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Wiley R H & Richards D G. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3:69-94, 1978. [Dept. Zoology, Univ. North Carolina, Chapel Hill, NC]

A review of the physics of sound transmission through the atmosphere suggested adaptations in animals' vocalizations to reduce the effects of frequency-dependent attenuation, refraction, amplitude fluctuations, and reverberation. [The *SCI*® indicates that this paper has been cited in more than 165 publications, making it the most-cited paper published in this journal.]

Evolutionary Adaptations for Communication

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This article had its beginning as an exercise in rumination. By 1976, I had selectively grazed through the field of physical acoustics, with an eye to relevance for acoustic communication in animals. That autumn, to aid in digesting the pickings, I dictated a summary.

The biological relevance of this physics had already attracted attention. As a graduate student in Peter Marler's group at Rockefeller University in the late 1960s, I noted the excitement over reports from a graduate student at Yale, Eugene S. Morton, who correlated measurements of frequency-dependent sound transmission through natural environments with the frequencies in birds' songs.[1] By 1976, Marler and his colleagues began their own investigations along these lines.[2,3]

My thinking had focused on reverberation and amplitude fluctuations as further sources of degradation in acoustic signals. A graduate student, Douglas G. Richards, joined me in applying ideas from signal detection theory to an investigation of adaptations in bird songs.[4] In 1976, however, there was no clear review of how the physics of sound propagation might influence the evolution of animals' vocalizations.

Within a month or so, a draft of my thoughts was thoroughly revised in discussions with Richards. We sent a copy to Marler, who, as I recall, thought it might be useful if published. Because the article entirely lacked new observations, we first submitted it to *Advances in the Study of Behavior,* which had a distinguished tradition of publishing reviews. The editors, however, quickly informed us that the paper did not include enough behavior! Indeed, the behavioral implications must have seemed a minor adjunct.

We next tried *Behavioral Ecology and Sociobiology (BES),* despite this new journal's explicit emphasis on experiments and observations. Our decision was probably influenced by a feeling that the relative immaturity of the journal at that time might tempt it to take some risks! The editor, Hubert Markl, replied, "Your manuscript...is recommended for publication in *B.E.S.* with only a few corrections. I enjoyed reading it, too. Nevertheless, as editor of the journal, I get some headache from it. *B.E.S.* is primarily...a data journal for original work. Your paper is, of course, mainly a review of the literature, and not very short for that. It is because I believe that many field-workers and experimentalists in bioacoustics need that type of introduction to the physical problems involved that I finally made up my mind to accept the ms." If *BES* had rejected this manuscript, would we have pursued the matter? Possibly not.

The subsequent popularity of this article perhaps indicates that it served as one of those citations useful for establishing authors' credentials with reviewers. We owe its publication to the somewhat agonizing flexibility of the editor of a fledgling journal.

The relevance of adaptations in the structure of animals' vocalizations goes back to the early days of ethology. Konrad Lorenz had argued that displays used for communication with conspecifics evolved in arbitrary ways, constrained only by mutual evolution of signaler and receiver, rather than by adaptations to the environment.[5] We now know that at least some features of communicatory signals are better explained by adaptation than by phylogeny.[6]

This application of physics to biology also has a deeper significance. The degradation of signals during transmission suggests that animal communication is often noisy and hence error prone. This situation in turn has fascinating implications for the evolution of strategies for signaling and receiving.[7]

1. **Morton E S.** Ecological sources of selection on avian sounds. *Amer. Naturalist* 109:17-34, 1975. (Cited 180 times.)
2. **Marten K & Marler P.** Sound transmission and its significance for animal vocalization. I. Temperate habitats. *Behav. Ecol. Sociobiol.* 2:271-90, 1977. (Cited 120 times.)
3. **Waser P M & Waser M S.** Experimental studies of primate vocalization: specializations for long distance propagation. *Z. Tierpsychol.* 43:239-63, 1977.
4. **Wiley R H & Richards D G.** Adaptations for acoustic communication in birds: sound transmission and signal detection. (Kroodsma D E & Miller E H, eds.) *Acoustic communication in birds.* New York: Academic Press, 1982. Vol. 1. p. 131-81.
5. **Lorenz K.** Vergleichende Bewegungsstudien an Anatiden (Comparative movement-studies on ducks). *J. Ornithologie* 89(Supp.3):194-293. 1941. (Cited 95 times since 1945.)
6. **Wiley R H.** Associations of song properties with habitats for territorial oscine birds of eastern North America. *Amer. Naturalist* 138:973-93, 1991.
7. ---------. Errors. exaggeration and deception in animal communication. (Real L, ed.) *Behavioral mechanisms in ecology.* Chicago, IL: University of Chicago Press. (In press.) Received October 6, 1992