

# Symposium on "Natural Selection for evolution of Quantitative Characters"

- Chairman : Dr. D.S. Balain  
*Director*  
*National Bureau of Animal Genetic Resources and National Institute of Animal Genetics, Karnal - 132 001*
- Convenors : Dr. V.K. Bhatia  
*Scientist (S.G.)*  
*Indian Agricultural Statistics Research Institute New Delhi - 110 012*

At the outset, Prof. Prem Narain, Secretary, ISAS and Director, IASRI, New Delhi in his introductory remarks, highlighted the importance and genesis of the topic of the symposium. He also stressed upon the role of natural selection in the evolution as well as in the improvement of the quantitative characters. Thereafter, he introduced Dr. D.S. Balain, Director, NBAGR and NIAG, Karnal as Chairman of the symposium.

Firstly, by accepting the responsibility of chairing the symposium, Chairman thanked Prof. Prem Narain and made his opening remarks by highlighting the role of cross breeding in relation to natural selection. He also laid emphasis on the maintenance of desirable genes by natural selection. After that, he invited the speakers to present their papers.

Prof. Prem Narain presented his paper entitled "On evolutionary dynamics of quantitative traits". In the beginning of his talk, he drew attention on some of the important aspects about quantitative traits under natural selection and the role played by stabilising selection which favour intermediate types. He particularly mentioned the problems regarding maintenance of genetic variability in natural population as well as genetic differentiation between populations. For studying them, he highlighted the characteristics of various genetic models particularly those relating to the number of allele per locus and the mutation scheme. To explain the nature of genetic

variability for polygenic trait in infinitively large natural population, the model involving step-wise mutation with discrete allelic effects was discussed in detail and the results obtained therein were compared with the findings obtained by other research workers based on 'house of cards' approximation for strong selection and of normal approximation for weak selection. Specific attention was drawn to the results which bring out clearly the behaviour of the genetic variability at equilibrium with changes in the mutation and selection parameters. He concluded that mutation and selection along with the number of allele at a loci are the crucial factors for the evolution of quantitative characters in natural populations.

Dr. Ravi Prakash presented his paper on 'Patterns of genic differentiation in *Zaprionus Indianus* populations'. He pointed that in order to study the evolutionary potential of a population it is desirable to have information on the amount of genetic variation occurring in the species populations. Thereafter he elaborated the cause of genetic variability which may arise due to speciation process or adaptation process. He focussed on the study undertaken by him for the analysis of genetic variability in Indian natural populations of *Zaprionus Indianus* because there are many gaps of information on genetic differentiation in *Z.Indianus* population whereas lot of information is available on genetic differentiation in *Drosophila melanogaster* populations from different regions of the world. He highlighted the procedure of his study as well as the characters considered by him for the study of genetic variability. In addition to various qualitative and quantitative characteristics considered by him, he also studied the effect of various physical characteristics such as latitude etc. Based on various techniques of genetic differentiation and on Wright's fixation index, he concluded his results about the variation patterns maintained by natural selection mechanism in *Z. Indianus* population.

Dr. V.K. Bhatia presented a paper on the 'Use of Spatial pattern analysis techniques in studying the evolutionary processes of natural population'. In his talk the use of spatial analysis techniques as advocated by various research workers was highlighted. Initially he emphasised on the assumptions which are necessary to be met for the use of spatial patterns analysis. After that he explained how this approach based on autocorrelograms called 'signatures' can be used to answer important questions imposed by evolutionists. Based on simulation studies carried by various research workers, he further discussed how different forms of natural selection change spatial distribution of genetic variation within populations and how

the relative fitnesses of different genotypes depend on their location in different micro-environments within the population. Finally, he concluded by throwing light on how spatial signatures get changed by the change of selection strength, amount of dispersal, mutation pressure and direction of selection.

After presentation of these papers, Chairman thanked all the speakers for their detailed presentations and invited delegates to react on these presentations and offer their comments/observations on the topic of the symposium, including new ideas and findings.

Dr. M. Gurnani, made comments based on his own experience and stated that in practice, a change has been observed in variance due to change in mean on account of artificial selection. Secondly he suggested that efforts should be made to study the evolutionary process of quantitative characters by considering the role of the environment as well as by taking into account genotype x environment interaction effects.

After appreciating the work done by Dr. Ravi Prakash for studies on genetic heterozygosity of *Drosophila* in Indian set-up, Prof. Prem Narain commented on Dr. Gurnani's point of view and observed that probably the results obtained in practice may have some deviations from the expectations on account of GE interactions. Prof. Prem Narain further made some observations on the spatial pattern techniques for the study of evolutionary process of quantitative characters which were subsequently clarified by Dr. Bhatia.

The observations made by the Chairman and his remarks in detail are presented at the end in the form of a special note. The Chairman pointed out that since evolution had been established to be a cumulative process and there has been advent of some newer theories, it should now be possible to study homologies for understanding evolutionary relationships. Further more, the role of natural selection towards evolution of quantitative characters at molecular level would be more clear by making use of discoveries in respect of chromosomal localisation of genes, the chemical nature of genetic material and genetic maps with specific DNA sequences. He further stressed that with the clear understanding on the role of gene, as a central part of the heirarchical organisation of biological systems, it would be desirable that linkages and communication might be established among physicists, mathematicians, statisticians, chemists, geneticists and biologists. He was also convinced that with the help of study of chemical basis of the nature of genes, many new and significant insights into the properties of

macro-molecules and their potential for creation of diversity in nature would be expected in near future.

The Chairman summed up the discussion by stating that all the newer concepts on the molecular genetic front will prove immensely useful in clarifying the evolution of not only the quantitative characters but also all other related aspects about the physiological adaptation and functions. At the end, Chairman emphasised his sincere thanks to the speakers for their presentations, to the delegates for making this session a useful and propitious and to the organisers for providing him such a good opportunity for participating in this important session.

Based on the papers presented and discussions held as well as on the Chairman's observations, the following recommendations were made.

- *There is a need to look into the problem of evolution from the molecular genetics point of view;*
- *Attempts need to be made to carry out studies on adaptation and evolution by taking into consideration genetic, environmental and G E interaction aspects;*
- *Efforts should be made to carry out comparative studies on traditional theory of evolution in relation to the newer "molecular evolution clock" theory;*
- *Involvement of mathematicians, statisticians, biologists and geneticists is warranted in undertaking studies dealing with the evolutionary process in natural populations.*

The extended summaries of the papers presented and the Chairman's view points are detailed on the following pages.

#### 1. *On Evolutionary Dynamics of Quantitative Traits.*

**P. Narain**

**IASRI., New Delhi- 110012**

To explain the nature of genetic variability for polygenic traits in infinitely large natural populations, a model involving step-wise mutation with discrete allelic effects and stabilizing selection of optimal type is considered. When the number of alleles at a locus is taken as finite instead of an infinitely large number, the properties of equilibrium seem to change. In particular, the case of five allele at the locus is discussed in detail. The results obtained encompass on the one hand Turelli's (1984) findings based on 'house of cards' approximation for strong selection and the results of normal

approximation for weak selection on the other. The results of Slatkin (1987) based on five allele approximation for intermediate selection are made more exact by solving the set of recurrence equations without assuming that the outermost allele are negligible in frequency. This approach brings out clearly the behaviour of the genetic variability at equilibrium as mutation and selection parameters change characteristically. It seems the number of allele considered at each locus could be a crucial factor in mutation-selection balance equilibria in large natural populations.

## 2. Patterns on Genic Differentiation in Zaprionus Indianus Populations

Ravi Parkash

Maharshi Dayanand University, Rohtak - 124 001.

Homogenates of single individuals were analysed electrophoretically for allozyme variation at fourteen loci in twelve natural populations of *Zaprionus indianus* from different regions of India. The latitudinally varying populations of *Z. indianus* revealed clinal variation at most of the loci examined. The allelic frequency patterns revealed lesser alternations with the latitude at *Est-1<sup>F</sup>*, *Est-4<sup>F</sup>* and *Mdh-1<sup>F</sup>* loci while the allelic frequency patterns at nine loci (*Est-2<sup>F</sup>*, *Est-5<sup>F</sup>*, *Est-6<sup>F</sup>*, *Est-7<sup>F</sup>*, *Adh<sup>F</sup>*, *Acph<sup>F</sup>*, *Acph-2<sup>F</sup>*, *Ao<sup>F</sup>* and  $\alpha$ -*Gpdh<sup>S</sup>*) were found to increase significantly with latitude. However, the data on allelic frequencies in geographical populations revealed significant correlation with latitude at six loci (*Est-1*, *Est-5*, *Est-7*, *Ao*, *Adh*. and  $\alpha$ -*Gpdh*). The analysis of Wright's fixation index (FST) revealed genetic differentiation at *Est-1*, *Est-5* and  $\alpha$ -*Gpdh* loci. The data on genetic identity (I) in different populations of *Z. indianus* depicted slight genetic differences in pairs of latitudinally varying populations. Thus, the observed latitudinal genic variation patterns could be maintained by natural selection mechanism in *Z. indianus* populations.

## 3. Use of Spatial Pattern Analysis Techniques in Studying the Evolutionary Processes of Natural Populations

V. K. Bhatia

IASRI, New Delhi - 110 012.

In this article, the use of spatial analysis techniques as advocated by various research workers in studying the evolutionary processes of natural populations are highlighted. With the understanding, that patterns of spatial variation of morphometric and other variables and especially of electrophoretic variats may reflect the working of evolutionary processes, various evolutionists

have tried to separate out the effects of several microevolutionary factors based on spatial autocorrelation analysis under the assumptions (a) spatial variation patterns (spatial response surfaces) can be summarized and characterised by a 'signature' obtained through spatial autocorrelation analysis, spectral decomposition and related techniques (b) similar deterministic factors result in similar spatial response surfaces (c) stochastic processes with the same parameters yield independent and different spatial surfaces but these surfaces will have similar signatures suggesting similar generating processes and (d) changes in these parameters will be reflected by change in signatures.

Based on these assumptions, the researchers attempted mainly to study the evolutionary processes of natural populations. They are Moran's measure of spatial correlation of allele frequencies as well as the co-efficients of Kinship. Spatial patterns are found for the selectively neutral loci in populations with limited symmetrical dispersal. Marked patch structures quickly develop from local stochastic events and assortative matings. Homozygous genotypes become concentrated into separate large areas or patches and these patches are surrounded by heterozygotes. Researchers have shown further through detailed theoretical investigations based on simulation studies that how different forms of natural selection change spatial distribution of genetic variation within populations. In these simulations the relative fitness of different genotypes depend on their location in different microenvironments within the population. Their results showed that microenvironmental selection can change spatial patterns of genetic variation, but the exact forms of changes depend on the spatial distributions of microenvironments, the strength of selection and the amounts of dispersal. Further it has also been shown that immigrations into the margins of a population can also change spatial autocorrelation. Likewise the effect of directional selection showed its influence on the spatial patterns of the genetic variation in natural populations.

#### 4. *Natural Selection and Evolution of Quantitative Characters : Recent Developments*

**D. S. Balain**

**National Bureau of Animal Genetic Resources &  
National Institute of Animal Genetics, Karnal- 132 001.**

Since the rediscovery of Mendel's ideas at the turn of this century, progress in all branches of genetics has occurred by quantum jumps. This is also likely to continue in the foreseeable future.

Evolution has been established to be a cumulative process. Population genetics principles governing especially the inheritance of quantitative traits are also based upon the cumulative or additive effects of genes. As such these two aspects bear similarity. "It is only through comparative studies of organisms, from closely and distantly related taxonomic groups, that we distinguish the general from the particular, the common from the peculiar, in the phenomena and processes that we study." In the past, such comparative work from the point of view of genetics was difficult and time consuming. However, with the availability of DNA sequence data banks, this task has become somewhat easy. As such it is now possible to study homologies which can go a longway in reflecting evolutionary relationships. More work in this direction is warranted. The fact that genetic material as well as the mechanisms of gene action have chemical basis, has provided biology with a unifying theoretical structure that complements, at molecular level, natural selection. So, it may now be possible to explain the role of natural selection towards evolution of quantitative characters in molecular terms as more discoveries are being made in respect of chromosomal localisation of genes, the chemical nature of genetic material, and the correspondence of maps and specific DNA sequences.

By now it has been established that genes are something concrete, having a metastable and variable, macro-molecular structure, but are fundamental and essential for life. Thus the genetic theory by now has become a formidable unifying power in biology. Also it is now practicable that genes can be handled and manipulated by genetic engineers. In this way, great practical powers stand conferred upon genetics in recent years which can be made use of in explaining the role of selection-be it natural or artificial- upon quantitative characters.

The emerging role of genes as a central part of the heirachical organisation of biological systems has enabled communication and linkages to be established among physicists, mathematicians and statistician, chemists, geneticists and biologists, the like of which was unknown previously in science.

Thus, more and more explanations are in the offing regarding finding solution to the twin problems that heredity is a primary mathematical formulation and mechanism implemented through Mendelian laws of the Mendelian factors, and also that it concerns the cell, the egg and the sperm.

Also with the help of the study of chemical basis of the nature

of the genes, many new and significant insights into the properties of macromolecules and their potential for creation of diversity in nature, have been gained. "The accidental consequences of thermal disorder in the molecular landscape of the gene is a major factor in creating genetic 'information', and with selection, the genetic 'programs' of genomes." This is the material basis of adaptation through natural selection, and ultimately of the uniqueness of the quantitative traits as well as that of the individual as a whole. It is expected that in the near future, more light will be thrown on these aspects.

Motoo Kimura (1989) has explained the main tenet of his neutral theory of molecular evolution in an article published in *Genome* 31(1): 24-31. He has contended that great majority of evolutionary changes at the molecular level are caused not by Darwinian selection but by random fixation of selectively neutral (or very nearly neutral) allele through random sampling drift under continued mutation pressure. This theory also propounds that the majority of protein and DNA polymorphisms are selectively neutral, and that they are maintained in the species by mutational input balanced by random extinction rather than by "balancing selection." According to him, this neutral theory is based upon simple assumptions which has enabled him and his co-workers to develop mathematical theories (using the diffusion equation method) that can treat these phenomena in quantitative terms and that permit theory to be tested against actual observations. Dr. Kimura has further contended that although this neutral theory has been severely criticized by the neo-Darwinian establishment, supporting evidence has accumulated over the last 20 years, and in particular, the recent burst of DNA sequence data has helped to strengthen the theory a great deal. It is believed that this neutral theory has also triggered reexamination of the traditional "Synthetic theory of evolution."

In this paper, Dr. Kimura has also extensively reviewed the present status of the neutral theory, including discussion of such topics as "molecular evolutionary clock," very high evolutionary rates observed in RNA viruses," "a deviant coding system found in *Mycoplasma*", "the concept of mutation-driven neutral evolution", and the origin of life". In short, he has presented a worldview based on the conception of what is called "Survival of the luckiest".

All such striking revelations on the molecular genetic front will prove immensely helpful in clarifying the evolution of not only the quantitative characters but also of all other related aspects about their physiological adaptation and functions.