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IN MEMORIAM

Peter R. Marler, 1928–2014

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Peter Marler, a "maestro" of ethology, arrived in the United States from the United Kingdom in 1957 to take a faculty position at the University of California, Berkeley. Over nearly 50 years, his presence in the United States had a major impact on the study of communication in birds and in nonhuman primates. He single-handedly fostered a tremendous growth in the field of vocal learning and development in songbirds. His prodigious efforts, and those of his students, spawned a new subdiscipline of ethology—the neurobiology of birdsong learning, perception, and production—that continues to thrive today.

Peter Robert Marler was born in Slough, near London, on February 24, 1928, to Robert and Gertrude Marler, and died in Davis, California, on July 5, 2014, at the age of 86. Starting as a young boy in England, he was a keen naturalist with a strong interest in birds. He rescued local birds that had run into trouble and even kept a pet Rook, foreshadowing his long career of hand rearing birds for experimental purposes. He earned a B.Sc. (1948) and a Ph.D. in botany (1962) from University College, London. While collecting mud samples in the Lake District of England during his Ph.D. research and a subsequent job at the Nature Conservancy surveying possible nature reserves, he noticed that the songs of Chaffinches changed systematically with location across England. This observation fascinated him, and he decided he wanted to focus on animal vocalizations, especially in birds. That decision prompted him to join the group of Professor William Thorpe, who had recently set up the Madingley field station in Cambridge. There he joined Robert Hinde, who had recently completed his D.Phil. at Oxford under David Lack. Because of the peculiarity of the Oxford–Cambridge culture not recognizing Ph.D.'s from other institutions, Marler decided to undertake a second doctorate in zoology at Cambridge, completing it in 1954. While there, he published a seminal paper describing the phenomena of call convergence among songbird species in the structure of mobbing calls and a different structural convergence in their alarm calls that he observed in a variety of songbird species (*Nature*, 1955). His thesis on Chaffinches included a comprehensive documentation of their behavior, including thorough descriptions of their vocal repertoire. Also while at Cambridge, he became fascinated with the field of vocal development, based on his interactions with Thorpe.

Peter Marler at the International Meeting of the Society for Behavioral Endocrinology in Lisbon, Portugal, in 2004. Photo credit: courtesy of Greg Ball

Marler left Madingley and the UK in 1957 to accept a professorship at the University of California, Berkeley. There he began a series of very influential studies on the White-crowned Sparrow, documenting their dialects in the San Francisco Bay area (Marler and Tamura, *Science*, 1964). He also initiated experimental studies with hand-reared sparrows that showed that the geographic variation in song that he had observed in the wild was a learned behavior. His studies of hand-reared sparrows clearly demonstrated that normal song development required that the sparrows be exposed to conspecific song prior to reaching sexual maturity (*Journal of Comparative and Physiological Psychology*, 1970). Although Marler was a

naturalist at heart and sensitive to the importance of understanding the full complement of animal behavior as it occurs in nature, he also had the strong mechanistic orientation toward understanding causes of behavior championed by pioneering ethologists such as Niko Tinbergen. This orientation was apparent in the highly influential textbook he authored with William Hamilton, *Mechanisms of Animal Behavior* (Wiley, 1966).

This mechanistic orientation was also apparent in the thesis projects of some of his students at Berkeley. For example, Masakazu (Mark) Konishi arrived at Berkeley from Japan to work on a Ph.D. with Alden Miller. Unbeknownst to Konishi, Miller was away in South America, but Marler had just arrived at Berkeley and Konishi knew his reputation based on the 1955 *Nature* paper. Konishi therefore worked with Marler and completed a thesis on the critical role of auditory feedback in vocal development in White-crowned Sparrows and other songbird species. Fernando Nottebohm joined Marler's lab as a Ph.D. student when Konishi was close to finishing his dissertation, and he took on the question of proprioceptive feedback and its role in vocal development. He discovered by careful nerve cuts that in certain songbird species, such as canaries, there is a left-side dominance in the role played by the tracheosyringeal nerves in regulating syringeal function. This immediately suggested analogies between the regulation of song development in birds and the control of human language. The path-breaking work of both of these Marler students at Berkeley laid the foundation for the discovery of the avian song control system by Nottebohm in the 1970s and the remarkable development of the field of birdsong neurobiology.

Like many ethologists, Marler became curious about how generalizable his work might be to primates and humans. This led to a stint in Africa, where he studied colobus monkeys in East Africa as well as chimpanzees at Gombe. Though he failed to find evidence for dialects and vocal learning of the sort he had observed in songbirds, he did complete novel analyses on the acoustic structure of primate calls and how they might be perceived. At this point in his career, he had moved to Rockefeller University in New York, where Detlev Bronck, the president of Rockefeller, had decided to expand the intellectual scope of the university by making a major investment in the study of behavior, a novel approach for a university so tied to biomedical research. Peter joined Donald Griffin, who had moved from Harvard, in setting up lab groups dedicated to the study of ethology who were well aware of the cognitive complexity of animals but were also committed to a highly mechanistic approach. At Rockefeller he initiated a major research program on vocal development in songbirds by comparing learning processes in two congeneric sparrow species common in New York State, Song Sparrows and Swamp Sparrows. This work was conducted at the Rockefeller Field Research Station in Millbrook, New York. Marler was joined there by Fernando Nottebohm, who also maintained a research program at the Rockefeller campus in New York City.

At Millbrook, Marler sponsored many doctoral and postdoctoral students investigating mechanistic and functional aspects of avian vocal learning and perception, and whether these emerging biological principles might extend to primates and human speech. Over the years at Rockefeller, such noted avian behavioral biologists as William Searcy, Donald Kroodsma, Ken Yasukawa, Steven Nowicki, and Douglas Nelson conducted fieldwork and lab work on songbirds as part of Marler's group. Marler consistently reached beyond his own immediate focus to attract students and postdocs to his research group from related fields, including Peter Tyack and Christopher Clark, who worked in marine mammal acoustic communication, and Robert Dooling, a hearing scientist with a psychophysical approach to the perceptual side of birdsong. Always, there was an eye toward the broader implications of the birdsong work for primate and human acoustic communication, especially with the fieldwork showing semantic communication in vervet moneys by Thomas Strushaker, Robert Seyfarth, and Dorothy Cheney. Other primatologists of note were Steven Greene, John Mitani, and Harold and Sally Gouzoules.

Marler's commitment to integrating mechanistic and functional approaches attracted John Wingfield to the Field Center, and John's group included postdoctoral fellows such as Marilyn Ramenofsky, Robert Hegner, Alfred Dufty, Jr., and Gregory F. Ball. This group documented how environmental stimuli affected hormone concentrations in wild songbird populations, and produced collaborative studies with Marler on the hormonal basis of song learning in sparrows and European Starlings.

Marler left Rockefeller and moved to the University of California, Davis, in 1989, where he completed additional studies on song development and function before retiring in 1994. In retirement he continued to actively promote the field of birdsong study, editing key integrative books such as *Neuroscience of Birdsong* with H. P. Zeigler (Cambridge University Press, 2008) and *Nature's Music* with Hans Slabbekoorn (Elsevier, 2004).

Marler received numerous accolades for his scientific achievements, including being elected an Elective Member of the American Ornithologists' Union in 1961 and a Fellow in 1974. He was also a Fellow of the Animal Behavior Society, of which he was a founding member and former president, and received its Distinguished Animal Behaviorist Award in 1992. In 2009 he received the Lloyd and Alden Miller Research Award from the Cooper Ornithological Society for his lifetime of scientific achievement. He was also elected to the U.S. National

Academy of Sciences and, in 2008, was elected a Foreign Member of the Royal Society of London, a rare combination of achievements for someone who started as a field biologist. His nomination for the latter honor begins, "Peter Marler is an extraordinarily distinguished behavioural biologist. He and his many graduate students, post-doctoral workers, and colleagues have played a central role in elucidating mechanisms of development of behaviour and brain."

Peter married Judith Gallen, also from Slough, in Edinburgh on September 1, 1954. Their nearly 60-year union produced three children, Christopher, Catherine, and Marianne. Judith, the three children, and two grandchildren, Carson Drury and Kelsie Drury, survive.

We both were members of Marler's laboratory at Millbrook, although we did not overlap temporally. We have great appreciation for Peter's intellectual generosity, his deep commitment to and curiosity about understanding birdsong from all angles, and his remarkable wisdom in mentoring a generation of scientists. His gentle, disarming manner at seminars was undergirded by an extraordinarily deep understanding of critical questions. There is no dimension of this field, whether it be adaptive significance, evolution, mechanism, or development, that he did not touch. His scientific legacy will last for generations; we owe him so much, and we miss him greatly.

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