OBITUARIES

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Robert R. Capranica (1931–2012) and the Science of Anuran Communication

Field herpetologists—and field biologists generally—have been entertained, soothed, and sometimes even seduced by the nocturnal serenades of frogs and toads. A harbinger of spring in the temperate zone and of the rainy season in the tropics, those who have not experienced a frog chorus have missed out on one of Nature's great spectacles.

Aristophanes, the comic playright of ancient Athens, was the first to describe a frog's mating call in written form (in 405 BCE). It wasn't until 1905, however, that Robert M. Yerkes, then a psychologist at Harvard University, showed conclusively that frogs could actually hear the calls! Two Cornell University ornithologists, Arthur A. Allen and Peter Paul Kellogg, made the first sound recordings of frog calls (on the optical sound track of movie film in 1935). The original use of "sonagraphs" (sound spectrograms) to visualize frog calls was by W. Frank Blair of the University of Texas at Austin (1954), and Bernard S. Martof, then at the University of Georgia, was the first to conduct playback experiments with tape-recorded calls (1958). During this same period, Charles M. Bogert, of the American Museum of Natural History, provided a functional classification of frog vocalizations and addressed many issues about the biological significance of frog calls including their role as isolating mechanisms in reproduction.

It could be attested, however, that the subject of anuran communication did not truly become a rigorous experimental science until the research performed by a young electrical engineer–turned-neuroscientist was initiated in the early 1960s. Robert R. Capranica, one of the founders of neuroethology (a branch of biology that seeks to understand the neural basis of natural animal behaviors), began his research career in the Department of Sensory and Perceptual Processes at Bell Telephone Laboratories in Murray Hill, New Jersey, and then, in 1969, moved to the Department of Neurobiology and Behavior at Cornell University in central New York State. It was Capranica who pioneered the use of quantitative behavioral analyses to determine key features in a frog's complex vocal signal and later combined these studies with electrophysiological analyses of the frog's auditory system, thus firmly establishing the connection between brain and behavior. He set the stage for numerous investigations that linked hearing and decoding mechanisms in frogs with both their ecological setting and their evolutionary diversification. Capranica forever changed the standards for bioacoustics research, and he trained and inspired several generations of biologists and engineers to study animal communication from this same broad biological perspective. In doing so he made frog communication one of the best-studied phenomena in biological science.

Robert Rudy Capranica, who died last year a few weeks shy of his 81st birthday, was born in Los Angeles, California, on 29 May 1931, and raised in southern California. His formal education was entirely in electrical engineering (University of California at Berkeley, B.S. 1958; New York University, M.S. 1960; Massachusetts Institute of Technology, Sc.D. 1964). Since 1958 he had been working at the famed Bell labs where they had supported his research on the auditory system of frogs, which formed the basis

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for his doctoral dissertation. What he produced has been referred to as ". . . arguably the most elegant dissertation research ever completed in animal bioacoustics." This was published as a book by MIT Press in 1965—entitled "The Evoked Vocal Response of the Bullfrog [*Lithobates catesbeianus*]. A Study of Communication by Sound"—and is now a classic in the field. In it he pioneered the use of synthetic calls for playback experiments, showed that the mating call of the bullfrog was species-specific, and systematically demonstrated that the two principal components of the bullfrog's mating call (its high- and low-frequency energy bands) must be present simultaneously to evoke a vocal response from an isolated male. It was a first attempt to answer the query, "What does the frog's ear tell the frog's brain?" and he spent the rest of his career attempting to answer this fundamental question.

Although Capranica devoted much of his time studying the function of calls of various species in the field and the lab, his ultimate goal was to understand how acoustic signals are processed. Prior to his work, it was thought that the decoding of sensory information was done solely in the brain and that the ear was simply a passive conduit for information. He demonstrated that much of the signal processing was, in fact, done within the inner ear organs themselves, an example of what is called "peripheral processing." Capranica and his colleagues also followed this message to the brain and determined how information is processed through a series of brain nuclei, culminating in a "mating call detector" in the frog's midbrain.

After arriving at Cornell, Capranica the engineer also became an accomplished field naturalist. His first overseas field trip was to Puerto Rico in 1973, together with his wife (Patricia), a new postdoc from Murray Littlejohn's lab in Australia (Jasper Loftus-Hills), and one of his first graduate students (Peter Narins). He was involved in all aspects of the field work, experimental design, and testing. Narins was searching for an appropriate species to study for his dissertation research and thought that the ubiquitous and abundant Puerto Rican Coqui (*Eleutherodactylus coqui*) would be a likely candidate. He wanted a frog that produced a call with a sequence of simple notes to replicate in the time domain what Capranica had studied with bullfrogs in the frequency domain, in order to determine if the normal note sequence was required for a natural behavior. The coqui frog seemed to be ideal because males produce a two-note call ("co-qui"); each note is spectrally simple and easily synthesized (a Cornell graduate student, Bruce Land, built the first portable "co-qui" synthesizer in 1972); and this species is large enough to permit electrophysiological recordings from its auditory system.

On this first trip to Puerto Rico, a series of acoustic playback experiments with male coquis revealed that the natural (actually, a synthetic version of the natural) two-note call evoked a characteristic one-note ("co" only) response from males in the field nearly half the time it was played. Moreover, both the sequence-reversed call ("qui-co") and the single note ("co") were equally effective at evoking the one-note response, but the "qui" note alone was almost completely ineffective. Capranica's enthusiasm for these field experiments was infectious and inspiring to everyone around him.

Capranica financially supported field studies by his own students and postdocs, and also by those working in other Cornell labs. Loftus-Hills was not directly involved in these Puerto Rican experiments, but on this same trip he discovered a spectacular new species of coqui calling from water-filled bromeliads 10 m above the ground, on the basis of its previously unrecognized call. After his untimely death in 1974, the frog was named for him by George Drewry and Kirkland Jones in *Journal of Herpetology* (1976). This species—the Golden Coqui (*Eleutherodactylus jasperi*)—was the first and is still the only ovoviviparous frog known from the Western Hemisphere. Narins returned to Puerto Rico in 1974 to continue his field studies, accompanied by a fellow graduate student in another lab, Kent Wells, who was thus introduced to Neotropical frogs and their behavioral ecology.

Many in his own field of neuroethology were unaware of Capranica's influence on studies of animal speciation. Species-recognition studies in frogs offered important proof that behavioral isolation could drive speciation. Blair, Littlejohn, and Carl Gerhardt, Capranica's first postdoc, all made seminal contributions to this field by showing how the mating call and its recognition resulted in species-specific mating preferences by females. All of these results were consistent with Capranica's studies of how the auditory system, inner ear, and brain bias the perception of females to find calls of their own species more attractive.

Capranica also teamed up with the noted Israeli biologist, Eviatar Nevo, to extend the concept of species recognition to that of dialect recognition. Combining ecological surveys of the calls of cricket frogs (*Acris*) throughout much of the United States with detailed studies of auditory neurophysiology, Capranica and his colleagues showed how variation in calls and the neural mechanisms that decode them can co-vary from one population to the next even within one species. Although he was trained as an electrical engineer and practiced as a neuroethologist, he knew how important sexual communication was to evolutionary biology. As such, even the evolutionary biologists who spent time at his bench, such as Michael Ryan, were made to feel welcome.

Capranica's lab at Cornell was home to an interdisciplinary hive of graduate and postdoctoral students drawn from engineering, psychology, neuroscience, and animal behavior. They studied communication and the evolution of sound processing in a diverse array of anuran taxa including *Ascaphus* and *Xenopus* and in representatives of many families of advanced frogs. They also studied the lateral-line sensory organs in *Xenopus*. Among the young scientists he mentored were his own graduate students (including Karen Mudry Avil, Christine Boake, Deana Bodnar, Eliot Brenowitz, Martha Constantine-Paton, Frank Dodd [his only student who worked with reptiles—on the vocalizations of geckos], Albert Feng, Peter Narins, John Paton, Gary Rose, David Yager, and Harold Zakon), his postdocs (Carl Gerhardt, Jasper Loftus-Hills, Michael Murray, Andrea Megela Simmons, Walter Wilczynski, and Nigel Woolf), and rotational students from other labs (Stephen Nowicki and Michael Ryan).

In the lab, Capranica worked closely with his long-time technician, Anne Moffat, and together they carried out long electrophysiological experiments in which they would record from single fibers in the auditory systems of frogs. Their studies were usually done on Fridays, a day that was held sacred and thus unavailable for student lab research, but the students would often hang around the lab on those days simply to watch the master at work. The experiments would begin in the morning when the animals were anesthetized, the surgery was done, and the frogs were then placed in the soundproof chamber and the electrode was poised to enter the auditory nerve. The recordings were done in the afternoon but often extended beyond dinner and into the late hours of the evening.

Capranica also served his discipline as a highly dedicated associate editor for section A (sensory, neural, and behavioral physiology) of the *Journal of Comparative Physiology* (1974–1986) and thereby helped to raise its standards to become the leading journal for neuroethology. In attracting manuscripts from around the world, he would often re-write entire papers into proper English in order to help make neuroethology a more international discipline. In the early 1980s, together with a small group of Europeans and Americans, he founded the International Society for Neuroethology, which now awards the Capranica Prize each year for the best paper published in the field of neuroethology. His well-known sense of humor and infectious laughter made him a popular teacher, lecturer, and friend.

Only on one occasion did Capranica attend a herpetological meeting. At the SSAR meeting in 1976, held at Miami University in Ohio, he participated in a symposium, entitled "Reproductive Biology of Amphibians" (published the next year under the editorship of Douglas Taylor and Sheldon Guttman). After listening to a speaker remark how he tested the toxicity of skin secretions of frogs—by requiring his entire class of students to lick them—Capranica exclaimed, "You herpetologists really are crazy." One might infer from this comment that he did not consider himself to be a card-carrying herpetologist, but his research nevertheless is counted among the most important bodies of work ever conducted with amphibians.

Capranica's major research accomplishments include: 1) multiple studies showing that the auditory systems of different species of frogs have different spectral sensitivities; 2) the discovery of acoustic dialects in frogs and the existence of distinct call types in allopatric populations; 3) the introduction of the concept of the "matched filter" to provide an underlying basis for the co-evolution of sender and receiver; and 4) studies on the remarkable temporal sensitivity found in the cells of the anuran central nervous system that are often closely matched to advertisement call features. Together with his Cornell colleague, Watt Webb, an engineering physicist, he applied the then-novel technique of laser Doppler vibrometry to measure the nano-scale vibrations in the eardrums of frogs and other animals. LDV is now a standard technique in the auditory mechanics community.

Robert Capranica died on 11 May 2012 in Tucson, Arizona, where he had retired in 1993. He is survived by his wife, Patricia Alna Capranica (née Mullen).