

Amitabh Joshi

Equations, Fruit Flies, and History: Five Months in Paradise



My roots are in the Himalayas in far northern India. I was born (1965) and grew up in Agra, an old Mughal capital, went to the university in Delhi (B.Sc. Botany, M.Sc. Genetics), another Mughal capital, and since 1996 I have been on the faculty of the Jawaharlal Nehru Centre for Advanced Scientific Research at Bangalore in southern India. In between, I spent eight and a half years in the USA, during which I obtained my Ph.D. from Washington State University working on the coevolution of competing fruit fly species. In the past 14 years, I have been involved in experimental and theoretical research in evolutionary genetics and population ecology and have co-authored a book on *Stability in Model Populations* (Princeton University Press, 2000), in addition to various research papers on population growth, competition, developmental rates, biological rhythms, ecological specialization, density-dependent selection, and the cost of sex. The latter, believe it or not, is actually a respectable area of intellectual endeavour in evolutionary biology. When not busy justifying my spending “tax-payers” funds on evolutionary research, I like to listen to music – especially traditional *Qawwali* – and indulge in my passionate hobbies of history, philosophy, and reading and writing poetry in Urdu and English. – Address: Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, P.O. Box 64 36, Jakkur, Bangalore 560064, India.

The fourth Mughal emperor of India, Jahangir, was very fond of vacationing in Kashmir, no doubt to enjoy the Himalayan climate when Agra was scorchingly hot. One of the poets accompanying the emperor on his summer vacation is said to have remarked of Kash-

mir: “گر فردوس به روزمین است همین است همین است همین است” (if there be paradise on earth, this is it, this is it, this is it!). Although I agree the Himalayas are like no other place on earth, I would have to add, after having spent five wonderful months at the Wissenschaftskolleg, that the poet, unfortunately, had not had the opportunity of being an intellectual in residence at Wallotstraße 19. For me, the time spent at the Kolleg has been wonderfully satisfying both academically, in its broadest sense, as well as on a much more personal level. For an experimental biologist who occasionally does theoretical work and has had a long abiding interest in medieval Indian and Islamic history and in more recent German history, it is nothing short of paradise to be free from the more mundane aspects of running a laboratory in order to do some theory and some serious writing and thinking (incubators that treacherously malfunction just when you have set up an experiment after weeks of tedious preparation being just one of the pitfalls of laboratory evolution), to find oneself in Berlin (a city at the heart of modern German history), and, as if this were not enough, to be in the company of several distinguished scholars of Indian and Islamic studies.

When I had originally submitted my proposal of what I intended to do while at the Kolleg, I had planned to start work on a book on life-history evolution in *Drosophila*, in addition to working with Somdatta Sinha (a colleague in the Demography and Evolution of Eusociality Group) on developing mathematical models of *Drosophila* population dynamics that could then be extended to a spatially structured context and form the foundation for serious experimental work in metapopulation dynamics. This proposal was predicated upon my finishing an earlier writing project before I came to Berlin. This, of course, did not happen and, moreover, I began to revise my plan about the *Drosophila* book in order to change my point of view a bit to accommodate recent advances in genomics that have important consequences for how we can study life-history evolution. So, while at the Kolleg, I actually ended up working on a different book: an expository text aimed at students (as an adjunct to formal textbooks) as well as a more general audience, titled *The Dance of the Genes: An Introduction to Population Genetics*.

I had finished one chapter of this book in Bangalore, and I am happy to say that I managed to finish another six and a half chapters while I was in Berlin, this together accounting for almost 75% of the book. I was also able to rework the proposal for the life-history evolution book. Even more satisfying was some theoretical work I managed to do here that I had been wanting to do for the past couple of

years but had never been able to get around to actually doing. I find it difficult to do theoretical work unless I can singlemindedly focus on it, which is hard when one is at the mercy of heavy teaching schedules and treacherous laboratory equipment. In the peaceful surroundings at the Kolleg, with all the messier details of life taken care of by the wonderful staff, I was actually able to finish this piece of work, which involved making the case for a broader view of density-dependent selection in an argument that drew upon a combination of some new theory, reinterpretation and integration of previous theory from several different areas of evolution and ecology, and new experimental results from my laboratory that provide support for this argument. This work resulted in two manuscripts that have been submitted for publication: (1) “*K*-selection, α -selection, effectiveness, and tolerance in competition: density-dependent selection revisited”, and (2) “Laboratory evolution of faster pre-adult development in *Drosophila melanogaster* leads to reduced competitive ability”. A review article, “Development and competition in fruit flies: a tale of two densities”, and a general article on “Genomics and evolution” were also submitted for publication.

The collaboration with Somdatta Sinha was fruitful; we laid the foundations for the type of modelling effort we wanted to engage in and managed to write up a research proposal titled “Theoretical and empirical investigation of local and global dynamics in metapopulations”, which is shortly to be submitted to the Department of Science and Technology in India for funding. In the course of discussing population growth models and how and why we should model the growth of *Drosophila* populations in a particular way, we also realized that there was an interesting point that had been missed in most prior work on density-dependent selection theory. Population growth models typically ignore genetic considerations and focus on the dynamics of population numbers. An important development in population ecology has been the realization that high per capita growth rates can give rise to very complex dynamics (including chaos), even in extremely simple models. Population genetics, on the other hand, tends to ignore the dynamics of population numbers by assuming a large population at equilibrium for size, and then focuses on the dynamics of the genetic composition of the population under various scenarios of selection. The theory of density-dependent selection has been one of the few areas in which population genetics and population ecology have tried to come together. Yet, even though different genotypes are assigned fitnesses explicitly based on a population growth equation, none of the standard models of

density-dependent selection has addressed the issue of what happens to the parameter values of the growth equations that would result in complex dynamics. We have begun to explore this issue theoretically and hope that this work will eventually yield interesting and important results.

Discussions with Leticia Avilés and Raghavendra Gadagkar, other members of our working group, and with participants at a workshop on social evolution in May broadened my horizons in evolution considerably and, in particular, convinced me that I need to study recent developments in multi-level selection theory. This task is substantially simplified by the fact that, thanks to the amazingly efficient *Bibliothek*, I now have all the relevant literature on multi-level selection with me, including many papers it would be difficult to find in India. Frau Bottomley and her colleagues have, in my opinion, actually succeeded in creating the perfect utopian library, and among the things I take back with me to Bangalore is a priceless treasure they managed to obtain for me: a copy of Fisher's 1918 paper, published in a relatively obscure journal, that laid the foundations of population genetics, the discipline in which I work.

Another great benefit of being in Berlin for several months was the opportunity to travel to other universities in Europe and, thus, to be enriched by discussions with a variety of colleagues working on life-history evolution in *Drosophila*. These discussions and the peace of mind afforded by residence at the Kolleg also led me to do some serious thinking about longer-term research directions for my laboratory and have been directly responsible for my decision to initiate experimental studies on selection in fluctuating environments. To this end, I have finished a draft outline of a research project proposing to examine experimentally the possible impact of fluctuating environments on the evolution of canalisation.

Berlin itself was a pleasant surprise, being far greener and far less crowded than I had imagined. Getting around was easy, people were very nice and helpful, and the pleasure of being able to walk on streets that I had read so much about since my teenage years is an experience that I find myself unable to describe in words. Wolf Lepenies and all his colleagues at the Kolleg appear to have perfected the art of ensuring that one feels at home practically the minute one arrives, and one is also thereafter free of all distractions from the vicissitudes of daily life that normally obstruct intellectual activity. Getting to know the other Fellows was one of the greatest pleasures of being at the Kolleg. I enjoyed and learned from numerous discussions I had with many of the other Fellows on topics

ranging all the way from the evolution of cooperative behaviour to issues of identity, causation, Sufi thought and Persian poetry and, of course, thanks to Gerhard Neuweiler and Hans-Ulrich Schnitzler, the innate qualities of people from Swabia (I must say that their personalities make it easy to believe their laudatory statements about Swabians). I also managed to do a lot of reading outside my subject, something I had not done for the past few years because I was busy setting up a new laboratory after taking up my appointment in Bangalore. It was a particularly interesting experience to read works by colleagues at the Kolleg, because then I could actually talk to the author about the book I had just read, which is a rare privilege indeed.

Frau Hund did an extremely good job of teaching us German, but, I am sorry to say, I could not find the time to do even one-tenth as good a job of learning it. Consequently, my German is still not good for much more than deciphering (partially) the labels on products in supermarkets. However, that itself is of some practical benefit. On my second day in Berlin, I spent an hour in a supermarket looking for salt, which I knew was *Salz* in German. Unfortunately, all I found was *Speisesalz*, and not having any idea of what *Speise* was, I refrained from buying it because I was afraid of ending up eating what, for all I knew, could have been bath salts. After a couple of weeks of German class, shopping slowly lost the element of uncertainty; it is truly reassuring to be able to confidently buy what you want, instead of making wild guesses and hoping for the best.

To sum up, I am not happy to be leaving, even though I am going home. I wish I could have actually been here for the full academic year, but that, unfortunately, was not possible due to other commitments and responsibilities. Certainly, I did not finish all that I, perhaps over optimistically, had hoped to. On the other hand, I did some work that I had not originally planned to do; this was work that originated from the discussions and experiences at the Kolleg and is, therefore, more precious to me than the book that I could always have written in Bangalore.