Journal of Entomology and Zoology Studies

Available online at www.entomoljournal.com

E-ISSN: 2320-7078
P-ISSN: 2349-6800
JEZS 2019; 7(3): 1561-1564

Received: 22-03-2019
Accepted: 24-04-2019

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Importance and utilization of non-additive genetic variance in farm animals

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Abstract
The phenotypic expressions of quantitative traits *viz.* milk production, egg production are under the control of large number of genes which interacts together to express a particular trait. There expressions depend not only on the genotype, but also due to interaction of genotype with an environment. The genotype of a trait, in turn, depends on both additive and non-additive type of gene action. For low heritability and complex traits such as fitness/survival or reproductive traits, the additive genetic variance does not show much of the impact. For a breeding program to be effective, mate selection along with appropriate breeding method is important to control inbreeding depression and to get maximum heterosis due to non-additive type of gene action. These methods includes various type of out breeding programs such as crossbreeding, recurrent selection, recurrent reciprocal selection, etc., mainly in species with short generation intervals like swine and poultry.

Keywords: Quantitative traits, genetic variance, selection, breeding program

Introduction
With the increase in world's global population that may reaches up to 9 billion by 2050 [1], the demand for livestock products as a food will also be increased [2]. Thus, it will exert a tremendous pressure on the livestock sector to fulfil this demand. To mitigate this situation effectively, the genetic improvement in livestock is one of the methods that can be employed to improve the production efficiency of livestock. The genetic variation (or phenotypic value) in quantitative or complex traits can be partitioned into many components due to genetic and environmental effects. These genetic effects, which are caused due to action of genes, are further partitioned into additive, dominance and interaction effects of genes [3]. The dominance and interaction effects of genes are called as non-additive type of gene action.

$V_P=V_G+V_E+V_{GE}$
$V_G=V_A+V_D+V_I$

Where,
V_P = Phenotypic variance
V_G = Genetic variance
V_{GE} = Variance associated with the interaction of genetic and environmental factors
V_E = Environmental variance
V_A = Additive genetic variance
V_D = Dominance variance
V_I = Variance due to epistasis

In additive gene action, two or more genes source a single contribution to the final phenotype, or when alleles of a single gene (in heterozygotes) combine so that their combined effects equal the sum of their individual effects, however, in non-additive type of gene action, the value of offspring is not exactly equal to that of their parents. The non-additive genetic effect includes dominance, over dominance and epistasis [4]. In dominance and over dominance, the interaction between two alleles occurs at same locus, whereas, in case of epistasis, interaction between two alleles occurs at different locus. The additive genetic variances are heritable and are highly transmitted from parents to next generation offspring. In an offspring, the contributions that occur due to non-additive genetic variances are usually lesser, still the traits

With low heritability such as fitness/survival traits have substantial variation from non-additive gene action which cannot be ignored, as such non-additive effects poses a substantial contribution to variation of complex traits [5]. However, non-additive genetic effects have been ignored in the genetic evaluation of livestock for several reasons such as the lack of informative pedigrees, such as large full-sib families, the calculations involved are more complex, the fact that statistical additive variance captures biological dominance or higher order interaction effects and the difficulty in using dominant values in practice (mate allocation). As a consequence, estimates of non-additive genetic variances are scarce in livestock populations [6]. Thus, to improve the accuracy of prediction of breeding values along with response to selection and to get maximum benefit of mate selection/breeding methods because of non-additive genetic variance, their estimation is of utmost importance [7, 8].

Utilization of non-additive genetic variance

The main genetic consequence that occurs during non-additive genetic action (dominance, over dominance and epistasis) which is commonly utilized by animal breeders for improving the performance of animal is heterosis. The heterosis is the average superiority of an offspring as compared to the average of it's selected parents. The heterosis may be in both positive or in negative direction. The heterosis on positive direction is called as hybrid vigour. The extent of heterosis varies with the type of genotype of an individual i.e. the magnitude of heterosis increases with increase in hetrozygosity and decreases with an increase in homozygosity. Thus, amount of heterosis will be higher, if greater will be the differences among genotype of selected parents and more intense will be the form of out breeding. The amount of heterosis expressed for a particular trait is inversely related to the heritability of a trait. The animal's performance is very strongly associated with gene combination value rather than breeding value [9]. In general, the heterosis causes the greater improvement for traits with low heritability *viz*. reproductive, survival and fitness traits (At least 10%), moderate improvement for moderately heritable traits *viz*. production traits (At least 05%) and lowest improvement for traits with high heritability like structural and anatomical traits [10]. Since, the heterosis in animals arises due to the effects of gene combinations, thus the genetic principle employed for utilizing the heterotic effects in offspring depends upon differences in the frequencies of different alleles at each locus that contributes to a trait [11]. Larger these differences, greater will be the heterozygosity and more will be the heterosis effects. In farm animals and field conditions of India, selection of parents with greater variability and crossbreeding is the most common method of out breeding employed for improvement in vitality and performance of livestock. Among different species of livestock, those which are highly prolific and with shorter generation interval like swine and poultry, the suggested procedure to exploit the non-additive genetic variation is based on combination of selection and crossing. Hence, due to non-additive effects of genes, an individual in certain mating combinations (having high heterotic value) has a special breeding value [12, 13].

In large animals, breeds that are least closely related show the most heterosis when crossed [14]. Thus, crossing of breeds or lines that vary greatly in gene frequencies is always desired. In such cross breeding programs, the parent line should be selected in such a way so as to improve the performance of an offspring, which is generally carried out by reciprocal recurrent programs. In such cases, to predict the value of a parent's crossbred offspring various markers can be utilized by comparing with a crossbred reference population. This should cause the heterosis in the cross to steadily increase [15].

Breeding technologies employed in farm animals

The breeding technology refers to the method adapted for crossing between the best selected individuals as parents, so as to get the offspring with best performer genotype. The aim of all these different breeding methods is to get maximum advantage of heterosis through various non-additive genetic effects [16]. The heterosis may be parental (maternal or paternal), referring to the performance of animals as parents or may be individual heterosis, referring to non-parental performance of an individual. The most commonly used breeding technologies in the farm animals that can be used are as follows:-

1. Cross breeding:- It is refers to the crossing between two different pure breeds. It is mainly used for producing commercial animals in an attempt to take the advantage of hybrid vigour. The breeding value of offspring produced by crossbreeding is usually lower, however, the judicious crossing of breeds that complement each other results in increases vigour. Thus, the economy of crossbreeding depends upon whether the increase in production is more enough to balance the reduction in breeding value of the crossbred individuals and increase in cost of replacement of purebred breeding stock under a cross breeding system. It is more profitable in those species where the fertility rate is high and the cost of replacement of females is lowest. Therefore, it has wider application in those species which are prolific and is having short generation interval like pigs and poultry as compared to cattle [17]. The cross breeding can be practiced in different ways depending upon the number of breeds used and the manner of their crossing [18]. It may be of two breed cross/continuous F_1 production (takes advantages of individual heterosis only and not maternal heterosis [9], three breed crosses (takes advantages of individual as well as maternal heterosis [19], inter se mating (gives 100% heterosis in F_1, which reduces by 50 % in next generation [4], four way/double cross (forms double hybrids and is extensively used in commercial poultry production), backcross (takes full advantage of maternal heterosis and a part of individual heterosis [20], rotational crossing/sequence breeding, in which two or more breeds are used in sequence/rotation on crossbred female populations. The levels of heterosis/hybrid vigour achieved in rotational crossbreeding vary with number of breeds involved [9].
2. Breeding approaches for combining ability:- It includes the general and specific combining ability. The mean performance of the line in all of its crosses with other lines expressed as deviation from mean of all possible crosses is called the general combining ability (GCA), while the specific combining ability (SCA) is the performance of a particular cross of two lines and is expressed as a deviation from the sum of general combining ability of the two lines. This is due to dominance, over dominance and epistasis. In general, recurrent selection and recurrent reciprocal selection methods of breeding are used to improve GCA and SCA.

The recurrent selection involves testing different segregating populations against a common broad based tester population and then selecting individuals within varying populations on the merit of their cross progeny performance. The selected individuals are mated to members of their own population to produce the next generation. This process is repeated through successive cycles. The two selected populations are the crossed which is expected to result in the production of superior hybrids. In reciprocal recurrent selection, instead of using constant tester strain, two segregating populations were used and selected for combining ability. The parents are selected on the basis of performance of the progeny and then selected parents are re-mated to the members of their own lines to produce the next generation of parents. The whole cycle is repeated each generation to form the best commercial hybrids.

Species wise utilization of non-additive genetic variance in farm animals

The non-additive genetic variance had been utilized in different species of livestock with varying breeding programs. This has improved the production and performance of these animals. In cattle, crossbreeding is effective because of heterosis (NAGA) and breed complementarity (AGA) [17]. There has been increase in the productive performance - 38, 1.57, and 5.46 kg higher for milk, fat, and protein yields, respectively as compared to the random matings [21]; reproductive - F_1 Holstein-Jersey crossbred was 7 days younger at first calving, had a 9-day shorter calving interval, a 6 percentage unit greater pregnancy rate in the first 42 days of the breeding season and a 3 percentage unit greater survival rate to next lactation as compared to the parental mean [22] and better calf growth and lifetime productivity [23].

In swine, although the additive genetic effect plays a greater role on growth and carcass traits however, non-additive genetic effects *viz.* Dominance effect were important for all traits, particularly in back fat thickness [24], in daily weight gain [25]. Similarly, non-additive gene action causing heterosis and recombination significantly increases number of nipples, weight at puberty, lactation weight loss, litter size, and litter birth weight in pigs [19]. Thus, in pigs, terminal system, rotational and combination system of crossbreeding are employed for the utilization of non-additive genetic variance [17].

In poultry, crossbreeding is the most common technique employed for production of crossbred chickens, improvement of indigenous native chicken breeds or for creating a synthetic breed that has desirable traits of one or more breeds within the shortest time. Crossbred birds have better performances as significant differences among the F_1 progenies is observed for body weight, average feed intake and feed conversion ratio due to the positive heterotic effects [26]. In poultry, Dominance variance accounted for a significant proportion of the total genetic variance in different seven feed related traits, ranging from 29.5% for $trait_1$ to 58.4% for $trait_7$ [27]. However, long-term and simple strategies are necessary as there is the need to efficiently exploit the potential of indigenous breeds. It must be achieved while also considering the variable socio-economic and cultural values of livestock in different societies or regions [28].

Conclusion

To improve the performance of livestock animals, the genetic intervention is one of the methods. These genetic potential can fully be exploited by using the non-additive genetic variance component. For utilizing the non-additive genetic variance, particularly all types of heterosis, only mate selection is not sufficient but also requires the improved and appropriate breeding techniques. In most of the livestock species, cross breeding technique, in varying forms may be employed, however, it should be used judicially to improve production performance along with considering the socio-economic and cultural values of livestock in different societies or regions.

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