Ronald Maxwell Savage, 1900–1985: a tribute

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ne of the less endearing aspects of science is that, excepting the authors of major discoveries, enterprising researchers who make groundbreaking contributions can all too often be forgotten in the light of newer studies. In the worst cases, papers appear years or decades later that virtually reinvent wheels in apparent ignorance of what has gone before. This is as true of herpetology as any other science, and came home to me forcefully when re-reading a book that I first came across as an undergraduate in the 1960s. R. Maxwell Savage's "Ecology and Life History of the Common Frog Rana temporaria temporaria", published by Pitman in 1961, is testament to a remarkable pioneer of amphibian research in Britain. Savage carried out extensive fieldwork night after night around ponds in Hertfordshire during the 1930s, investigating very successfully (and without modern aids such as radiotracking) the migrations of frogs to their breeding sites and factors influencing their spawning times. He also spent hours watching frog behaviour in specially designed tanks, so he could observe pairs from underneath while eggs were laid. Survival and growth rates of tadpoles were compared among ponds, and, remarkably, he initiated and collaborated in biochemical work on the protective jelly around the egg capsules. Savage was an interdisciplinary biologist long before it became fashionable. Yet, despite all this, I could find no obituary and nothing about him on the worldwide web. So who was this man?

Born in 1900, the youngest of three children, Ronald Maxwell Savage went up to Queens College Cambridge in 1918 and graduated with a BA in Natural Sciences in 1921. This was converted to an MA by proxy in 1944. Most of his important work on frog ecology was carried out during the 1930s and published in a series of papers, mainly in the Proceedings of the Zoological Society of London (predecessor of the current Journal of Zoology). Some of this work, on tadpoles, was accepted as a PhD submission by Birkbeck College, University of London, in 1950–1951. The main hypothesis emerging from his research, the possibility that frogs migrate to ponds by following the smell of algae that emanates from them, continued to occupy him in his later years. His central idea was that frogs respond to algae because tadpoles use it as their main food source. The evidence for this from the field was largely circumstantial, and with common frogs he never demonstrated an unequivocal link – perhaps not surprising considering the various technical difficulties of experimenting with Rana temporaria. He did, however, provide some convincing correlations of spawning times with environmental variables in the preceding weeks (temperature, rainfall etc), which have attracted interest again, decades on, in an era of climate change biology.

Savage's view was that the climatic factors were acting indirectly on the frogs by affecting the growth of algae. In later years, using laboratory experiments with Xenopus, he took this idea further and showed that these aquatic frogs could be induced to spawn in response to a particular volatile chemical (glycolic acid) released by algae into the water.

Of course things have moved on since Savage's day, and we now know that many amphibians rely on a variety of cues, not just smell, when migrating to their breeding ponds. Even so, it is disappointing to see how rarely Savage's impressive work is referenced in the recent scientific literature. He broke new ground, and there is nothing to suggest that in the specific case of the common frog his hypothesis is wrong or inadequate to explain much of migration and breeding behaviour in this species.

And what of the man himself? I'm grateful to his daughter Vivienne Kynaston and his two grandsons Roger and Matt for most of the following information, as well as a lot more that unfortunately there is insufficient space to include here. Ronald Savage spent all his working life as chief chemist for a small pharmaceutical company. It was his first job after he graduated from Cambridge in 1921, and he worked there until his retirement in 1965. It was here that he met Violetta. They married in 1931, and Vivienne was born in 1941.

During the war he stayed in London and volunteered as an ARP warden, but he ran the chemistry laboratory throughout, and in the 1950s worked closely with researchers at Oxford University who had developed a treatment for haemophilia based on derivatives from animal blood. He took a keen interest and pleasure in both



Photo: Violetta and Ronald Savage at Welwyn.

the medical and scientific aspects and in the humanitarian rewards of enabling people to live healthy lives.

Starting in the 1920s, and later with his family, he travelled extensively for holidays in Europe at a time when this was still rather unusual. A casual reference in his book to finding amphibians in France suggests that at least some of these trips had a fieldwork component. Vivienne recalls lovely memories of family expeditions in their Ford Prefect car to the local Hertfordshire ponds where he did his research.

Savage lived in north London, in Mill Hill and then Hadley Wood, throughout his working life, but on retirement he and Violetta moved to Welwyn where he died in 1985. His grandsons remark on how effectively he conveyed to them an interest in the natural sciences, as well as being fun to be with. Evidently he made a lasting impression on both of them, teaching them how to play chess and enjoy scientific experimentation. The affection in which they held him is very evident from their accounts to me

R.M. Savage was a Fellow of the Zoological Society and of the Royal Institute of Chemistry, and an early member of the British Herpetological Society (founded in 1947). Between 1955 and 1957 he edited the society's journal, then the British Journal of Herpetology, and in 1967 he was presented with the Stamford Raffles Award from the Zoological Society of London for contributions to zoology, presented by the Duke of Edinburgh. "Ecology and Life History of the Common Frog" is a seminal achievement, bringing all his earlier work together in one book as

a very readable monograph. The research is all the more remarkable because it was carried out in his own time, with no external funding - just his own energy and enthusiasm. Among other things, the book also hints at how dramatically frogs declined in the countryside between the 1930s/1940s, when he found ponds with thousands of spawn clumps, and the late 1950s, when only a few of his old study ponds had any spawn at all. Savage evidently became concerned about the future of amphibians in Britain, particularly the increasing numbers he saw killed on roads. Arnold Cooke, the only person I know who met him in his retirement home, recounted his pleasure that there was ongoing interest in his work. He was still experimenting with Xenopus in 1974, probably in the same garage laboratory where one of his grandsons recalled sleeping on a camp bed "under the whir of the aquariums where my dreams were soaked in croaks and plops". In the preface of his book, Savage makes a statement that surely resonates among herpetologists of all generations: "I have no recollection of a time when I was not interested in zoology in general and the Amphibia in particular". I wish I had taken the trouble to meet him myself.

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