



Breeding techniques to exploit non-additive gene action for improvement of Livestock

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ABSTRACT

The architecture of a trait is influenced by both additive and non-additive gene action. In the infinitesimal model, a very large number of genes each with very small additive effects contribute to a trait. Conversely, for a finite locus model, changes in genetic variances owing to truncation selection can be permanent as some or even all loci could get fixed for the favorable allele. That the additive genetic variance should decrease in a finite population because of genetic drift, is a well established principle of evolutionary biology. On the other hand the increase in non-additive variance in a population experiencing genetic drift could be explained by both dominance and epistasis (GCV). The non-additive genetic variation in some traits like viability and fertility is very important in all species of farm animals, and for this the inbreeding depression to a large extent has been observed in these traits. The breeding technologies that used to take advantage of livestock farm animal are cross breeding, terminal sire mating, composite breeding and reciprocal recurrent selection technology. The non-additive genetic variation is very important for viability and fertility in all species of farm animals. Several methods have been adopted to exploit non-additive genetic variation based on a combination of selection and mating that utilized in cattle and buffaloes through cross breeding and in poultry and pigs through terminal sire crossing.

Keywords- Breeding techniques, Cross breeding, GCV, Livestock, Non-additive gene effect, Rotational Crossing, Terminal sire crossing

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INTRODUCTION

The genetic architecture of a trait can greatly influence the effect of both additive and non-additive gene action. In the infinitesimal model, a very large number of genes each with very small additive effects contribute to a trait (25,41). When truncation (or divergent) selection is applied to the infinitesimal model, the change in genetic variance is temporary because linkage disequilibrium is induced between the selected genes. As soon as selection ends, genetic variance tends to be restored to the original level (12). The number of generations of random mating required to restore the level of genetic variance depends on the degree of linkage disequilibrium in the population (21). Conversely, for a finite locus model, changes in genetic variances owing to truncation selection can be permanent as some or even all loci could get fixed for the favorable allele. Recently, the rapid expansion of molecular methods for determination of quantitative trait loci (QTL) has given support for the presence of major genes behind many characters (4,46). Fisher (25) also emphasized that the genetic variation underlying a quantitative trait could be partitioned into different components using a least-square principle. The partition includes an additive part due to the additive effect of an individual locus, a dominance part due to within-locus interactions, and an epistatic portion due to between-locus interactions (34). Cockerham (20) and Kempthorne (38) proposed a parameterization to interpret how different genetic effects contribute to the genotypic value, including dominance and epistasis. Cockerham (20) used the concept of two parental populations' model to construct an F₂ reference population with two loci in Hardy-Weinberg equilibrium, and derived an orthogonal partition of the genetic variance in the F₂ population. Crow and

Kimura (21) and Mather and Jinks (42) both the group independently applied the two-locus genetic model to examine epistasis, but unlike Cockerham, they used an F2 reference population (pure lines derived from selfing). While most genetic models utilized by the following researchers Crow and Kimura (21), Mather and Jinks (42), Kao and Zeng (36) and Zeng *et al.* (59) were further extended form of Cockerham's genetic model to include multi-locus gene interactions in a segregating population for the purpose of QTL analysis. The additive genetic variance usually decreases in a finite population because of genetic drift that is a well accepted principle of evolutionary biology proved by Crow and Kimura (21) and Falconer and MacKay (24). On the other hand the increase in non-additive variance in a population experiencing genetic drift could be explained by both dominance and epistasis (31,54,40). Willis and Orr (56) investigated the role of dominance variance in a bottleneck population, where they emphasized that a different degree of dominance may increase the additive variance towards a particular phenotype. The effect of epistatic to additive genetic variance in a bottleneck population has been studied theoretically by Cheverud and Routman (18) and Naciri-Graven and Goudet (45). Wang *et al.* (54) using data on viability in *Drosophila melanogaster* going through bottlenecks to quantify the effect of dominance. Also, Waldmann (52) and Jannink (35) suggested that high levels of additive variance in a small population of the plant *Scabiosa canescens* could be explained by the presence of dominance. This phenomenon has also been verified experimentally in the housefly by Bryant *et al.* (11) and Bryant and Meffert (10), in *D. melanogaster* by López-Fanjul and Villaverde (39) and García *et al.* (27) and in mouse by Cheverud *et al.* (19). Under the finite locus model, when directional selection is acting on a population for a certain quantitative trait, the additive genetic variation is also expected to decrease according to traditional quantitative genetic model (21,24). However, some theoretical studies of selection suggest that the level of additive variance can be sustained or even increased when non-additive variance is present in a manner similar to the action of genetic drift (35,16). Experimental evidence for this phenomenon was found by Martinez *et al.* (41) when they selected for body fat in mice, and by Sorensen and Hill (49) that performed a short-term selection experiment for abdominal bristle number in *D. melanogaster*. Furthermore, in a recent study, Carlborg *et al.* (15) and Carter *et al.* (16) showed that epistatic interactions between four loci mediated a considerably higher response to selection of growth in chicken than predicted by a single-locus model. However, none of these studies have compared the development of variance components between different genetic models in situations of directional selection. Theoretical investigations of the effect of selection on the re-distribution of additive and non-additive genetic variances are scarcer than for the drift situation (16). Pair wise epistatic gene interactions affecting a trait have been simulated for the directional truncation selection process (28,58,26). However, few simulations have been performed on multiple interacting genes. The effect of multi-locus genetic interactions is important for understanding the outcome of evolution and artificial selection as they could change the additive effects as the genetic composition of the population changes (6). Simultaneously, the genetic variance and selection response are also affected by the presence of non-additive genetic variances in a trait subjected to directional truncation selection.

GENE ACTION

Gene action refers to the behavior or mode of expression of functional units, genes that govern the development of various characters in an individual⁵⁰. Genes actually control the synthesis of proteins which ultimately govern the expression of various traits of an individual. It was first studied by Archibald Edward Garrod in 1902.

TYPES OF GENE ACTION

There are two types of gene action i.e. additive and non-additive. *Additive gene* action is also known as the breeding values (BV). Breeding value defined as the parental value that is the value of an individual as a contributor of genes to the next generation. In other words it represents only that part of genotypic value that can be transmitted from parent to offspring. But it does not appear in the basic model for quantitative traits, i.e.

$$P = \mu + G + E$$

In fact, it is the only truly genetic component in the model of genotypic value (G) as mentioned below. *Non-additive genetic* variation results from interactions between genes that represents the different degree of dominance and epistasis (53). Interactions between genes at the same locus are called dominance, and interactions between genes at different loci are called epistasis (36,34). Although many studies have shown that non-additive effects have a substantial contribution to variation of complex traits, this source of variation is generally ignored in the genetic evaluation of complex traits as by Bourdon (13) and Goodfellow (30). Thus the total value of a given genotype (G) is determined by its additive value (A) together with interaction effect of genes i.e. deviations caused by dominance (D) and epistasis (I) (50). Finally, we can say that genotypic value can be indicated as

$$G = A + D + I$$

The dominance and epistatic effects are known as non-additive effects of genes. So, apart from breeding value the remaining portion of genotypic value is called gene combination value (GCV). Gene combination value is the part of an individual's genotypic value for a trait that is due to combined effects- dominance and epistasis (40,34). Because individual genes and not gene combinations survive segregation and independent assortment during meiosis, gene combination value cannot be transmitted from parent to offspring. An animal's breeding value and gene combination value together constitute its genotypic value for a trait. In model form,

$$G = BV + GCV$$

The sole purpose of selection is for the improvement of the trait to increase the frequency of desirable genes controlling the trait with additive effects in particular but at the same time non-additive effects of genes cannot be ignored (29,15). The selection theory for each type of gene action is different. Thus once the kind of gene action is identified, the selection system which should maximize the effect of both types of gene action may be followed. So, Bourdon (13) gave the basic model for quantitative traits that can be expanded to include both breeding value (BV) and gene combination value (GCV). Mathematically,

$$P = \mu + BV + GCV + E$$

where, P = Phenotypic value or performance of an individual animal for a trait,
 μ = the population mean or average phenotypic value for the traits for all animals in the population,
 BV = Breeding value of an individual animal for the traits,
 GCV = Gene combination value of an individual animal for the traits

IMPORTANCE OF NON-ADDITIVE GENE ACTION

The selection response gradually declines and finally ceases as a consequence of continuous selection for several generations applied to closed population. This is explained due to the exhaustion of additive genetic variance (26,47). However, in some cases the lines continue to show genetic variation, which is partly or mainly of non-additive in nature. The non-additive genetic variation in some traits like viability and fertility is very important in all species of farm animals, and for this the inbreeding depression to a large extent has been observed in these traits (47). Walsh (53) and Carlborg *et al.* (15) independently suggested procedure to exploit the non-additive genetic variation, based on combination of selection and crossing and found their useful application in improvement of pig and poultry. As a result of these non-additive effects of genes an individual in certain mating combinations has a special breeding value (13,14). Unlike breeding values, gene combination values of individuals are rarely, if ever, predicted. This is partly because prediction of gene combination values is difficult, but mostly because a prediction of gene combination value has little practical use as given by Beckett and Ludwick (7) and Hu *et al.* (34). Gene combination value is not, after all, transmitted from parent to offspring. To the contrary, an individual's gene combination value for a trait can have a great influence on its own performance revealed by Walsh (53). Inbreeding depression and hybrid vigor or heterosis are two manifestations of the same phenomenon (22,31,53). Hybrid vigor and inbreeding depression are just alternative names for favorable and unfavorable gene combination value. Beckett and Ludwick (7) mentioned that the importance of gene combination value depends on whether the trait is important for a seed stock producer or commercial producer. Seed stock producers market breeding potential, so breeding value is of primary concern to them. Commercial producers market performance, and to the degree that gene combination value is of concern to them (3).

Inbreeding depression comes from the increase in homozygosity brought on by inbreeding and the accompanying expression of unfavorable recessive alleles occurring in homozygous combinations (50). Hybrid vigor derives from the increase in heterozygosity resulting from out breeding and the attendant masking of the expression of unfavorable recessive alleles occurring in heterozygous combination (44). As both the inbreeding and heterosis are functions of gene combination value and not breeding value, they cannot be inherited. The offspring of a mating between two highly inbred but unrelated individuals that suffer from inbreeding depression is not inbred at all and, in fact, should exhibit a high degree of hybrid vigor was illustrated by Carlborg *et al.* (15) and Ahlborn-Breier and Hohenboken (1). Likewise, the offspring of a mating between two outbred but closely related individuals that enjoy considerable hybrid vigor is inbred and may show signs of inbreeding depression. So, inbreeding depression and hybrid vigor are maintained in populations not through inheritance, but through mating systems designed to influence homozygosity and heterozygosity (36,57). In fact, both inbreeding and hybrid vigor are affected not only by the relative numbers of homozygous and heterozygous loci influencing a trait, but also by the degree of dominance exhibited at each locus (33). Traits that exhibit substantial vigor and inbreeding depression are heavily influenced by the effects of dominance (i.e., gene combination effects). Bourdon (13) developed a very important concept on non-additive effect satisfying to the previous findings of Van Der

Werf and De Boer (50) that animal performance is very strongly associated with gene combination value rather than breeding value. If performance of a particular trait of an individual is closely tied to gene combination value, then the relationship between performance and breeding value is therefore weak. In other words, heritability is low. On the other hand, traits that show little or no hybrid vigor or inbreeding depression are influenced very little by gene combination effects. Performance in these traits is much more likely to be associated with breeding value than gene combination value as established by Calus (14). That's why the heritability of these traits is likely to be higher. Usually in order to exploit the non-additive genetics effect breeding techniques has been adopted time immemorial to improve the genetic merit of farm animals in terms of breeding value to increase their productivity to meet the increasing demand of growing population.

BREEDING TECHNOLOGIES- It stands for the different technologies that used for mating between the selected individual to exploit a weighted combination of traits defining aggregate breeding value (14). The advantage of cross breeding on non-additive gene effects is through heterosis (44) and that of additive gene effects is through complementarity when two or more characters complement each other (36,1). The amount of heterosis depends on the environment, genetic variability between two populations involved in crosses and the non-additive gene effects (44). The heterosis may be parental (maternal or paternal) referring to the performance of animals as parents and the individual heterosis referring to non-parental performance of the individual. The breeding technologies in the farm animals can be guide by four techniques as mentioned below-

1. Cross Breeding
2. Terminal Sire Mating
3. Composite Breeding
4. Reciprocal Recurrent Selection Technology

1) CROSS BREEDING: - It is refers to the crossing between two different established breeds or strains to take the advantage of heterosis for improvement of breeds (43). It is also undertaken to practice the good quality of both the breeds/strains in complementary action. The cross breeding can be practiced in different ways depending upon the number of breeds used and the manner of their crossing (9).

a) Two breed cross: When two pure breeds are mated together and their cross bred progeny are not used in breeding programme. The two breed cross system produces first cross, or F1, progeny. In this system, the progeny resulting from the cross of two breeds are usually all sold for slaughter or to another commercial breeder (32). The system is most useful for situations in which females of a specific breed are well adapted to a given environment.

b) Three breed cross: In this system of crossbreeding three breeds are used. The bulls of three breeds are used in rotation in successive generations of crossbred females of the previous generation (37,55). This is thus called the rotational crossing. This system is practiced to maintain heterozygosity and to utilize heterosis for maternal ability of the crossbred dams (55). Three breed cross requires the input of three separate breeds (55). Along similar principles as with backcross, all first cross male progeny are sold. First cross females are joined with bulls of a third unrelated breed, instead of with one of the parent breeds as in the backcross. All progeny of F1 dams are sold for slaughter (55). This system takes advantage of both maternal and individual heterosis, and of the complementarity of three breeds (54,17). An example would be the a case where the first two breeds are chosen to achieve maternal heterosis and adaptation to an environment, while the third breed (terminal sire breed) produces the most acceptable animals. This use of the F1 female is generally considered to produce the greatest lift in productivity, but it is influenced by the quality of pure breeds that are maintained to breed the F1 females (55).

c) Backcross: In a backcross system, all male calves produced from the first cross are sold for slaughter. Female F1 crossbred progeny are mated to males of one of the parental breeds and all progeny are sold for slaughter growth (32). This breeding system takes full advantage of heterosis for maternal traits such as fertility of the cow, and milking/mothering ability (as the mother expresses 100% of possible heterosis) and half of the possible heterosis for (37,44). This approach is most useful where adaptation to a specific environment is required from a particular maternal breed but where characteristics from the other parental breed are desired for carcass or growth traits (5). The crossbred F1 female would also have satisfactory environmental adaptation. Continual backcrossing is the system used by producers to upgrade or change from one breed to another without having to buy purebred cows, such as in development of Brahman herds in Queensland (51).

d) Inter-se mating: This term is generally used to crossing of crossbred progeny having the same level of inheritance of the two breed like crossing of F1 with F1.

e) Four breed crosses or Double two way crosses: The crossbred females produced by crossing two breeds (A and B) are mated with crossbred males produced from crossing another two breeds (C and D). Thus the mating is between (AB) X (CD).

f) Rotational cross

Rotational crossbreeding, sometimes referred to as sequence breeding, is when males of two or more breeds are mated to crossbred females. Over a number of years, each breed will have contributed its strengths and weaknesses equally. Variation seen in the progeny in early years of a rotational crossbreeding program may make it more difficult to consistently meet a specific market requirement in this production system (51). When the breeds used are similar, consistency of performance is less likely to be a problem, although levels of heterosis will also be lower if breeds or breed groupings are relatively closely related. Levels of heterosis achieved in rotational crossbreeding depend on the number of breeds involved (54). Once stabilized after many crosses, with a number of breeds (n) contributing equally, the level of retained heterosis may be expressed as:

$$(2n-2) / (2n-1)$$

It can be 3 breed 4 breed or n breed rotation crossing for example in 3 breed rotation crossing the males are used in following pattern-

g) Two-Breed Rotational cross- A two-breed rotation is started by breeding cows of breed A to bulls of breed B. In each succeeding generation, replacement heifers are bred to bulls of the breed that is the opposite of their sire (48). Two breeds of bulls are required after the first two years of mating. The two breeds chosen should be comparable in birth weight, mature size, and milk production. This minimizes calving difficulty in first-calf heifers and simplifies management.

h) Three-Breed Rotational cross- This system follows the same pattern as the two-breed rotation, but a third breed is added. The three-breed rotation maintains a higher level of hybrid vigor than the two-breed system (32). Mating plans can be confusing, but individual cows are not moved from one breeding group to another. Three distinct groups of cows are eventually created, and they are mated to the sire breed to which they are least related. This scheme continues for the life of the cow. After several generations the amount of retained heterosis stabilizes at about 86% of the maximum calf and dam heterosis, resulting in an expected 20% increase in the pounds of calf weaning weight per cow exposed above the average of the parent breeds (5).

2) TERMINAL SIRE SYSTEM -

Terminal sire crossbreeding systems are systems in which maternal-breed females (purebred or crossbred females that excel in maternal traits like conception rate, litter size, milk, and mothering ability) are mated to paternal-breed sires (sires that excel in paternal traits like growth rate and carcass yield) to efficiently produce progeny that are especially desirable from a market stand point⁵. Terminally sired females are not kept as replacements, but are sold as slaughter animals. These systems produce ample amounts of hybrid vigor, but their most important attribute is breed complement (17).

a) Two-Breed Terminal Sire cross- A two breed terminal cross system uses straight bred cows of one breed and a sire(s) of another breed and no replacement females are kept, therefore, must be purchased (48). Since all calves are marketed it is a terminal sire system. Charolais or Limousin sires used on Angus cows would be a common example. Implementations of two breed terminal sire systems are not desirable or recommended as they do not employ any benefits of maternal heterosis as the cows are all straight bred.

b) Three-Breed Terminal Sire Cross- This system uses a two-breed cross (F1) cow and a bull of a third breed. It produces maximum hybrid vigor in the cow and calf. This is an excellent system because hybrid vigor is realized for both growth rate and maternal ability. Replacement females for this system must be purchased or raised from another source. This is a good system for any size herd if high-quality replacement females are available.

c) Two Breed Rotational-Terminal Sire- The two-breed rotational with terminal sire system is sometimes called a rota-terminal system. It includes a two-breed rotational crossbreeding system of maternal breeds A and B. VanRaden and Sanders (51) describe that this portion of the herd is charged with producing replacement females for the entire herd, so maternal traits of the breeds included are very important. In this system approximately half of the cow-herd is committed to the rotational portion of the breeding system and half to the terminal sire portion. This system retains about 90% of the maximum calf heterosis plus capitalizes on 67% of the maximum dam heterosis; it should increase weaning weight per cow exposed by approximately 21% as calculated by Sölkner (48).

d) Three breed Rotational-Terminal Sire- This system involves the use of rotational mating of maternal breeds (breeds A and B) in a portion of the herd to provide replacement females for the entire herd. The older crossbred cows are then mated to the terminal sire breed (breed C) explained by Wang (55). The entire terminal cross off spring is marketed as described by Katpatal (37). This system maintains a high

level of production but also requires a high level of management. It almost does away with heifer selection since nearly all heifer calves produced by the rotational mating must be kept to maintain herd numbers.

e) Terminal Cross with Purchased F1 Females- The terminal cross system utilizes crossbred cows and bulls of a third breed. This system is an excellent choice as it produces maximum heterosis in both the calf and cow (51). As such, calves obtain the additional growth benefits of hybrid vigor while heterosis in the cows improves their maternal ability. The terminal cross system is one of the simplest systems to implement and achieves the highest use of heterosis and breed complementarities (17,44). All calves marketed will have the same breed composition. A 24% increase in pounds of calf weaned per cow exposed is expected from this system when compared to the average of the parent breeds.

3) BREEDING FOR COMPOSITE -

Development of a composite or synthetic breed results from the crossing of two or more existing breeds (43). There are many examples of this in Queensland: Santa Gertrudis, Drought master, Braford, Charbray, Brangus and Belmont Red. The primary advantage of forming composite breeds is that after the initial crosses are made, management requirements are the same as for straight breeding. McDowell and McDaniel (43) postulated that a market signal indicate the change in characteristics of the composite breed. Although, the initial selection of a breed depends on the desirable trait for a particular environment and target market. The percentage of heterosis increases as more breeds contribute in the initial mating program (17). While the heterosis will not be as high as that achieved with a rotational crossbreeding program with the same number of breeds, the management requirements will be reduced. For instance, if there are three breeds in a given composite, the amount of retained heterosis would be expected to be $(3-1) \div 3$ or two-thirds or 67%. Inbreeding is not usually significant when numbers are greater than 200 or 300 breeders. In the extreme case where a herd uses only one bull all heterosis is lost after approximately eight generations or 40 years. When two-, three- or four-breed composite are formed they retain 50%, 67%, and 75% of maximum calf (individual) and dam (maternal) heterosis and improve productivity of the cowherd by 12%, 15%, and 17%, respectively. Thus, these systems typically offer a balance of convenience, breed complementarities and heterosis retention (32).

a) Inbred crossing or line crossing- The inbred lines are those populations which have inbreeding coefficient (F) above 0.3375. The inbred lines are crossed to incorporate desirable characters and to get maximum amount of heterozygosity for commercial purpose (51). This is very commonly used in species like poultry and swine which are prolific breeder and, hence can undergo inbreeding for formation of inbred lines. The inbred crosses are generally called "incross hybrids". In some cases, more than two inbred lines are mated to produce a commercial stock for getting maximum heterosis (44).

b) Strain crossing- In this, different strains of a particular type of animals/ breeds are crosses. These strains are mildly inbred (<40%) and possess some characters unique to them. This type of crossing helps in infusing a character in commercial animal/flock which was absent earlier. It also helps to generate some milder form of hybrid vigor (48). This is now most commonly used in poultry to evolve new strains. This has an advantage over line crossing that it minimized the extinction of line due to inbreeding depression.

4) RECIPROCAL RECURRENT SELECTION:

Randomly selected individuals from each of the two non-inbred strains are progeny tested in crosses with each other. Those individual giving the best results in crosses from the two strains are inter- se mated to continue their respective strains. The crosses are made reciprocally like $M1 \times F2$ & $M2 \times F1$ & the parents are evaluated on the basis of cross progeny performance. The best performer male and female lines are selected. The selected lines are mated to member of their own line to produce the next generation of individuals which are to be tested by mating them with individuals of the second line produced in the same way. Thus RRS is the kind of progeny selection. This cycle is repeated over & over. The initial difference of gene frequency between the two lines is a pre-requisite of this method.

PREDICTION OF CROSSBREEDING PERFORMANCE AND MATE SELECTION

The use of molecular markers can help to solve the problem of deciding which combination of lines to test. Studies from cattle tend to suggest that there is a positive relationship between the genetic distance between the lines, as estimated from AFLP markers, and the amount of heterosis in the crossbred progeny (2). Genetic distance between two populations is a measure of the number of generation they have diverged from a presumed common ancestor, and is usually calculated from differences in allele frequencies between the populations at a number of loci (8). Although the correlation between genetic distance and heterosis is not always large, this method might target specific line combinations which are more likely to produce fit, high performing progeny (2). If this technique of combining lines for crossbreeding works, it should also be possible to use the same principles for mate selection. To achieve a

better commercial animal, the exploitation of non-additive variation in purebred lines should aim to produce the favourable allelic combinations in the crossbred generation. Selection methods such as Recurrent Reciprocal Selection (RRS) may be implemented to select the purebred lines at the nucleus level, with or without the use of molecular markers (23). RRS is a traditional selection method in which purebred parents are selected for purebred breeding on the basis of their predicted crossbred performance. RRS is theoretically efficient in the presence of over dominance, however, to our knowledge there is little evidence for over dominant gene action in livestock (and other) species. RRS used to be practiced in poultry breeding, but less so at present.

CONCLUSION

Non Additive Genetics effect (NAGA) is important to select animal for Specific Combination Ability (SCA) means to take advantage of hybrid vigour. The causes of NAGA for difference in SCA of the lines in crosses are dominance, over dominance or epistasis. Selection on the basis of individuality is not effective when traits are largely affected by NAGA but the improvement in such traits depends upon heterozygosity through cross breeding resulting in the expression of heterosis. Thus the ultimate goal is to produce breeds or varieties each of which is homozygous which will produce the desired phenotypic merit when crossed with each other. This is important when epistatic effects and over dominance is important. The non-additive genetic variation is very important for viability and fertility in all species of farm animals. Several methods have been adopted to exploit non-additive genetic variation based on a combination of selection and mating that utilized in cattle and buffaloes through cross breeding and in poultry and pigs through terminal sire crossing.

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