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Heterosis–Genetic Basis and Utilization for Improvement of Dairy Cattle: A Review

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Abstract
The phenomenon in which progeny of crosses between inbred lines or purebred populations are better than the expected average of the two populations or lines for a particular trait is known as heterosis. Utilization of heterosis is the main goal of crossbreeding. The amount of heterosis maintained in a herd depends on the type of crossbreeding system selected for breeding. Heterosis includes greater viability, faster growth rate and greater milk production in dairy cattle. The genetic basis of heterosis is nonadditive gene action (dominance, overdominance, pseudo-overdominance, and epistasis). The main requirements for heterosis are there must be genetic diversity between the breeds crossed and there must be some nonadditive gene effects present for the particular trait involved. No heterosis was observed for traits governed by additive gene action. However, it tends to be greatest for traits with low heritability and least for traits with high heritability in nature. Traits of low heritability (reproductive traits) are generally most benefited from heterosis as compare to high heritability (growth rate). They can be improved through the adequate use of crossbreeding systems.

Keywords: *Crossbreeding, heterosis, cattle*

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INTRODUCTION

Heterosis has been defined as the superiority of a hybrid organism when compared with its parents. If the performance of the crossbred animal is different from the midparent average for a particular trait, heterosis exists for that trait. Depending on the economic value of the difference, heterosis can be positive or negative, large or small and it may be considered to be favorable or unfavorable. Heterosis for a trait is specific for the two breeds involved in the cross. For example, heterosis for production and fertility may not be the same in Holstein-Sahiwal and Holstein-Tharparkar crosses.

This heterosis may be superiority of a single attribute or may be expressed as hybrid vigor for a number of traits. Heterosis arises from the effects of gene combinations means effects of pairs of genes [1]. Heterotic effects in the crossbred progeny depends upon the differences in the frequencies of the different alleles at each locus that contributes to the trait [2]; larger these differences greater the heterozygosity and the heterosis effects. Crossbred animals often show improvement in performance traits. This is known as heterosis or hybrid effect. The word ‘Heterosis’ was given by Shull in 1914 after observing the stimulation of heterozygosis upon cell division, growth performance and other physiological characters in maize. According to Shull, the developed superiority of the hybrid is hybrid vigour and the mechanism by which superiority is developed is heterosis. Lippman and Zamir [3] described that offspring from parents with greater genetic diversity are genetically superior to offspring of parents with lesser diversity.

The highest level of heterosis is most commonly seen in low heritable traits or functional traits affecting reproduction, survival and overall fitness of the animals. These traits often show at least 10% heterosis and low heritability. Production traits affecting milk yield and growth showed about 5% heterosis and a moderately high heritability [4]. Heterosis level differs depending on the type and number of breeds in the crossbreeding system, subsequently the expected level of heterosis is difficult to predict [5]. According to Lammers *et al*. [6], those traits having low heritability show more heterosis as shown in Table 1 in which main benefits of heterosis are seen in fitness and health traits. About 16% increase in the pounds of calf weaning weight per cow exposed above the average of the parent breeds [7]. Crossbreeding as a mating system optimizes the additive genetic and non-additive (heterotic) breed effects of *Bos taurus* and *Bos indicus* cattle in sustainable breeding systems [8].

The main aim of crossbreeding is to increase the dairy cattle production through new combination of genes in different breeds [9]. Crossbreeding can also result in adverse effects such as recombination loss. Separation of favorable gene combinations that are accumulated in the parental breeds results in recombination loss. This loss can be difficult to estimate although it has been seen to reduce the level of heterosis [10]. Two basic genetic requirements for a trait to exhibit heterosis are genetic diversity between the breeds crossed and presence of some non-additive gene effects for the particular trait involved. Absence of either one of these conditions being fulfilled for a particular cross for some trait would result in that trait exhibiting no heterosis in crossbred animals.

In such a case, the expected performance of the crossbred offspring would simply be the average of the performance levels of the particular purebred parents involved in the cross. For those traits that express heterosis, the magnitude of heterosis will be dependent upon how much genetic vaiablity exists between the two parent breeds. Degree of genetic similarity or dissimilarity that exists between the two breeds is known as genetic diversity. Non-additive gene effects refer to the kinds of gene actions that exist with regard to the many gene pairs that are involved in determining a particular performance trait. These effects fall in two categories: (1) non-additive gene effects that are expressed by individual gene pairs (due to level of dominance); and (2) non-additive inter-allelic interaction between the effects of genes present at one locus with the effects of genes at one or more loci (epistasis).

The continued maintenance of breeds and crossing them to find the highest performance levels combinations under broad range of existing management and environmental conditions is the practical way of using heterosis in beef cattle. This procedure will work irrespective of kinds of non-additive gene effects are responsible for the heterosis. Since increased heterozygosity was involved in the crossbred individual, intermating among crossbred individuals results in increased genetic diversity. Consequently, crossbred populations are less likely to breed true than the purebred populations.

Intermating crossbreds leads to decline in the numbers of heterozygous gene pairs and as a result a regression toward the average performance of the base parents. Thus, it seems very difficult, if not impossible; to fix heterosis, i.e., to maintain heterosis and its resulting high performance by mating those crossbred individuals having the highest degree of heterosis. Accordingly, to fully capitalize on increased productivity due to heterosis, it is necessary to restore the crosses among each generation of purebreds. Various environmental factors significantly affected the milk production efficiency traits indicating the scope of improvement in Jersey crossbred animals [11,12].

Table 1: *Relationship between Heritability and Heterosis of Different Traits.*

Traits	Heritability	Heterosis
Fertility, Mothering ability, Calf survival	Low	High
Birth and weaning weight, Milking ability and Feedlot gain	Medium	Medium
Mature weight, Carcass quality	High	Low

Table 2: *Average First Lactation Milk Yield in F_1 and F_2 Generations of Crossbreds.*

Genetic group	F_1	F_2	% decline	References
BS	2898	2183	24.67	Bhatnagar *et al.*, 1976 [28]
BS	3548	2805	20.94	Taneja and Chawala, 1978 [29]
JH	1679	1328	20.91	Parmar *et al.*, 1980 [30]
JR	1929	1115	42.20	Parmar *et al.*, 1980 [30]
FH	1933	1349	30.21	Parmar *et al.*, 1986 [31]
FG	3391	2533	25.30	Taneja and Bhat, 1986 [32]
JK	2547	2031	20.26	Patel *et al.*, 1989 [33]
FH	1926	1293	32.87	Bala, 1981 [34]
JH	1610	1139	29.25	Bala, 1981 [34]
KS (B × S)	3247	2380	26.70	Saha, 2001 [35]
KF (F × T)	3747	3105	17.13	Saha, 2001 [35]

F, Friesian; B, Brown Swiss; J, Jersey; S, Sahiwal; H, Hariana; K, Kankrej; R, Red Sindhi; G, Gir

The objective of choosing a three-way cross as compared to the traditional two-way cross was to exploit hybrid vigor in the future generations. About 86% hybrid vigor is maintained in later generations in case of three-way cross, while a two-way cross will level off at 67% and a four-way cross at 93% [4]. The decision to pick a three-way cross over a four-way cross can be explained by the complexity and dilution of individual breeds traits from generation to generation and by the minimal improvement of hybrid vigor at 6% in later generations as compared to a three-way cross program. Three-way crosses leads to increased heterosis along with longevity, protein and fat components, and calving ease [13].

In a three-way cross program, the F_1 and F_2 generations are both able to maintain 100% hybrid vigor as compared to a two-way cross program where hybrid vigor drops to 50% in the F_2 generation [14]. The F_2 crossbred cows had declined (17–42%) production performance on inter se mating between the F_1 animals. Crossbred performance in F_1 and F_2 generations of dairy cattle is given in Table 2 [15]. F_1 crosses yielded more milk (147%), were milked for more days and had shorter calving interval [16]. Studies in France have shown that the F_1 crosses tend to be above median average of the two breeds for milk but closer to the Normande for components [17]. Heterosis can also increase longevity of cows by 1.3 years and can increase the total calf weight weaned per cow by 30% over the life span of a dam [18]. Loss of heterozygosity in inter se mated populations does not occur if inbreeding is evaded [19]. Cows exhibit more hybrid vigour in first and second parities than at later parities [20].

UNDERSTANDING OF HETEROSIS

Complementary to phenomenon of inbreeding depression, hybrid vigor or heterosis is opposite. When inbred lines are crossed, the progeny showed an increase of those characters that previously suffered a reduction from inbreeding or in general term, the fitness lost in inbreeding tends to be restored on crossing. The amount of heterosis, expressed as the difference between crossbred (F_1) and inbred means (midparent values) is obtained by substituting the under mentioned equation:

$HF_1 = MF_1 – MP$
Where, MF_1 = Mean of F_1 progeny; MP = Mean ofparents
$HF_1 = \sum dy^2$
Where, d = Sum of dominance deviations of these loci that have different alleles in two lines and y = square of difference of gene frequency between thepopulation.

Thus, heterosis just like inbreeding depression, depends for its occurrence on dominance, loci without dominance (i.e., loci with d = 0), causes neither inbreeding depression nor heterosis. The amount of heterosis following a cross between two particular lines or populations depends on square of difference of gene frequency (y) between the populations. If population crossed do not differ in gene frequency there will be no heterosis, and heterosis will be greatest when one allele is fixed in one population and other allele in otherpopulation.

The amount of heterosis shown by HF_2 is the difference between F_2 and midparent value,
$HF_2 = MF_2 - MP$
Where, MF_2 = Mean of F_2 progeny; MP = Mean ofparents
$HF_2 = \sum ½ dy^2$

Thus, heterosis shown by F_2 is only half as great as that shown in F_1. In other words, the F_2 is expected to drop back half way from F_1 value. Now consider the joint effect of all loci at which the two populations differ. If genotypic values attributed to separate loci combine additively, we may represent the heterosis produced by joint effects of all the loci as sum of their separate contributions.

Effects of favorable genes are generally dominant to unfavorable genes. When lines homozygous for different genes or lines whose gene frequencies are different are crossed, the resulting offspring will be heterozygous and favorable dominant gene will mask the unfavorable recessive genes. The performance of hybrid will thus surpass that of parents; or even the better parent, if both favorable and unfavorable gene were present in each parental lines. In other words, each-pure bred with homozygous for some loci for favorable genes at some, for unfavorable genes at other. If first line complements the second line, the hybrid will have favorable genes at many loci than either of parents. Consequently, when favorable genes are dominant, the performance of hybrid will be superior to that of either of parental line.

Cunningham and Syrstad [21] had broadly reviewed the crossbreeding of different cattle breeds in tropics. Maximum experiments have been performed for dairy cattle crossbreeding in India and other Asian countries and a few in Africa, Australia, and Latin America. The production and reproduction performance of crossbred cattle indicated broad range of variation in different tropical countries based on the environmental and feeding management. They concluded that the average lactation milk yield of crossbred cattle under tropical environmental conditions fall in the range of 2000– 3000 kg. Main conclusions were as follows:

- Heterosis was estimated as 28% for milk yield, 14% for age at first calving and -6% for calving interval and this was due to crossbreeding.
- It may be due to epistatic effects that performance of F_2 for milk yield was below expectation (between mid-parent mean and F_1) for a simple additive plus dominance model.
- In *Bos Taurus* cattle, having up to 50% exotic inheritance, there was linear improvement in all the traits and above that inheritance there was no clear trend except a slight increase in calving interval.

TYPES OF HETEROSIS

Dickerson [19] had described three main types of heterosis on the basis that some of the traits have three genetic components, i.e., Direct, Maternal, and Paternal heterosis.

Individual (Direct) Heterosis

The direct component of a trait is due to the effect of an individual's gene on its performance and the improvement in performance of an individual animal due to these genes, relative to the mean of its parents, which is not attributable to maternal, paternal or sex linkage effects is called individual heterosis. According to Spangler [22] advantages of crossbred calf are given in Table 3, which showed individual heterosis.

Maternal Heterosis

Maternal heterosis is the heterosis in a population due to the effect of gene in the dam, which influences the individual's performance via the environment provided by crossbred dam; e.g., milk production, improved prenatal environment, large litter size, etc. According to Spangler [22], advantages of crossbred cow are given in Table 4, which showed maternal heterosis.

Paternal Heterosis

Paternal heterosis is the advantage of a crossbred sire over the average of purebred sires [23] i.e. enhancement in production and reproduction traits of the bull.

Examples of paternal heterosis are reduced age at puberty, improvements in scrotal circumference, improved sperm concentration, increased pregnancy rate and weaning rate when mated to cows. The heterosis in F_1 is attributable to the individual effect; the maternal effect is zero whereas in F_2 the individual effect is lost about half the heterosis in F_1 but the maternal component show full heterosis.

Table 3: *Advantages of Individual Heterosis are shown by Crossbred Calf.*

Trait	Observed improvement	% Heterosis
Calving rate	3.2	4.4
Survival to weaning	1.4	1.9
Birth weight	1.7	2.4
Weaning weight	16.3	3.9
ADG	0.08	2.6
Yearling weight	29.1	3.8

ADG average daily gain

Table 4: *Advantages of Maternal Heterosis are shown by Crossbred Cow.*

Trait	Observed improvement	% Heterosis
Calving rate	3.5	3.7
Survival to weaning	0.8	1.5
Birth weight	1.6	1.8
Weaning weight	18.0	3.9
Longevity	1.36	16.2
Cow lifetime production		
Number of calves	0.97	17.0
Cumulative weaning Wt., lb.	600	25.3

Heterosis on the Basis of Origin and Nature

Euheterosis or True Heterosis

Dobzhansky (1952) proposed to distinguish between euheterosis and luxuriance according to whether the heterozygotes are adaptively superior to the homozygotes or not.

a. *Mutational Heterosis:* Heterosis resulting from the sheltering of deleterious recessive mutants by their adaptively superior dominant alleles in populations of sexually reproducing and cross-fertilizing organisms.
b. *Balanced Heterosis:* Heterosis due to the occurrence of mutations and gene combinations which confer a higher adaptive value or a higher agricultural usefulness on heterozygotes than is to be found in the corresponding homozygotes; balanced euheterosis permits the maintenance of a multiplicity of genotype in a population and may be adaptive in different ecological niches occupied by the population.

Pseudoheterosis or Luxuriance

It is the term proposed to designate those cases in which hybrids between species, varieties, or strains are larger, faster growing, or otherwise exceed the parental form in some characters when this is evidently neither the result of sheltering of deleterious genes nor of balanced gene combination (Dickerson, 1952) [24].

Heterosis on the Basis of Types of Estimation

Relative Heterosis

When heterosis is estimated over mid parental values, or we can say, average of two parents it is known as average or relative heterosis.
Average heterosis = $[(F_1\text{-MP})/ \text{MP}] \times 100$

Heterobeltiosis

When heterosis is estimated over better parents, it is called asheterobeltiosis.
Heterobeltiosis = $[F_1 - \text{BP}] / \text{BP} \times 100$
Where, BP = Value of better parent

Useful or Standard or Economic Heterosis

When heterosis is estimated over standard commercial hybrid, is known as standard heterosis. It has practical importance in plant breeding.
Economic heterosis = $[F_1 - \text{SH}] / \text{SH} \times 100$
Where, SH = Standard commercial hybrid

GENETIC BASIS OF HETEROSIS

Dominance Hypothesis

The dominance hypothesis was proposed by Charles Davenport (1908) [25]—most widely accepted hypothesis among the other explanations for heterosis. According to this hypothesis, heterosis results due to superiority of dominant alleles over the harmful recessive alleles by masking their effect and heterosis is in direct proportion with number of dominant genes contributed by each parent.

Overdominance Hypothesis

Edward M. East (1908) [26] and George Shull (1908) [27] independently developed overdominance hypothesis. According to this hypothesis, heterosis is due to superiority of heterozygote over its both homozygous parents, due to complementation between divergent alleles. Here, heterosis is in proportion with heterozygosis.

Pseudo-overdominance

Genetic intermediate of dominance and overdominance is called pseudo-overdominance, which is actually a case of simple dominance complementation, because of tight repulsion phase linkage and appears to be overdominance.

Epistasis Theory

As per this theory, gene interactions are responsible for heterosis. The epistasis model is based on nonallelic interactions between two or more loci that lead to superior phenotypic expression inhybrids.

UTILIZATION OF HETEROSIS IN DAIRY CATTLE

Utilization of heterosis in dairy cattle have various advantages like it helps to introduce desirable characters into a population in which they have not existed formerly and paternal, maternal and individual heterosis are exploited; crossbred animals usually exhibit an accelerated growth, vigor and fertility; used to produce commercial stock to meet market demand; and effective for the improvement of traits which are highly influenced by nonadditive gene action. But some constraints of heterosis in dairy cattle such as traits that are highly heritable are affected little by heterosis. To produce crossbreds, two or more purebreds have to be maintained, lack of quality feed and fodder availabilty for exploitation of heterosis and better management related to health and breeding are required for exploitation ofheterosis.

Amount of heterosis maintained in a herd depends on the type of crossbreeding system selected for breeding. Heterotic effects in cattle as consequences of crossbreeding are given in Tables 5 and 6 and production performances in synthetic crossbred cattle of India are given in Table 7. The results obtained from various crossbreeding experiment have revealed that performance of crossbreds was definitely better as compared to native breeds because it utilized heterosis.

Table 5: *Heterotic Effects in Cattle as Consequences of Crossbreeding.*

Breeds involved	Result	References
Brown Swiss x Red Sindhi halfbreds	Produced 53% more milk than Red Sindhi cows.	Stonaker, 1953 [36]
Jersey x Red Sindhi halfbreds	Produced two times more milk than the native component.	Agarwala, 1966 [37]
Friesian x Hariana halfbreds	Showed 188% improvement in milk production.	Bhasin and Desai, 1967 [38]
Ayrshire-Holstein and Brown Swiss- Holstein crossbreds	Increase in heterosis 8 to 10% for milk yield and milk fat, respectively.	McDowell and McDaniel, 1968 [39]
Crossbred Holsteins and Guernseys cows	Increase in heterosis for milk and fat yields resulting from of 6.4% and 7.5%, respectively.	Touchberry, 1970 [40]
HF x Sahiwal crossbreds at MDF, Jabalpur	Heterotic effect of 34% had been reported that was gradually declined as the fraction of Holstein inheritance deviated from 50%.	Katpatal, 1977 [41]
Holstein x Sahiwal	Heterosis for birth weight from 1.8 to 7.1% had been reported.	Katpatal, 1977 [41]
Sahiwal x Friesian crosses at different MDF	About 4.97% heterosis for FLMY was reported based on large volume of data.	Taneja, 1973 [42]
Sahiwal x Friesian crosses at different MDF	Beneficial heterosis of -4.63% for AFC, -11.4% for SP, -22.4% for number of dry days and -8.53% for CI was reported.	Taneja, 1973 [42]
Holstein Friesian x Sahiwal halfbreds	Lower AFC by 14 months and produced 3.5 times more milk than Sahiwal cows.	Parmar and Jain, 1986 [31]
Crossbred cow (HF & Jerssy),	Heterosis for milk fat yield 7.2% of the parental mean.	Breier *et al.*, 1991 [43]
Crossbred Holstein-Golpaigani cows	Increase in milk yield, fat yield and fat% were 20.86 kg, 0.712 kg, and 0.041%, respectively.	Rekui, 2000 [44]
Crosses between DH and DR	The degree of heterosis range from 2.2% (crosses between DH	Norberg *et al.*, 2014

and crosses between DR and DJ	and DR) to 6% (crosses between DR and DJ) for peak yield.	[45]

Table 6: *Heterotic Effects in Cattle as Consequences of Crossbreeding.*

S. No.	Breeds	Traits	Estimate of heterosis	References
1	Jersey x Ongole	AFC	-14%	Rao *et al*., 1996 [46]
2	Temperate x Zebu	AFC	Heterosis Percent	Singh *et al*., 2003 [47]
	FH		-19.2	
	BH		-15.9	
	JH		-25.1	
	FBH		-17.0	
	BFH		-10.9	
	FJH		-20.8	
	JFH		-17.6	
3	Holstein Friesian x Hariana	AFC (days)	39.86	Dahiya *et al*., 2005 [48]
	Jersey x Hariana	AFC (days)	-113.38	
4	Brown Swiss x Ayrshire	Milk yield Heterotic (%)	-0.7 (1st lactation)	McDowell and McDaniel, 1968 [39]
5	Friesian x Ayrshire	(1st lactation) (2nd lactation)	6.7 2.3	Donald, 1977 [49]
	Jersey x Ayreshire	(1st lactation) (2nd lactation)	4.1 3.1	
6	Guernsey x Brown Swiss	(1st lactation)	4.5	Brandt *et al*., 1966 [50]
7	Holstein x Ayreshire	(1st lactation)	8.1	McDowell and McDaniel, 1968 [39]
	Holstein x Brown Swiss	1st lactation	9.9	
8	Holstein x Gurensey	1st lactation)	2.0	Bereskin and Touchberry, 1996 [51]
9	Ayershire x Friesian	1st lactation 2nd lactation	8.2 0.7	Donald *et al*., 1977 [47]
	Friesian x Jersey	1st lactation 2nd lactation	3.6 5.7	
	Ayershire x Jersey	1st lactation 2nd lactation	7.5 4.9	
10	Brown Swiss x Guernsey	Fat yield (%)	3.7%	Brandt *et al*., 1966 [48]
	Brown Swiss x Holstein		-0.4%	
11	Guernsey x Holstein	Fat yield (%)	4.8%	Bereskin and Touchberry, 1966 [49]
12	Ayershire x Friesian	Fat yield (%)	8%	Donald *et al*., 1977 [47]
	Ayershire x Jersey		4.0%	
	Friesian x Jersey		1.8%	
13	Ayershire x Holstein	Fat yield (%)	7.9%	McDowell and McDaniel, 1968 [39]
	Ayershire x Brown Swiss		-0.02%	
	Brown Swiss x Holstein		10.4%	
14	Ayershire x Friesian	CI	9.5	Donald *et al*., 1977 [47]
	Friesian x Jersey		5.6	
	Ayershire x Jersey		9.2	
	(A X F) X J		-2.4	
	(F X J) X A		0.0	
	(A x J) x F		-3.3	

15	FH	Calving interval (%)	-5.6	Singh *et al*., 2003 [45]
	BH		-8.4	
	JH		-9.6	
	FBH		8.3	
	BFH		11.8	
	FJH		4.2	
	JFH		0.6	
16	Jersey x Hariana	CI (days)	-61.96	Dahiya *et al*., 2005 [46]
	Holstein Friesian x Hariana		-72.05	
17	Jersey x Ongole	Lactation length	11.8%	Rao *et al*., 1996 [44]
18	Jersey x Hariana	Lactation length (days)	37.00	Dahiya *et al*., 2005 [46]
	Holstein Friesian x Hariana		76.03	
19	FH	Service period (%)	-18.1	Singh *et al*., 2002 [45]
	BH		-19.8	
	JH		-23.9	
	FBH		21.6	
	BFH		31.0	
	FJH		11	
	JFH		3.7	
20	Holstein Friesian x Hariana	Service period (days)	-60.02	Dahiya *et al*., 2005 [46]
	Jersey x Hariana		-64.74	
21	FH	Dry period	-30.3	Singh *et al*., 2002 [45]
	BH		-30.3	
	JH		-34.5	
	FBH		-15.5	
	BFH		-10.9	
	FJH		-16.7	
	JFH		-9.7	
22	Holstein Friesian x Hariana	Dry period (days)	-146.80	Dahiya *et al*., 2005 [46]
	Jersey x Hariana		-111.54	

H, Hariana; F, Holstein Friesian; B, Brown Swiss; J, Jersey; DMI, Dry matter intake; RFI, residual feed intake; RG, residual BW gain; RIG, residual intake and BW gain; HCW, harvest individual carcass weight; LM, Loin muscle area; TMY, total milk yield; M90, milk yield at 90d; M305, milk yield at305d.

Table 7: *Production Performances in Synthetic Crossbred Cattle due to Heterosis.*

Breed	TMY (kg)	305 DMY (kg)	References
Karan Fries	4678 ± 50	4114 ± 56	Japheth *et al*., 2015
Frieswal	2921 ± 47	2766 ± 43	Rathee, 2015
Karan Swiss	3495	3082	ICAR-NDRI, 2014–15
Phule -Triveni	2855 ± 43	2647 ± 39	Ambhore, 2015
Vrindavani	3220 ± 41	3047 ± 34	Singh *et al*., 2011

Sunandini	3400	2500	KLDB, 2000

CONCLUSIONS

The main advantage of crossbreeding is heterosis, which helps to introduce desirable characters into a population in which they have not existed formerly. Heterosis leads to increase in the genetic level in a hybrid offspring as compared to the average of the parent breeds. Heterosis exploits the paternal, maternal and individual heterosis in crossbred animals. Crossbreeding schemes is the most profitable breeding strategy that can assist improved growth, reproduction, production and maternal traits, health and overall fitness by taking advantage of heterosis. The challenge of maintaining heterosis and minimizing inbreeding can only be met using large populations of dairy cattle. It is difficult to improve the traits of low heritability such as fertility, milk yield and longevity through pure breeding but are greatly improved through crossbreeding leading to improvements in survival, reproductive efficiency and growth rates. Heterosis is effective for the improvement of traits, which are highly influenced by non-additive gene action and used to produce commercial stock to meet market demand.

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