

Obituary

Suresh D. Jayakar, one of Europe's leading population biologists and an editor of the present journal, died on the 21 of January this year after a long period of illness.

Jayakar was born in Bombay in 1937 into a highly cultured Indian family. He obtained his Master degree in Mathematical Statistics from the University of Lucknow in 1958, after which he went to Calcutta to continue his studies at the Indian Statistical Institute. Here he met J. B. S. Haldane and Helen Spurway who just had arrived from England, and Jayakar decided to specialize in genetics. Haldane wrote at the time that his most important work was to get young Indian scientists started on their scientific careers. He mentioned four students whom he found particularly promising, and among them we find Jayakar's name. Jayakar worked closely with both Haldane and Spurway, and he joined them when they in 1962 moved to Bhubaneswar where the Government of Orissa had created a Genetics and Biometry Laboratory specifically for Haldane. After Haldane's death in 1964, Jayakar succeeded him as the Director of the Laboratory.

Jayakar's contract with the Government of Orissa was terminated in 1967, at which time he was invited by Professor L. L. Cavalli-Sforza to join his research group in the Pavia Section of the International Laboratory of Genetics and Biophysics. In this beautiful Italian city with one of the world's oldest universities Jayakar arrived with his family and came to stay for more than twenty years. He held various research and teaching positions and was at his death Associate Professor of Genetics at the University of Pavia.

In 1985 a severe seizure gave the first sign of a malignant brain tumor. He had two big operations, underwent radiotherapy, and was treated with anti-epileptic drugs. Nevertheless, he continued to lead an active life as a scientist and went, for example, for a working visit to Stanford in 1986. Though obviously not well he attended also the Founding Congress of the European Society for Evolutionary Biology in August 1987. A few months later he was hospitalized, and he died in January 1988 leaving a family with two teen-aged sons and many colleagues and friends in deep sorrow.

Jayakar's scientific contributions range over a wide spectrum in biology. Most of his early articles describe detailed studies on insect and bird behaviour, investigations often performed with Helen Spurway. As a well trained statistician and human geneticist he came also to participate in a number of studies concerning human variation, in particular an analysis of polymorphisms in African Pygmies (with L. L. Cavalli-Sforza) and a search for the genetic basis of obesity in Italian children (with L. Zonta).

But to most of us he is known as a very thoughtful theoretical population geneticist. This is a field where one can find similarities between his and Haldane's work. Both of them found it natural to present an evolutionary problem in terms of a

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formal genetical model accompanied by a mathematical analysis. However, the formal construction and the mathematical treatment is never performed for its own sake; instead, the analysis is always in close contact with the biological problem under consideration. I would like to mention three areas where Jayakar made important theoretical contributions.

The effect of fluctuating selection

In 1963 Haldane and Jayakar published an article which gives the condition for a genetic polymorphism when the fitness values of the genotypes vary over time with e. g. seasons or years. This article, with its simple conclusion that a polymorphism is protected if the geometric mean fitness of the heterozygotes is greater than the corresponding values for the homozygotes, has become a classic and must be one of the most cited papers in population genetics. In one of his last articles Jayakar, together with L. Zonta, returns to the same question in a discussion of the effect of fluctuating selection for a quantitative trait.

Ecological fitness interactions

In most population genetical models the fitness values of the genotypes are treated as fixed parameters. The simplicity thus gained often overrules the concomitant loss of realism in the model. However, at other times the assumption of fixed fitness values must be challenged. There is a whole range of interesting evolutionary problems that requires that the fitness values are treated as dynamic variables, i.e. that the fitness values themselves are modeled. The need for dynamic fitness values is particularly strong when ecological interactions between genotypes are considered. Jayakar, alone or in cooperation with C. Matessi, made a number of interesting studies of models of this kind. Thus, we find his name on early and important articles on the joint evolution of predators and prey, the evolution of altruism, and the coevolution of species in competition.

Sex ratio evolution and the evolution of sex determination systems

In India Jayakar studied the mating behaviour and sex ratios of wasps with H. Spurway, and he continued as a theoretician to take an interest in the sex of insects. With G. Maffi he wrote in 1981 a fascinating study of a two locus model for a sex-linked meiotic drive system. The model describes a complex situation found in the mosquito *Aedes aegypti*, and it leads to one of the few examples in population genetics of a stable limit cycle which is not due to ecological interactions between the genotypes.

In his last major theoretical analysis he considers the sex determination system in the housefly (*Musca domestica*), where there is a cline in sex determination mechanisms between an "autosomal" system and the "standard" chromosomal system. Here he runs into the situation, so hard for population geneticists to explain to ecologists, that no simple deduction can be given about the future evolution of a particular sex determination system. All depends, not only on the selective properties of the new mutations occurring, but on their transmission properties—something which is difficult to map naturally into a fitness-set representation.

The Pavia laboratory under Jayakar became one of the most important nodes in the informal network of population biologists that developed in Europe during the last decades and led to the creation of the European Society for Evolutionary

Biology. Jayakar organized, for example, a very successful conference in Pavia at the centenary of Darwin's death in 1982, which resulted in the book "Evolution and the Genetics of Populations", published as a supplement to *Atti Associazione Genetica Italiana*. Jayakar was a good speaker and he participated at many meetings, workshops and courses. I myself met him already as an undergraduate in 1969, when he taught at an international course in theoretical population genetics in Pavia. The topic, the city and Suresh made a lasting impression on me. In particular, I remember the Sunday lunch that Suresh kindly invited me to, and where he and his wife served Indian chicken curry. He had asked me beforehand, polite as ever, if I disapproved of hot food for lunch, whereby I had claimed that we always had hot food for lunch in Sweden—not realizing the double meaning of the word in English. Little did I know what Indian hot food *really* tasted like. The chicken was unforgettable, and so were the ragas that we listened to the whole afternoon.

Suresh was to me, and to many other European population biologists, like an admired and helpful elder brother. In discussions he was knowledgeable and interesting and never severe in his criticism. His home was open to us when we visited Pavia. He was enviably handsome and very distinguished and his manners showed us the meaning of true civilization.

He was absolutely unique. A gentle man, and a friend. His death was so unnecessary and we miss him terribly; more than words can say.

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