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ANNOUNCEMENTS

NOTED BIOLOGIST BILL HAMILTON DIES

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Bill Hamilton, one of the most prominent and original evolutionary biologists since Darwin, died March 7 in London, England, following a six-week-long struggle with complications from an intestinal ulcer and from malaria contracted in the Congo region of Africa. He was 63.

Educated at Cambridge, where he studied genetics, Bill moved to London for his Ph.D., which he obtained from University College and the London School of Economics. His annotations to his papers in the first volume of his collected works, *Narrow Roads of Gene Land,* suggest that although he was convinced at an early age that the genetics and evolution of altruism was a worthwhile line of study, few shared his enthusiasm. While slightly daunted by this lack of support from a scientific community still recovering from the eugenics movement of the earlier part of the twentieth century, Bill nevertheless went on to develop the idea he is best known for, inclusive fitness or kin selection theory. The idea is deceptively simple: self-sacrificial behavior can evolve if it benefits relatives of the altruist, because they share the altruist's genes. This explanation forms much of the foundation of sociobiology and behavioral ecology, and it also helped establish the gene-centered approach that has proven so fruitful in modern evolutionary biology. The two papers explaining the genetic bookkeeping involved in such behavior are often cited, but regrettably rarely read. The reader who makes the effort finds not only an interesting theoretical journey but also an insight into Bill's gift for natural history, a gift that infused his theory and set his work apart from many more mathematically talented but less biologically intuitive scientists.

After receiving his doctorate, Bill took a position as Lecturer at Imperial College, where he was based at Silwood Park. In 1978 he became a Professor in the Museum of Zoology at the University of Michigan, and in 1984 moved back to England as a Royal Society Research Professor at Oxford, where he remained until his death. In addition to his work on altruism, Bill wrote about the evolution of animal groups in his aptly titled paper, ''Geometry for the Selfish Herd,'' about sex ratios, about aging and senescence, and about the origins and function of cooperation and fighting. He became intrigued with one of the greatest problems of evolution, the existence of sexual reproduction, and this led to an interest in parasites and their effects on host ecology, behavior, and evolution that lasted for the rest of his career. When I first met him, Bill spoke of being disturbed by redwoods. The trees themselves did not bother him; it was their vegetative reproduction combined with such a long life. Anything so likely to be out-evolved by its parasites should by rights have to reproduce sexually, he thought.

Most of the accolades of the scientific world came Bill's way; he received the Kyoto Prize; the Crafoord Prize, Sweden's Nobel equivalent for nonmedical biology; the Distinguished Animal Behaviorist Award from the Animal Behavior Society; the Sewall Wright Award; and many others. Many fields—evolutionary biology, animal behavior, genetics, entomology—claimed him as one of their own, testimony to the broad application of his ideas. Although pleased to receive the recognition that he had been denied early in his career, he generally accepted these awards sheepishly and was relieved to be taken into the field after the ceremony where he could see some new bird or plant or insect.

Although Bill had many extraordinary ideas in his life, many people failed to understand that his genius lay not in the quality of his ideas, but in their sheer abundance. It was often amusing watching others try desperately to find a kernel of brilliance in every thought he expressed, even though this was often not possible. My own explanation is simple. Say, for example, that the general frequency of brilliant ideas is one in ten, and that frequency is unchanged among individuals. The difference between Bill and most other people was that he had a total of over one hundred ideas, with the result that at least ten of them were brilliant, whereas the rest of us have only four or five ideas as long as we live, with the result that none of them are. Bill was not afraid of saying outrageous things, perhaps especially unsubstantiated outrageous things. Most of them were wrong, and some were even ridiculous, but the ones that were right were gems.

Bill was a very visual thinker, and he often suggested three-dimensional analogies for complex mathematical concepts. I am much more verbal in my own thought processes, and although I appreciated his efforts to clarify theory, they were rarely helpful. Linkage disequilibrium, the nonrandom association of genes in a population, was, he said, ''like water sloshing about in a bath,'' an explanation that only made sense to me after I had worked through the math and understood the concept anyway. When we were working on models of antagonistic coevolution between hosts and parasites, Bill constructed a toy to demonstrate the genetic interactions. It was a lovely and ingenious device, consisting of a flat block of wood, four long screws, eight metal nuts in two colors (one for the host and one for the parasite), two extra-large rubber bands, and two bicycle spokes. The only problem was that I hadn't the slightest idea of how to play with it, which somewhat defeated the intended purpose. Again, its illustrative role became clear well after I figured out the model.

Many of the anecdotes about him seem to turn into parables about what he tried to do in his life and why it was so important

that he do it. The last time I saw Bill, we went hiking in the Italian Alps with his companion Luisa and my husband. We walked for some time along one side of a river, and Bill was his usual expert self as we spotted birds and caterpillars and startled several chamois among the boulders.

I do not remember whether we eventually lost the trail on our side of the bank or whether Bill had simply decided that we needed to return on the other side for the novelty. Regardless, he was determined that we cross the river, and he was undeterred by the absence of a bridge and the depth and speed of the water. Amidst my loudly voiced skepticism, he enthusiastically set about constructing a bridge from fallen branches and bits of debris, which he laid across the water with much splashing and dislodging of soil. He was, after all, the son of an engineer. Finally the connection was arranged to his satisfaction and he prepared to cross. I was quite convinced it would not support us and kept pointing out that it wasn't important that we get to the other side in any event. He insisted, both Luisa and I protested, and in the end he dragged each of us bodily across. Of course the bridge held. Once Bill envisioned that he needed to get somewhere, he knew that all he had to do was keep at it and get everyone else to see that they could get there too.

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REMEMBRANCE OF GEORGE LEDYARD STEBBINS

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Ledyard Stebbins holding specimens of *Antennaria virginica* Stebb. near Salineville, Ohio, May 13, 1979.

George Ledyard Stebbins, Jr., died on January 19, 2000, at age 94. With his passing, botany lost the greatest plant evolutionist of the last century. His books, articles, and ideas have influenced generations of botantists. Most evolutionists considered Stebbins a central figure in plant evolution since the publication in 1950 of his classic *Variation and Evolution in Plants.* As one of Ledyard's last long-term collaborators, let me relate some of my experiences resulting from our twenty year association.

Ledyard was born on January 6, 1906, in Lawrence, New York. From an early age he was keenly interested in natural history. He entered Harvard University as an undergraduate in 1924 and continued at Harvard for his Ph.D. (1928–1931) on the cytology of *Antennaria.* This work followed on the early work on apomixis in European species of *Antennaria* carried out by H.O. Juel (1900). These years were turbulent not only because of the personalities involved in this thesis (M. L. Fernald and E. C. Jeffrey), but also because his father, a wealthy businessman, wanted him to become a lawyer or physician and did not approve of his studying botany. From 1931 to 1935 he held a position at Colgate University in upstate New York, working mainly on the cytogenetics of *Paeonia.* In 1935 he moved west to the University of California, Berkeley, to work with the eminent geneticist Ernest B. Babcock on the interactions between polyploidy and apomixis in *Crepis.* Ledyard remained at Berkeley until 1950 when he was asked to help establish the department of genetics at the University of California, Davis. He remained at Davis until his retirement in 1973.

I first encountered Ledyard's work as an undergraduate at Cornell University working on a cytogenetics project on *Quercus* under the direction of Charles Uhl. I read the 1947 article by Stebbins, Matzke, and Epling entitled, ''Hybridization in a population of *Quercus marilandica* and *Quercus illicifolia,*'' (Evolution 1:79–88) with great fascination and thought ''I want to conduct research like this.'' I began my M.Sc. with Daniel Crawford at Ohio State University in 1978 just as Ledyard came to Ohio State as a distinguished visiting professor. While looking for a suitable thesis project, Dan suggested that I visit Dr. Stebbins because he had a possible thesis project for me to consider. When I went to his office he was bending over some specimens of the genus *Antennaria.* He explained that sexually reproducing populations of *Antennaria* were dioecious, but that agamospermous populations were gynoecious, consisting entirely of pistillate plants. He had noticed that herbarium specimens of *Antennaria parlinii* from northern (glaciated) parts of Ohio seemed to lack staminate plants and that ones from the southern (unglaciated) part of Ohio usually had both staminate and pistillate plants, and he wondered whether there was a correlation between glaciation and amphimixis and agamospermy in this species. The next week we set out on our first field trip to take gender ratios in local populations. As we got into the elevator, he said, ''It has been fifty years since I have gone into the field to specifically study *Antennaria.*'' Ledyard and I developed a close friendship and went on numerous field trips during his year at Ohio State. I soon realized that *Antennaria,* which had been

neglected by systematists due to its seemingly incomprehensible morphological variation, was an ideal tool to study the evolution of polyploid agamic complexes.

Ledyard contributed a great deal to evolutionary biology, but perhaps his most significant contributions were in studies of natural hybridization, polyploid evolution, and apomixis. His writings on the evolution of polyploid complexes greatly influenced many of us who work on groups where polyploidy is prevalent. He was very encouraging about all aspects of my work on *Antennaria* and it impressed me that this great man would take such interest in my work. Ledyard was always keen to listen to scientists talk about their research, offer encouragement, and make suggestions about further avenues of research. After returning to Davis in January 1980, Ledyard wrote me to say that he was being awarded the highly prestigious National Medal of Science from President Carter in recognition of his influential work on plant evolution. In his own words he was the first ''grass roots'' botanist to receive the medal.

I decided to continue my studies on the origin of polyploid complexes in *Antennaria* for my Ph.D. at Ohio State. Because several complexes occur in the Rocky Mountains, Ledyard suggested a field trip to the northern Rockies—Wyoming and Montana—in July 1980. The flora and mountains were all new to me and I quickly became aware of Ledyard's amazing breadth of knowledge. Although he is remembered primarily as a plant geneticist and evolutionist, he had a keen interest in taxonomy, knew the flora of western North America very well, and had an encyclopedic knowledge of geology and plant geography. You could never go into the field with him and not come away without having learned a great deal about plant evolution and natural history. In his mid 70s at this point, Ledyard's health was still good except for his failing eyesight. During this field trip he told me that he wished he could turn back the clock to be my age again as he still had so very much he wanted to accomplish.

I continued collaborating with Ledyard following my Ph.D. We produced a series of joint papers on *Antennaria* between 1981 and 1993, the last one a synopsis of the genus in 1993. He had come full circle in his research, beginning with cytology of *Antennaria* and ending with a taxonomic account of the genus based largely on evolutionary concepts of the polyploid agamic complexes developed in his work with Ernest Babcock on *Crepis.* We accomplished a great deal with *Antennaria,* going from essentially alpha taxonomy to a classification based on an evolutionary synthesis.

My last mountain hike with Ledyard and Helen Michaels was on August 8, 1988, to the west slope of North Sister (Three Sisters Wilderness, near Bend, Oregon) to collect material from a sexual/agamospermous population of *Antennaria media.* This was a long hike for an 82-year-old, and it was obvious that his eyesight and knees were failing. He wanted to keep hiking to continue studying plant evolution in the field, but his body would not allow it. His last letter to me, dated January 9, 1997, ends by saying, ''Aside from my eyesight and the fact that I cannot walk long distances, I am in good health. . . . I am therefore optimistic about being around and interested in evolution for a while longer.''

We will remember Ledyard Stebbins for the enormous contributions he made to the evolutionary synthesis. Those fortunate enough to know him personally will remember him as an extraordinary teacher, tireless advocate for the study of botany and evolution, great proponent of conservation, and as a kind and caring person who was always willing to give a bit of his time to others. We shall miss him very much.