama, in July 1983. A tape loop of a whine-plus-two-chucks call was broadcast over a system consisting of a Nagra III tape recorder, a Kudelski Paudex speaker-amplifier, and a speaker (7·5 cm diameter, Realistik, full-range, dynamic audio speaker). Calls were recorded on two channels of a stereo Sony TCD-5M tape recorder with metallic tape and two Sennheiser ME 80 microphones with KU-3 power modules. The frequency response of the recording system is flat (within 1 dB) for the frequency range of the frog calls. The microphones were placed at distances of 1 m and 11·6 m from the source.

The frequency response and the directionality of the speaker were determined. The output of the speaker varied $\pm 1·6$ dB over the range of frequencies contained in the *P. pustulosus* call, with the exception of the 3000-Hz signal ($\pm 3·0$ dB). The output of the speaker was symmetrical, and thus was measured at four positions around a hemisphere at 1 m from the speaker: $0°$ (directly in front of the speaker), $45°$, $90°$, $135°$ and $180°$. Relative to $0°$, the average output was $-5·8$ dB at $45°$, $-8·7$ dB at $90°$, $-11·4$ dB at $135°$, and $-18·7$ dB at $180°$. Directionality patterns are not known for *P. pustulosus*. Some anurans are omnidirectional sound sources, while others are directional (e.g. Gerhardt 1975).

Prior to recording the artificially-broadcast calls, the calls of three male *P. pustulosus* were recorded using the same recording system with the microphones in identical positions. The males were positioned in a triangle, each within 10 cm of his nearest neighbour. One male was facing the transmission line, one circa $180°$ from the transmission line and directly behind the previous male, and the third male was facing circa $45°$ from the transmission line. After the natural calls were recorded, the males were removed and the speaker was placed in the centre of the area from which the males were calling.

Calls were analysed on a Data 6000 digital waveform analyser. Calls recorded at the far distance were first filtered by a Krohn-Hite model 3100R filter with high pass at 400 Hz and low pass at 3500 Hz to reduce masking, especially by higher frequency insect calls. Amplitude was measured in volts. I determined the peak amplitude for each component recorded at 1 m and at 11·6 m. The amplitude of each component at the far distance relative to the amplitude at the close distance was computed in decibels for both the natural calls and the artificially-broadcast calls. The null hypothesis that the attenuation rate of each component did

not differ for natural and artificially-broadcast calls was tested by comparing the attenuation rates with a Mann–Whitney *U*-test.

Twenty-two artificially-broadcast calls and 31 natural calls were analysed. In all cases, the peak amplitude of the whine was greater than the peak amplitude of the chuck (Fig. 1), although the mean difference between peak amplitudes of the two components was greater for the broadcast calls than for the natural calls. For both natural calls and artificially-broadcast calls, the chuck component attenuated more than did the whine component: 7·8 dB for natural calls and 4·2 dB for broadcast calls. The difference in the amount of attenuation between natural and artificially-broadcast calls was remarkably small: 1·9 dB for the whine and 1·7 dB for the chuck. The differences in the amount of attenuation of the chuck for natural
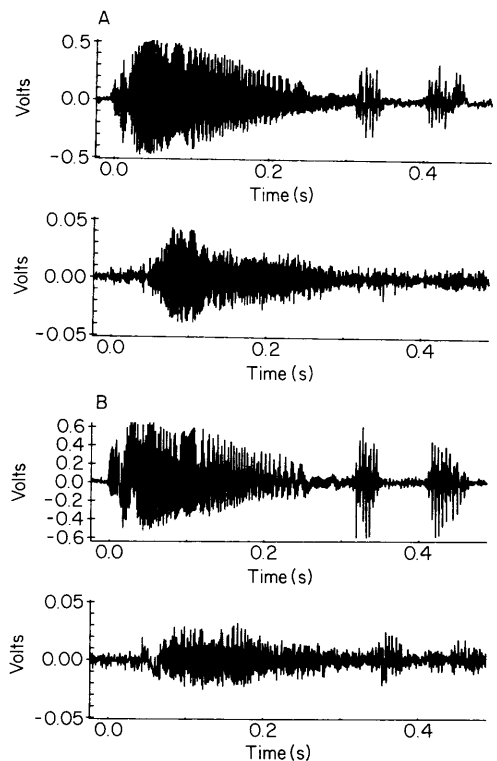

Figure 1. (A) An oscillogram of an artificially-broadcast mating call of *Physalaemus pustulosus* consisting of a whine and two chucks recorded at 1 m (top) and 11·6 m (bottom) from the speaker. (B) An oscillogram of a naturally-broadcast mating call of *Physalaemus pustulosus* consisting of a whine and two chucks recorded at 1 m (top) and 11·6 m (bottom) from the frog.

and artificially-broadcast calls were not statistically significant (Mann–Whitney U-test, $z = 1.09$, $P = 0.22$). Although the difference in the amount of attenuation of the whine for natural and artificially-broadcast calls is also relatively small, this difference is statistically significant ($z = 4.28$, $P < 0.0001$).

These measures of the relative attenuation of the whine and chuck are consistent with previous results. Ryan (1985) conducted similar experiments in three habitats: open grassland, a gravel pit with no vegetation, and dense forest. *P. pustulosus* commonly breed in the first two areas, but not in the forest. In all habitats and over several distances, the chuck attenuated at a greater rate than did the whine. The proximate explanation for this phenomenon is that the chuck has its energy concentrated in higher frequencies, while the whine has its energy concentrated in lower frequencies. This is consistent with a number of bioacoustic studies demonstrating relatively lower rates of attenuation for low frequencies (e.g. Brenowitz 1982), as well as with acoustic theory that makes the same prediction (reviewed by Wiley & Richards 1982).

These results suggest that, at least in this study, broadcasting the animal's signal gives qualitatively similar results to those obtained by measuring the attenuation of the signal actually produced by the animal. This technique is further supported by the fact that Ryan (1985) showed similar results in different habitats using a different broadcast system. This is the first demonstration of the validity of this technique for studies of environmental bioacoustics. However, this study also suggests caution in interpreting results of such studies. Although the results are qualitatively similar, they are not quantitatively the same in the comparison of the attenuation of the whine. The fact that there was no significant difference in the chuck, but there was in the whine, highlights the potential difficulties with such an experimental design. Of course, although the differences are significant statistically, they are so small that they might not be meaningful biologically. This study suggests that the technique of broadcasting an animal's signal through the environment for purposes of characterizing rates of attenuation might be fairly robust, although the cautions of Michelson (1978) should still be heeded.

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Infanticide of Nestling Noisy Miners, Communally Breeding Honeyeaters

Infanticide, once thought to be a rare phenomenon, occurs regularly throughout the animal kingdom, but its adaptiveness to individuals has been studied only recently (for a review, see Hausfater & Hrdy