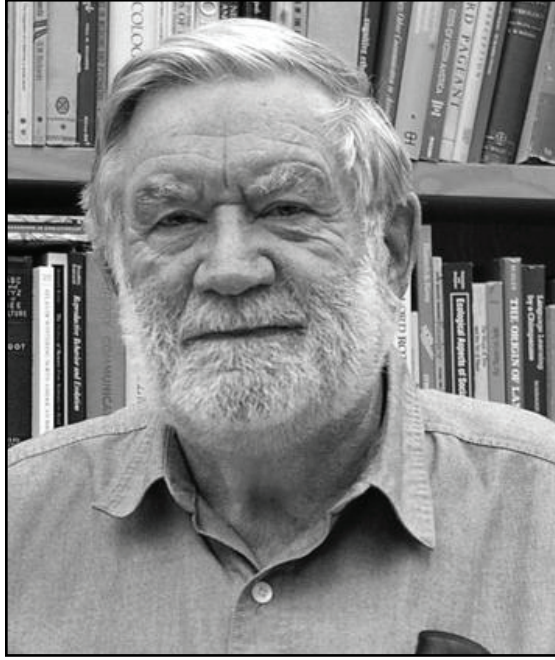


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PETER MARLER



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PETER MARLER died on 5 July 2014. He pioneered the study of animal communication, which until his involvement had been rather anecdotal. He set up a logical framework that looked at all aspects of the signals used (i.e., their physical structure, who produced them, in what context, and what responses they elicited). Answers to all of these questions then helped researchers infer what information the signals conveyed as well as the intention, or at any rate the benefit to the signaler. In the case of a male songbird singing in the spring, the message was species identity, individual identity, breeding condition, and marital status (e.g., single, shall welcome a mate). To other males, it stated, “This is my territory and I shall defend it.” In this manner, the same message could mean different things to different listeners.

Marler came upon this area of interest while working on his first Ph.D. (University College, London, 1952), which involved vegetation surveys of potential nature reserves in Britain, France, and the Azores. In his spare time, he collected recordings of chaffinch song from the same localities. It was while doing this work that he realized the variability in chaffinch song was not random. For example, the song of chaffinches in the Azores was simpler than that in Britain or France. He speculated that in simpler island avifaunas, species identity could be achieved with a simpler song. He also was struck, while doing field work in Scotland, by how chaffinch song changed as he traveled between adjacent valleys: each had its own dialect. These observations and others formed the body of his second Ph.D., in zoology, from the University of Cambridge (1954), under the tutelage of William Homan Thorpe and Robert Hinde. Memorably, this work also included the observation that chaffinches used different alarm calls to signal different kinds of danger. For example, an overhead hawk triggered a thin, sustained, high-pitched whistle that was very hard to locate; and a perched owl or a fox elicited sharp, broad-frequency, staccato calls that were easy to locate and thus helped recruit others to mob the enemy. Here Marler was making two points: (1) the physical structure of the signal was not arbitrary and (2) the signal itself could have a semantic value—it was not just an expression of emotion. Such findings were new.

Even as Marler pursued these studies in the field, Thorpe was working on his classic study of song learning in the chaffinch. In that study, Thorpe made several important discoveries:

- (1) Vocal ontogeny in the chaffinch followed predictable developmental stages, which he called *subsong*, *plastic song*, and *full song*. Subsong, he noted, was akin to babbling in infants (i.e., soft, variable, and rambling) and was produced even while a young bird was by

itself, often with its eyes closed, as if dozing. This observation struck a parallel between vocal ontogeny in songbirds and humans.

(2) Chaffinches made no attempt at imitating the song of other species, but readily imitated the song of wild chaffinches played over a speaker. From this finding, Thorpe inferred that juvenile chaffinches were selective learners.

(3) Exposure to a model, followed by imitation, occurred only during a sensitive period before sexual maturity.

Marler elaborated all of these concepts in studies using a diversity of songbirds, thus proving their generality. He subsumed these “innate predispositions” into what he called an “instinct to learn.” I remember his dictum: “If development depends importantly on learning, it is highly unlikely that the when, what, and how will be left to chance.” In this manner, song learning in birds yielded to Marler an important philosophical insight. He also showed that some songbirds learned a diversity of songs from models they heard but eventually sung only one of them, the one that most closely matched the song of a neighbor. To this day, we do not know why territorial birds like to counter-sing in kind, but it is thought that doing so indicates a high level of aggression and alertness and thus best protects territorial boundaries. It is as if each neighbor were calling the other by name, and then the latter reciprocates.

There were issues with Thorpe’s work as to whether the preferences of juveniles for the song of their own species were innate or reflected exposure to wild models before the nestlings were brought into the laboratory for hand-rearing. Marler met this challenge by collecting eggs, incubating them under canaries, and then hand-rearing the babies away from any exposure to unwanted models. The task of finding eggs and nestlings involved many in his laboratory, students and assistants alike. When it came to hand-rearing, this was the domain of Judith Marler, who, in addition to three of her own—Christopher, Catherine, and Marianne—would every spring look after dozens of nestlings.

Marler was, of course, interested in what birds and other animals might teach us about the evolution of human language, and as part of this interest, he spent time in Uganda and Tanzania studying the vocal repertoires and social behavior of Colobus monkeys and chimpanzees, respectively. The chimpanzee work was done in collaboration with the Grande Dame of chimpanzee studies, Jane Goodall. They recorded a thorough list of the sounds produced and their social contexts. To Marler’s disappointment, this communication system was rich and versatile, but he did not find there obvious precedents to the vocal skills of humans. One of his students, Tom Struhsaker, made more promising observations in African vervet monkeys. Vervets, he showed, had three different kinds of signals

to sound the alarm for hawks, mammals, or snakes. For each of these potential predators, the calls produced were different and so was the response—again, as in chaffinches, an instance of naming. Dorothy Cheney and Robert Seyfarth, two post-doctoral students working with Marler, then showed that playbacks of these signals elicited different and appropriate responses in free-ranging vervets.

Marler was the product of the ethological movement that became strong among European zoologists starting in the 1930s and was defined particularly by the work of Niko Tinbergen, Konrad Lorenz, and Otto von Frisch. These three had been interested in various signals used in aggression, courtship, and, in the case of bees, the waggle dance that indicated the direction and distance to a food source. Marler focused on vocal signals and, in particular, on vocal learning. The phenomena that Thorpe and Marler described so well in birds created a robust field on the basic biology of vocal learning over which Marler presided for many years. In time, his work spawned anatomical, physiological, cellular, and molecular studies on the basic biology of vocal learning. These studies were spearheaded by Marler's students.

Marler was a man of great charm, voracious curiosity and intellect, and very clear thinking. Students were drawn to him as if by a magnetic force. I was one of his early students at the University of California at Berkeley, along with Masakazu Konishi, Dietsy Neil, Keith Nelson, George Hersch, John Eisenberg, Ingrid Waldron, Tom Struhsaker, and many others. Peter, as we all called him, encouraged us to follow our own interests. Each of us, first at Berkeley, then at Rockefeller and UC Davis, chose our species and topic—flies, songbirds, tarantulas, electric fish, orangutans, macaques, whales, gerbils—and Peter would give us encouragement and advice, which included elegant and efficient editing of whatever we wrote. All doctoral work was published under the sole name of the student author. This policy was an example that Peter set for each of us. In addition, Peter was very hospitable. Evening seminars during the Berkeley years were at his house, and Judith and he would throw parties for visiting scientists to which we were all invited. Perhaps it is no wonder that after all of these years later, I still feel Peter's influence as depicted in the ceiling of the Sistine Chapel, where the hand of God touches that of a human and by doing so makes that human special. Peter had that effect on us, and we wore it as a badge of honor—we were members of Peter's clan. We knew there was a tradition that we would have to uphold—of excellence, integrity, generosity, and relentless curiosity. Truth was what we sought, not what we had found. Observations suggested explanations, but we never, ever, slid into the pit of dogma.

It is now 88 years after Peter Marler was born. The study of biology has become very molecular, and the Zeitgeist is all about reductionism. Marler was still a philosopher of nature, the kind of person who realizes that the questions asked can be more important than the answers. Answers come and go, but the questions remain.

Peter loved life and science, but above all, he loved his wife, Judith. Peter was the professional, but Judith matched every bit of professional expertise with an equal amount of common sense, humor, and grace. The two worked off each other like music, and we, the students, could hear it play. Those were the days.

Elected 1983

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