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Review Article

Mitochondrial DNA: A Molecular Tool for Assessment of Genetic Diversity

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Abstract

The most important component of any breed improvement programme is genetic diversity which is the major cause of genetic gain. Assessment of population structure and genetic diversity is a basic tool for genetic improvement. The decline in genetic diversity results in inbreeding and consequent reduction in the performance. Significant morphological differences exist among various breeds but little information is available on their genetic diversity and structure. So, it is more important to access the genetic diversity of a population. There are various ways to access genetic diversity and structure of the population and studying mitochondrial DNA diversity is one of them. Mitochondrial DNA with unique features of maternal inheritance, a relatively fast rate of evolution and lack of recombination has proved to be useful markers for assessment of genetic diversity. Hence the current review aims to discuss the importance of mtDNA for the assessment of genetic diversity.

Key words: Breed Improvement, Genetic Diversity, Maternal inheritance, Mitochondrial DNA

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Introduction

Domestic farm animals are always an invaluable resource in agriculture and play a major role in providing livelihood to millions of poor people. There is a vast array of domestic farm animal breeds which contribute directly or indirectly to the agriculture economy but most of the indigenous breeds have not been exploited to their full genetic potential. Due to higher production demands along with issues of patenting and intellectual property rights, it becomes very important to identify unique genes and gene combinations of livestock which possess a great diversity harboring trait of higher yield, better productivity and tolerance to stressful conditions.

Animal Genetic Resources (AnGR) exist in the form of a vast array of breeds and livestock population which continuously evolve according to a varied range of environmental conditions. Genetic diversity is essential for sustenance and long-term survival of the species or its population as it is the raw material for adaptation and evolution especially when environmental conditions have changed (Eriksson *et al.*, 1993; Rajora and Mosseler, 2001a). So, the central objective of any breed improvement or conservation plan is to maintain genetic integrity and natural levels of genetic diversity and to enhance them in areas where they have been eroded (Rajora and Mosseler, 2001a). Domestic animal genetic diversity which offers food varieties are in a drastic state of decline, so, there is urgent need of conservation as well as maintenance of diversity which will act as a raw material for future breeding plans and is becoming an important issue in international, regional and national agriculture planning.

Genetic variation forms the basis of selection and it is the basic tool with which an animal breeder works. This variation can be exhibited within a population or between populations. It is widely accepted that detailed molecular data on within and between breed diversity are essential for effective management of FAnGR (Weitzman 1993; Hall and Bradley 1995; Barker 1999; Ruane 2000; Bruford *et al.*, 2003; Simianer 2005; Toro and Caballero 2005; Toro *et al.*, 2009). The enormous diversity of population culminated in the formation of well-defined groups used for a variety of purposes with differing levels of performance (Groeneveld *et al.*, 2010). So, genetic diversity forms the primary component of adaptive evolution and is essential for the long-term survival probability of a population (Avise, 1995; Coltman *et al*., 1998; Reed and Frankham, 2003).

Methods of Genetic Diversity Analysis

Genetic diversity analysis can be done by various methods: e.g. morphological, cytogenetic, biochemical and molecular techniques. Among these cytogenetic and biochemical methods are not acceptable widely due to some limitations. Morphological and chromosomal markers usually are less accurate, less polymorphic and lack the power to resolve differences between closely related populations because of their low polymorphism (Meghen *et al*., 1994). Molecular markers are powerful tools for the analysis of genetic biodiversity, which are based on DNA sequence polymorphisms. DNA sequences determine the diversity of organisms, and therefore the techniques which are used to evaluate DNA polymorphisms directly measure the genetic diversity. Several molecular techniques to measure DNA polymorphism include PCR-RFLP, microsatellite and mini satellite, mtDNA variation and SNP chips.

Mitochondrial DNA sequences are the markers of choice for studies related to the origin and domestication of livestock species. The mtDNA genome is strictly maternally inherited. The sperm contributes no mtDNA when fertilizing the egg. Biological maternal relatives all share their mtDNA, yet their mtDNA is unique. Mitochondrial DNA sequencing has been used to explain the origins of many modern domestic livestock

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species. The existence of multiple mtDNA lineages and their mixing within breeds could be due to various domestication events or introgression between 2 or more different species or breeds. Worldwide, mitochondrial DNA sequence variation has been extensively exploited as an important powerful tool to identify ancestral haplotypes, to understand several genetic structure issues and evolutionary relationships and divergences between livestock breeds (Mannen *et al*., 1998; Mirol *et al*., 2003)

Characteristics of Mitochondrial DNA For Diversity Studies

Mitochondrial DNA contains 37 genes, all of which are essential for normal mitochondrial function. Thirteen of these genes provide information for making enzymes involved in energy generation or oxidative photophosphorylation. The remaining genes are responsible for making molecules called transfer RNAs (tRNAs) and ribosomal RNAs (rRNAs). The major reasons for the adoption of mtDNA as markers of choice are well known. Experimentally, mtDNA is relatively easy to amplify because it appears in multiple copies in the cell. Mitochondrial gene is strongly conserved across animals, with little duplication, no intron, and a very short intergenic region (Gissi *et al*., 2008).

Mitochondrial DNA consists of the coding region for proteins and tRNAs, except for the D-loop region. It contains 13 protein-coding genes, 2 ribosomal RNA (rRNA) genes and 22 transfer RNA (tRNA) genes (Gray, 1989). The D-loop region is non-coding and is involved in the control of replication and transcription (Clayton, 1992). It is located between the tRNA genes for proline and phenylalanine. The D-loop region contains several promoters and an initiation site for H-strand replication. The nucleotide sequences of the other D-loop region is therefore considered to be variable and without effect on transcription and replication. Mitochondrial DNA appears to evolve more rapidly than nuclear DNA (Brown *et al*., 1980).

Structure of mtDNA

The D-loop region contains a noncoding sequence and includes a hypervariable region (Greenberg *et al*., 1983). Changes or repeats in the hypervariable region are highly polymorphic. Mitochondrial DNA D-loop (control region) contains two hypervariable regions approximately 400 bp in length and termed as hypervariable region-I (HVI) and hypervariable region II (HVII). The rate of mutation in these hypervariable regions is significantly higher than in the rest of mtDNA (Greenberg *et al*., 1983). The pattern of nucleotide substitution in this region is quite complicated; the ratio of transitional to transversional nucleotide substitutions is very high (Brown *et al*., 1982; Aquadro and Greenberg, 1983) and the rate of nucleotide substitution varies extensively among different sites (Irwin *et al*., 1991).

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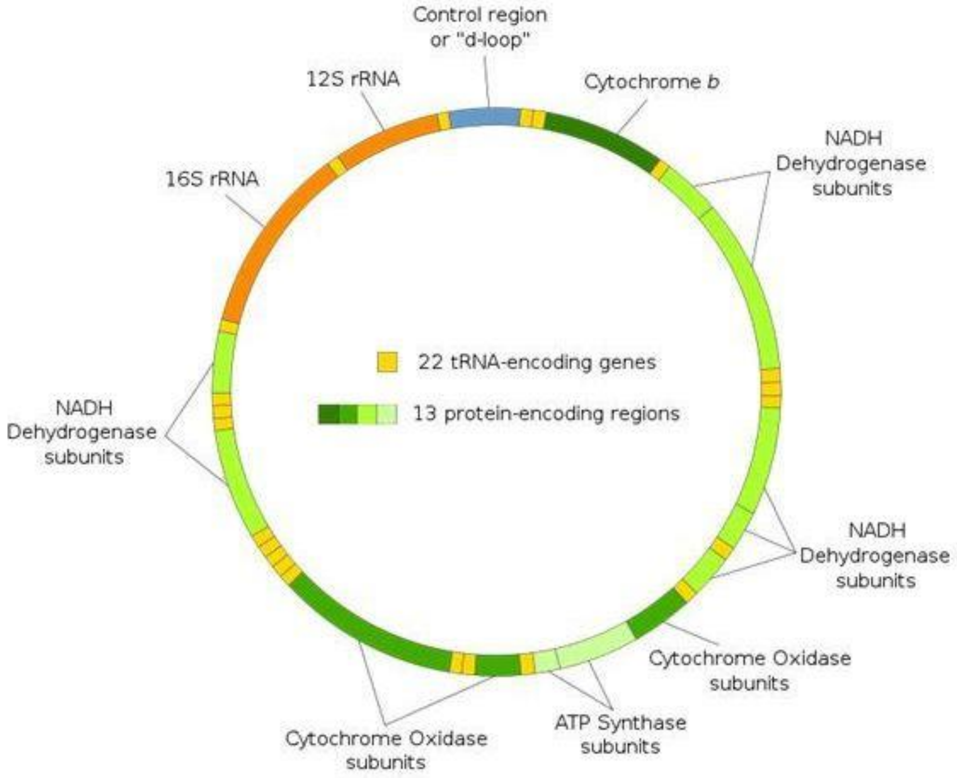

Fig. 1: Shows the structure of mtDNA having 13 protein-coding genes, 2 ribosomal RNA (rRNA) genes and 22 transfer RNA (tRNA) genes with a D-loop (Controlling region) (Park and Larsson, 2011)

Mitochondrial DNA has been the most popular marker of molecular diversity, for a combination of technical ease and supposed biological and evolutionary properties of clonality, near neutral nature and clock like nature of its substitution rate. Mitochondrial DNA (mtDNA) represents only a small fraction of the organism's genome size, yet it has been by far one of the most popular markers of molecular diversity in animals. Cytoplasm inherited mtDNA is free from genetic recombination and remains conserved for a species, making it particularly useful for reconstructing maternal based phylogenies unaffected by genetic exchanges. Measurements of mitochondrial DNA diversity are usually based on control region sequences, which exhibit greater variation than the rest of the molecule. This property makes mtDNA distinct from highly polymorphic microsatellite markers which are co-dominant in nature and makes it highly informative in evolutionary studies and in tracing maternal lineages (Bruford *et al.*, 2003). Variations in the mitochondrial DNA have proved extremely useful in studying recent genetic diversity.

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Assessment of Genetic Diversity by Mitochondrial DNA

Mitochondrial DNA with unique features of maternal inheritance, a relatively fast rate of evolution and lack of recombination have been proven to be useful markers for a variety of purposes such as genetic variation, parentage, breeds genetic diversity and determining population substructure (Ciampolini *et al.*, 1995; MacHugh *et al.*, 1998; Edwards *et al.*, 2000; Canon *et al.*, 2001; Tapio *et al.*, 2006; Ginja *et al.*, 2009; Li and Kantanen, 2009). Vertebrate mtDNA includes, in addition to coding regions, a non-coding segment the displacement loop (D-loop), which is the major region for mtDNA expression (Taanman, 1999). Therefore, sequence differences in mtDNA D-loop may alter the transcription and/or replication rates (Schutz *et al.*, 1994). Despite its functional importance, this region has a rate of nucleotide substitution five to ten times higher than that of nuclear DNA (Brown *et al.*, 1979). Initially, when 1st evolutionary studies using purified mitochondrial DNA were completed it became evident that besides its ease of isolation and small genome size mtDNA is maternally inherited (Lansman *et al.*, 1983). Mitochondrial DNA D-loop is mostly used to evaluate genetic diversity and phylogenetic relationship in many animal species including cattle (Bradley *et al.*, 1996; Loftus *et al.*, 1994; Mannen *et al.*, 1998; Mannen *et al.*, 2004), pig (Giuffra *et al.*, 2000), sheep (Hiendleder *et al.*, 1998), horse (Vila *et al.*, 2001) and goat (Luikart *et al.*, 2001; Mannen *et al.*, 2001).

Specific advantages of using D-loop of mtDNA for diversity analysis include : (a) its large allelic variation, which has not been affected by the loss of autosomal genetic variability in cattle since the introduction of artificial insemination (AI) (Taberlet *et al.*, 2008); (b) the copy number of bovine mtDNA molecules, ranging from 220 to 1720 per cell, and its applicability in severely decomposed samples in which nuclear DNA has already degraded (Xu *et al.*, 2009); (c) typing is efficiently performed by the widely used method of PCR-direct sequencing; (d) Although, it is a multi-allelic marker, but its direct sequencing is less prone to error than microsatellite genotyping and unlike single nucleotide polymorphisms (SNPs), it can quickly detect the samples containing DNA from multiple individuals by revealing more than two alleles per marker (Karniol *et al.*, 2009). The 1st mitochondrial genome which was sequenced entirely includes human (Anderson *et al.*, 1981), mouse (Bibb *et al.*, 1981) and cattle (Anderson *et al.*, 1982). Later the entire human mitochondrial DNA molecule was mapped. Soodyall *et al.* (1996) studied the utility of mtDNA in the reconstruction of human evolution and origin and in tracing population relationships and for analyzing ancient remains.

Virtually every molecular study of animal species involves mtDNA haplotyping at some stage. Recently a mitochondrial fragment, COX1, was elected as the standardized tool for molecular taxonomy and identification (Ratnasingham and Hebert, 2007). After Avise *et al.* (1987) and Moritz *et al.* (1987), many other population geneticists and molecular systematists have adopted this tool with little reserve. Mitochondrial DNA is highly variable in natural populations because of its high mutation rate, which can generate some signal about population history over a short time frame. Variable regions (e.g. control region)

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are typically flanked by highly conserved ones like ribosomal DNA, in which PCR primers can be designed. Certainly, mtDNA is the most convenient and cheapest solution when a new species has to be genetically explored in the wild. The only technical issues associated with the marker arise from illegitimate amplification of mitochondrial genes that have been inserted into the nuclear genome in some species (Bensasson *et al.*, 2001). Thus, mtDNA diversity has been the primary focus for researchers investigating domestic animal diversity and origin (MacHugh and Bradley, 2001) due to a combination of genetic characteristics like uni-parental mode of inheritance, lack of recombination and presence of hypervariable region.

The rapid rate of sequence divergence of mtDNA makes it suitable for the analysis of short-term evolutionary phenomena, while the maternal mode of inheritance allows the evolutionary relationships between lineages to be defined in terms of their phylogenetic divergence without the ambiguities caused by recombination. Therefore, mtDNA polymorphisms have been widely used to investigate the structure of populations, interspecies variability (Bradley and Cunningham, 1999; Cymbron *et al.*, 1999; Magee *et al.*, 2002; Troy *et al.*, 2001).

Limitations of Mitochondrial DNA (mtDNA) Marker in Livestock Diversity

Mitochondrial DNA has been used as a molecular clock, as it can be used for estimation of time of origin of the breed, its divergence and phylogeography. It is mostly because of the accumulation of neutral mutations occurring at an approximately constant evolutionary rate within the mtDNA. The mtDNA divergence level therefore roughly reflects the divergence in the population (Howell *et al.*, 2008; Galtier *et al.*, 2009). Mitochondrial DNA marker has been widely utilized in population studies particularly based on maternal lineages (Grechko, 2002; Kim *et al*., 2003) among the breeds of several species like buffalo (Kumar *et al.*, 2007), goat (Joshi *et al.*, 2004), pig (Larson *et al*., 2005), horse (Cozzi *et al*., 2004) and cattle (Bradley *et al.*, 1996; Cai *et al.*, 2007).

Although mtDNA is widely used for diversity and phylogeographic studies, in recent years issues arise due to the difference of mitochondria and nuclear genome at ploidy level, mode of inheritance, the degree of recombination, effective population size, mutation rate, repair mechanisms, etc. (Scheffler, 1999). It is also concluded by certain workers that inferring about the biology of the whole organism from a small fraction of the genome, such as mitochondria, is inappropriate as this single molecule alone may not always be sufficient to infer about the entire organism (William *et al.*, 2004). Further, allozymes were replaced by mtDNA in population history and diversity studies with the hypothesis that mtDNA diversity would reflect effective population size more accurately than allozymes (Foltz, 2003). Bazin *et al*., 2006 found that diversity of a given species does not reflect its average population size. Furthermore, mtDNA is unable to detect the male-mediated gene flow during evolution or during diversity analysis. So, for an overall

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diversity analysis, the approach of mtDNA need to be supplemented by other markers such as autosomal microsatellite markers and Y-chromosome DNA based information.

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