IN CONVERSATION

Amitabh Joshi

Amitabh Joshi is an evolutionary biologist with the Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Bengaluru. In an interview with *Current Science* he speaks about his research interests and their applications in other fields of biology.

What got you interested in pursuing evolutionary biology?

Evolutionary biologists typically develop interest in the subject in two broad ways. Some start with deep interests in natural history, whereas others start from an interest in understanding conceptual issues in biology. In my case it has been the latter. My basic training was in genetics. While I was pursuing my Master's degree in genetics, I took a course on population genetics which I thoroughly enjoyed. This was partly due to the richly conceptual nature of the subject, and its great explanatory power. An exceedingly inspiring teacher, C. R. Babu, taught the subject magnificently and with passion. He encouraged my interest in evolutionary biology and often gave me interesting papers to read on the topic.

In those days, there was no internet and as students we had no exposure to what kind of research was being done in evolutionary biology. Later, in 1987, I went to do a Ph D in evolutionary genetics at Washington State University. It was there that I was introduced to experimental evolution. My supervisor, Laurence D. Mueller, used to conduct multi-generational experiments using fruit flies (*Drosophila melanogaster*) to study how they adapted to extreme crowding. The idea of studying the evolutionary process itself, rather than the evolution of a trait or a taxon and the approach of experimental evolution, wherein one got to study the dynamics of evolutionary change in real time, were both very appealing to me, and I have stayed with experimental evolution since that time.

Please tell us about your research interests

Many evolutionary biologists are interested in the phylogeny of species, or in the evolution of specific traits, but those topics do not appeal to me. My interests lie in the dynamics of the evolutionary process itself. I am not interested in any single particular trait or behaviour or a taxonomic group, but on how ecology, heredity and development interact and generate the evolutionary process. I use fruit flies as a model system, and try to utilize the understanding gained from studying how they evolve in the laboratory in response to specific ecological challenges. This helps in developing better conceptualizations of how we think about, for example, the evolution of competitive ability. In some sense, this research uses flies but is not about flies; the flies act like a realistic computer simulation of the evolutionary process.

To see how *Drosophila* populations evolve to the challenges posed to them by a selection regime, we set up simple ecological conditions, contrasting one another. Through experimental evolution, we empirically study their evolutionary trajectories under controlled conditions and then use that information to address conceptual questions about the tempo, form and repeatability of the process of adaptive evolution via natural selection. For example, we have populations of fruit flies in our laboratory that have now been subjected to selection for rapid egg-to-adult development for over 600 generations. Essentially, all we do is to ensure that in each of the four replicate selected populations, only the first 20% of the individuals to reach the adult stage in each generation are allowed to produce the next generation. In the four matched control ancestral populations, everything is identical to the selected populations, except that all individuals that become adults are permitted to breed in each generation. The response to this selection for rapid development has been dramatic. Fruit flies normally take around 200 h to develop from egg to adult. In our selected populations, this duration has been reduced, over many generations of selection, to about 140 h.

Once the selected populations have shown evolutionary change in response to the selection pressure they faced, we can begin to ask how the adaptation occurred. In our faster developing populations, all life-stages (egg, larval instars, pupae) are reduced in duration. Gonadal maturation, which normally happens in the pupal stage, is postponed to early adulthood. There is an increased use of lipids as an energy source, rather than carbohydrates, during pupal metamorphosis, presumably because lipids yield more energy per unit mass. This, however, comes at a cost to the fruit flies because the more lipids they use during metamorphosis, the less will be available during early adulthood thereby constraining their fecundity. As a consequence of the reduced time available for the larvae to eat and pack on weight, the adults of the faster developing populations are smaller in size and have shorter lifespan than the individuals of the ancestral populations. Interestingly, it appears that this major size reduction has had the evolutionary effect of reducing levels of intersexual conflict in the selected populations, possibly aided by the fact that in the faster developing populations adults have less time to mate and multiply, compared to ancestral controls. In all species with separate sexes, there exists intersexual conflict at the genomic level. Intersexual conflict arises because the strategies for attaining high Darwinian fitness differ between males and females. For a female, the limiting factor for maximizing fitness is energy, because a lot of energy is required to produce eggs. For males, however, the limiting factor for maximizing fitness is the number of females they can inseminate. Sperms are relatively cheap to produce and therefore the males are limited by the number of females. This in turn creates some interesting dynamics. The optimum number of eggs laid by the female after a single mating, for example, can differ from the point of view of fitness of the male versus the female. Typically, it is in the male's evolutionary interest to make the females commit more eggs to be fertilized by his sperm. The males achieve this by transmitting peptides with the sperm to manipulate the female's neuroendocrine and reproductive systems. These signalling protein molecules 'hijack' the endocrine system of the female, inducing her to lay more eggs. The females as counter defence to this mechanism can evolve by having a mutant receptor for some of these peptides so that their endocrine system does not respond to the chemical signals of the male, thereby increasing the female's fitness. This can give rise to a co-evolutionary arms race between the male and the female, and is termed inter-locus genetic conflict as the alleles that respond to this mechanism are found on different loci in males and females. What we have found is that males of the faster developing populations have evolved to be less 'harmful' to females, and females of these populations have evolved reduced levels of tolerance to mate-harming by males. This evolution of reduced inter-locus sexual conflict in the faster developing populations appears to be driven largely, but not exclusively, by the reduction in body size. We are now developing this model system to study male–female co-evolution and sexual conflict by subjecting some individuals of the selected populations to reversed selection regime and examining whether conflict levels increase in the selected populations. One of the consequences of lowered level of inter-locus sexual conflict in these selected populations is that there is now partial reproductive isolation between the faster developing populations and their ancestral control populations. This is exciting, as it represents one of the early steps towards speciation following the classic allopatric model.

I am also interested in studying adaptations to extreme larval crowding in fruit flies, as it has bearings on the evolution of competitive ability. By implementing larval crowding in different species of fruit flies in slightly different ways, we have shown that they can adapt to crowding and enhance their ability to compete for scantily available resources using different underlying phenotypic mechanisms. We developed a hypothesis that it is not just larval density, but also the height of the food column in culture vials that determines which phenotypes will be better able to deal with a crowded culture. This is because a higher food column provides for a larger volume of food for nitrogenous wastes to diffuse into, while the feeding activity remains restricted to a band of about 10 mm depth from the surface. If waste concentrations are high in the feeding band, optimal feeding rates are lowered and hence faster feeding is not necessarily the best strategy. Experimental evidence supports the hypothesis showing that the development time and body weight distributions, and total larval survivorship, are indeed altered when one changes the height of the food column while holding the larval density per unit volume of food constant. We have now started new selection regimes to show that crowding at different food column heights leads to evolution of higher competitive ability using different underlying mechanisms involving a shifting balance between feeding rates, urea/ammonia tolerance and development time. We are also developing this into a broader view of competitive ability by emphasizing other aspects of the environmental context, such as total resource available, that actually interacts with density per se in determining density-dependent fitnesses. This view of competition should be applicable to species where larvae inhabit a discrete and ephemeral patch of food, be it a carcass or a rotting fruit. We have also shown that density-dependent selection can and does lead to the evolution of greater stability of population dynamics, both in terms of constancy and persistence. In collaboration with Sutirth Dey (IISER, Pune), we are trying to develop integrated models of the evolution of both density-dependent fitness and population dynamics. These results represent the first major conceptual advances in density-dependent evolution and population dynamics since Laurence Mueller's seminal work in this field in the 1980s and 1990s.

Another of my interests is population ecology, especially the ecology of spatially structured populations or meta-populations. In a meta-population, there are a number of small local populations which are isolated enough to have partly independent dynamics of how their numbers change over time, but are connected through some amount of migration and hence are not completely isolated. Understanding the dynamics of a meta-population is important, especially given the increasing habitat fragmentation. For example, if there are habitat patches with the species you want to conserve, and you want to introduce corridors so that individuals from one patch can move to the other, what kind of migration rates would be optimal for the stability of the system? Experimental work with laboratory meta-populations of fruit flies can be used to address such questions. For example, we have shown that if the local dynamics of populations making up a meta-population is unstable, intermediate levels of migration can help stabilize the system, but if there is too much migration then the entire system gets destabilized and has a higher risk of going extinct. In this context, we have been particularly interested in studying how different aspects of ecological population stability, such as constancy and persistence, are related and how the interaction between local dynamics and migration rates affects the overall stability and synchrony of the meta-populations.

Why do you use fruit flies as your model system? What are the advantages of doing so?

Fruit flies are a convenient system as their generation time is short, and they are cheap to rear in large numbers. Moreover, a lot is already known about their laboratory ecology. Some people also use *Escherichia coli* as a model system. *E. coli* has a shorter generation time than fruit flies and there are some advantages of using it as you can experiment with over 100,000 generations and answer questions that need longer experimenting periods. There is also the luxury of freezing generation zero of *E. coli* cultures and thawing them out when required. However, the dynamics of an evolutionary process in an asexually reproducing organism is completely different from that of a sexually reproducing organism. Therefore, the results of experiments done on *E. coli* do not translate in the same way in sexually reproducing organisms. In asexually reproducing organisms, the limiting factor for evolutionary change is the spread of new mutations by chance, whereas in sexually reproducing organisms there are many genetic variations in the population at any given time. This brings faster evolutionary responses. Also, in ecology, we need a more complex system than *E. coli*. Understanding of adaptation to crowding, competition and evolution of competitive ability has played a great role in forming ecological theories. Competition in *E. coli* does not relate well to the theory as it was made keeping in mind plants and animals. Fruit flies are therefore convenient and it is inexpensive to handle even large populations. It is labour-intensive work and does not require any fancy, expensive equipment. All you will find in my laboratory are vials, dissection microscopes and a couple of incubators. The only high-tech instrument we use is our brains.

Why is that there are very few people in India who are pursuing research in ecology and evolutionary biology?

Ecology and evolution are not properly taught in schools and colleges, and are also not properly represented in the curriculum. The textbooks used today are completely outdated. If you take a look at the ecology and evolution topics in our university curricula, it is almost as if nothing happened after Darwin or, at best after the Neo-Darwinian synthesis of the 1930s–40s. Can you imagine physics curricula ignoring Einstein's work and quantum mechanics? It sounds ludicrous, but that is what the state of affairs is with regard to ecology and evolution in our universities. Also, biology in India is increasingly being dominated by a reductionist viewpoint coming from the perceived importance of molecular biology. However, molecular biology and what one might call organismal biology are fairly different kinds of subjects. The epistemology of ecology and evolutionary biology is different from that of sub-organismal biology in being model-based rather than description-based. As a consequence, much like physics, ecology and evolutionary biology rest upon a solid theoretical foundation of formal mathematical theory. In India, that itself guarantees that many biologists will shy away from the field, shunning the dizzyingly attractive but also scary heights of concepts for the more mundane but reassuring solidity of a more descriptive and concrete world of facts.

Another problem is that in India science is viewed in a very utilitarian perspective, and ecology and evolution are (wrongly) believed to not have much applied significance. Science is ultimately about conceptualizations, not facts. It is about ideas, questions, curiosity and concepts and along these axes, ecology and evolution are perhaps the richest areas of biology. To my mind, the ultimate irony of our neglect of ecology and evolution in India is that these are the fields of biology in which we can excel internationally and to some extent already have, despite the small number of research groups studying these areas in India. This is because fields like ecology and evolutionary biology are not expensive or technology-driven, they are concept-driven. Therefore, even if you work in a university in some small town in India, it is much easier to do cutting-edge research in ecology and evolution than in molecular biology. Fields like molecular biology are technology-driven with research being hampered by technology gaps. So if one cannot afford it, he/she falls behind the competitors who are able to do so. In ecology and evolution you can compete with the best in the world on a level playing field because it is your brain against theirs, not your budget against theirs.

Ipsita Herlekar

Milind Watve

Milind Watve is an evolutionary biologist at IISER, Pune. He is the author of the book *Doves, Diplomats and Diabetes*, where he puts across an alternative model for understanding the cause of diabetes. In an interview with *Current Science*, Watve speaks about his research and the need for communication between scientists and the general public.

What inspired you to pursue research in the field of evolutionary biology?

My interest in evolutionary biology goes way back to my undergraduate college days. One of my teachers, M. T. Chauhan, was very enthusiastic about the subject. I pursued Masters in microbiology and later began a career in teaching. After 10 years of teaching, I had the opportunity of meeting Madhav Gadgil, who convinced me to pursue a Ph D, in order to equip me to teach better. While pursuing my Ph D at the Indian Institute of Science, Bengaluru, I was mentored by Nanjundiah, Gadagkar, Sukumar and Joshi. This rekindled my interest in evolutionary biology and behavioural ecology. On returning to Pune, I began teaching evolutionary biology at the undergraduate level, engaging the students in my research projects. Involving undergraduate students in projects that need data-intensive or technique-intensive work is difficult. However, as evolutionary biology is a conceptually rich discipline, it is possible for undergraduate students to take part in research projects.

What does your research currently focus on?

The work done in our laboratory focuses mainly on theoretical development in the field of behavioural physiology and medicine, supplemented by a few simple experiments. We mainly use secondary data from studies on rodents, primates and humans to conduct meta-analysis. The differences in the behavioural