In this issue

What exactly does evolution optimize? Mathematical physics provides an answer

If you are trained in mathematical physics, and have a serious interest in evolutionary genetics, you can directly skip to page 1159 of this issue. The article by Narayan Behera provides a charming account of the quest for optimizing principles in evolutionary dynamics, of the ups and downs before the strange and beautiful truth that emerges in the end—when visualized in Riemannian metric space of allelic frequencies, the trajectories move along the path that maximizes the increment in mean fitness. Lesser mortals may be better off looking at the highly simplified and probably correct description of the article, given below.

The Theory of Evolution means different things to different people. For the common woman, it is an amusing account that describes how men evolved from monkeys (no wonder she finds it easier to accept its incompleteness, non-directionality and reversibility). For school and college students, it is a welcome gift of half-a-dozen marks by writing a short note or comparing it with the theory of creation. For the young (and not-so-young) and bright (and not-so-bright) condensed matter theorist, it is just a special case of the chaos theory (or catastrophe theory, or fractals, or string theory—from phrases to be regularly updated with the latest buzzword). For the more sober and better informed scientists, it is the description of the outcome of the eternal competition between self-replicating entities, each trying to outdo the competitors in leaving behind more copies of itself. At the simplest level, evolutionary genetics describes competition between genes (rather alleles); different alleles are 'fit' to lesser or greater extent, and the fittest (fastest of the hares, most resistant of the plants, etc.) is the one that ultimately outcompetes every other allele. It is thus the only form that is thus seen in the population.

So, beginning with a mixture of many different alleles with different fitnesses, the mathematical theory of population genetics, developed by Haldane, Fisher and Wright in the 1920s and 1930s, allows us to compute the changes in the composition of the population from one generation to the next. Repeating the calculations over and over for many generations, we can obtain quantitative information on things like the rate of change of gene frequencies, changes in the average value of fitness, and so on. This is exactly like using Newton's laws of motion to predict the course of a hand of stones thrown in the air—the paths followed by them can be worked out by calculating their position from one instant to the next.

But this is a very simple-minded way, and the theoreticians would rather have something much more complex, subtle and obscure. This wish has been granted for mechanics! Instead of calculating the specific path followed by a set of particles, using a gigantic leap of imagination, we can examine all the possible paths that may be followed by the particles, and see if the actual one has some special quality. Amazingly, this expectation is fulfilled, at least in mechanics. Sometimes, it is the time taken to go from point A to point B; the actual path taken is the least time. In optics, the actual path of the ray occasionally takes the longest time. There is something innately beautiful and satisfying about the fundamental laws of nature being designed so intelligently.

Carrying over the analogy from mechanics to evolution, a very natural question is whether evolution too optimizes (maximizes or minimizes) something. The natural answer would be the fitness. After all, if the fittest survived, the fitness should be maximized. Fortunately or unfortunately, there is much more to making more copies of oneself than simple replication. There are many kinds of genes that influence each other. Gene complexes break and reform. So the simple expectation that fitness will be maximized turns out to be untrue in all but the simplest of the situations. In fact, it probably does not turn out to be fully correct even in the simplest situation of a single gene with many alleles. However, once the quest for optimization has begun, it cannot be given up easily. Relevance and applicability can be the first casualties; let us find something that is maximized—regardless of whether it is biologically relevant or useful. This led to a very imaginative though confusing and convoluted definition of change in average fitness—the change exclusively due to the change in allelic frequencies (as distinct from the changes that take place due to say changes in levels of heterozygosity). Even this, by itself, does not turn out to be enough—a further mathematical twist is needed. If say p1, p2, p3 are the frequencies of the competing alleles, then the path of evolution can be appropriately described as the movement of a point in three-dimensional space, where the rectangular X, Y and Z coordinate axes correspond to the three frequencies at any instant of time. Instead of this simple-minded description, if one uses a more elaborate function of the gene frequencies, evolution can then be described as the movement of a point on the surface of a sphere. In fact, all possible changes in gene frequencies correspond to distinct paths on the surface of this unit sphere. Finally, out of all these possible paths, evolution picks out the one along which the increase in the average fitness is maximized.

Lo and behold, we now know what exactly it is that evolution maximizes—never mind if it is in the simplest of the cases and never mind that we have no clue about the biological relevance of this—if any!

Coming back to the article 'Optimality principles in evolutionary genetics', Narayan Behera gives an extremely lucid and crisp description of the essentials of population genetics, including a clear explanation of technical terms easily under-
standable to non-biologists. In fact, motivated theoreticians with absolutely no background in genetics may even be able to launch their own quest on what the evolution optimizes under more and more complex (hence more and more realistic) scenarios. The article also presents a very readable survey of the various attempts (including a few by the author) towards capturing the elusive optimality principles governing evolutionary dynamics. A more appropriate illustration of 'purposeless research', so eloquently described in a recent editorial in *Current Science* will be hard to find; but then confining oneself to such 'pure' research was indeed a badge of honour especially among theoreticians. For those who have not come under the spell of the corporate culture of doing science, it will be difficult not to admire these attempts; even watching the quest for aesthetically pleasing theoretical constructs can be a rewarding experience.

N. V. Joshi

**Tropical cyclones**

Formation and intensification of tropical cyclones in the Indian seas has been the subject of active research in India for many years. This research received fillip with the introduction of the satellite monitoring through INSAT system. S. R. Kalsi (page 1175) has studied the multiple eye wall structure in the recent very severe tropical cyclone which struck Gujarat coast in May 1999. The evolution of the multiple eye wall structure, which is a rare event, has been clearly brought out in the paper with emphasis on inner core intensification and outer core strengthening of the cyclone.

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