

This Week's Citation Classic®

CC/NUMBER 11
MARCH 17, 1986

Marler P. Specific distinctiveness in the communication signals of birds.

Behaviour 11:13-39, 1957.

[Madingley Ornithological Field Station, Department of Zoology, University of Cambridge, England]

Bird vocalizations provide primary illustrations of many adaptive relationships between signal structure and function, especially in facilitating or hindering localization of the signal source. [The SC¹® indicates that this paper has been cited in over 115 publications.]

Peter Marler
The Rockefeller University
Field Research Center
Millbrook, NY 12545

January 27, 1986

Research on the communication signals of birds led me to conclude that, contrary to the view then extant, signal structure is by no means arbitrary. The physical properties of signals reflect not only the properties of the sense organs and brain mechanisms that receive and process them but also such factors as the transmission characteristics of different habitats, placement of the signaler in the environment, presence of other species competing for signal space, and adaptations for facilitating or hindering localization of the signal source. My primary focus was on vocalizations, the objective analysis of which had just been opened up by a new technique. The Bell Telephone Laboratories' sound spectrograph, developed for speech analysis, proved ideal for investigating the acoustic structure of animal sounds. William Thorpe, in the Department of Zoology at the University of Cambridge, was the first biologist to acquire one in England. He invited me to join him—first as a student and later as a research fellow of Jesus College, Cambridge—to explore its potential for analyzing bird sounds.

I was currently in thrall to the new ethology of Lorenz and Tinbergen, both enthusias-

tic exponents of the phylogenetic interpretation of species differences in behavior. Lorenz felt that the arbitrariness of animal signals rendered them especially reliable as cues to phylogeny and relatively free of the complications of evolutionary convergence.

My first clue that this might not be so came from a study of alarm calls. I discovered that several birds had independently evolved almost identical signals for use in extreme danger. During field work on an ethogram of the chaffinch, while under the tutelage of Robert Hinde, I found that this "hawk alarm call" has a curious ventriloquial quality. Sound spectrographic analyses revealed that these birds had, in fact, converged on a sound pattern that minimized the cues available for localization, disseminating alarm while reducing the risk of attracting attention. It then became obvious that many other signals are adapted to maximize localization cues, especially calls used in predator "mobbing." Most of the citations refer to this insight into the design of alarm calls, which has proved to be widely applicable to both birds and mammals.^{1,2}

The basic principles were laid out in more detail a couple of years earlier in a paper that, at the urging of J.B.S. Haldane, I published in *Nature*.³ It was reprinted a year later in a translation by the German ornithologist, Erwin Stresemann. Some details of my argument proved erroneous: for example, the high frequency of the "hawk alarm call"—a shrill, thin whistle—is probably designed for rapid attenuation with distance, to limit detection range rather than to minimize use of binaural phase differences in localization. In general, the line of reasoning has held up surprisingly well, however,^{4,5} bearing in mind that, 30 years ago, virtually nothing was known of the remarkable physiological specializations of avian predators for sound localization.^{6,7} It is still quoted as an illustration of how pervasive the relationship can be between animal signal structure and function.

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4. Konishi M. Locatable and nonlocatable acoustic signals for barn owls. *Amer. Naturalist* 107:775-85, 1973.
5. Klump G M & Shalter M D. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. *Z. Tierpsychol.—J. Comp. Ethol.* 66:189-226, 1984.
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7. Knudsen E I. Experience alters the spatial tuning of auditory units in the optic tectum during a sensitive period in the barn owl. *J. Neuroscience* 5:3094-109, 1985.