Review Article

An Overview on the Concept and Utilization of Heterosis in Livestock

Aayush Yadav[1], Asit Jain[2], Jyotimala Sahu[3*], Ashutosh Dubey[1], Rajkumar Gadpayle[1], Deepti Kiran Barwa[2], Sandhya Kasyap[1] and Anuj Singh[4]

[1]Department of Livestock Production and Management, College of Veterinary Science and Animal Husbandry, CGKV, Anjora, Durg-491001, Chhattisgarh, INDIA
[2]Department of Animal Breeding and Genetics, College of Veterinary Science and Animal Husbandry, CGKV, Anjora, Durg-491001, Chhattisgarh, INDIA
[3]Department of Livestock Production and Management, ICAR-National Dairy Research Institute, Karnal-132001, Haryana, INDIA
[4]Department of Animal Nutrition, College of Veterinary Science and Animal Husbandry, LUVAS, Hisar-125001, Haryana, INDIA

***Corresponding author:** smartjyoti83@gmail.com

Rec. Date:	Aug 30, 2019 08:20
Accept Date:	Sep 30, 2019 14:25
DOI	10.5455/ijlr.20190830082035

Abstract

Heterosis or hybrid vigour is the excellence of F_1 cross beyond the average performance of the two parents and noticeable across species. Heterosis, coined by Professor G.H. Shull in 1914 is well known to exploit the benefits of crossbreeding. Heterosis is usually positive but negative heterosis does occur and is uncommon. Heterosis is widely accepted to occur due to non-additive gene action i.e. dominance, over-dominance and epistasis. The heterotic effects are usually expressed in percentage and always highest in F_1 generation followed by a decline in later generations. This decline is mainly due to the recombination and segregation losses. Rotational crossbreeding systems are therefore followed to maintain levels of heterosis in later generations. Estimates of heterosis are high in low heritable traits followed by moderate in moderately heritable traits and negligible in high heritable traits. Besides improvement, there are some limitations to heterosis that shall overcome shortly.

Key words: Crossbreeding, Heritability, Heterosis, Hybrid Vigour, Non-additive Gene Action

How to cite: Yadav, A., Jain, A., Sahu, J., Dubey, A., Gadpayle, R., Barwa, D., Kasyap, S., & Singh, A. (2019). An Overview on the Concept and Utilization of Heterosis in Livestock. International Journal of Livestock Research, 9(11), 26-37. doi: 10.5455/ijlr.20190830082035

Introduction

In 1914, Professor George Harrison Shull proposed the word heterosis. In current usage, heterosis and hybrid vigour are used as synonyms and interchangeable. The term heterosis measures the ability of crossbred offspring to outperform the expected abilities transmitted by their parents. In other words, heterosis refers to the excellence of F_1 in fitness and vigour beyond the average parental values (Singh, 2000). Heterosis is frequently considered as the opposite of inbreeding depression where inbreeding depression operates in a small population and is due to the mating between related parents that produce offspring with traits largely governed by the homozygous recessive genes having a negative influence on their survival and fitness. In context to the trait to be improved, heterosis can be either positive or negative and is distinctively described in terms of percentage improvement of the trait. The heterotic effects are the outcome of non-additive gene action i.e. three principle genetic mechanisms as; dominance, overdominance and epistasis and, the widest possible concept known among the three is dominance. Filial generation 1 (F_1) always express the maximum level of heterosis i.e. 100% which reduces to half in later generations of a cross as a consequence of segregation and recombination losses (Sendros, 2002). It becomes a matter of concern as hybrid vigour reduces in later generations or to preserve it, for which several authors have recommended a criss-cross breeding programme (Wakchaure *et al*., 2015b). In general, crosses of genetically diverse breeds show maximum heterosis and are genetically sound or healthier due to greater heterozygosity than the crosses of genetically resembling breeds (Lippman and Zamir, 2006). Moreover, the dominant "like" genes of one parent disguise the recessive "unlike" genes of the second parent in heterosis. Cattle, swine and poultry species depend to a great extent on heterosis to exploit breed differences, improve growth, fertility, productivity and efficiency of production (Hansen, 2006). This article addresses the concept of heterosis, factors influencing heterosis and the benefits among livestock.

Heterosis is Outlined in Different Ways

A lot of researchers have outlined heterosis in different ways in their literature, some of which are presented below-

1. Hybrid vigour or heterocyst is the phenomenon in which progeny of crosses between inbred lines or purebred populations are superior to the expected mean of the two lines or populations for a particular trait (Wakchaure *et al*., 2015b).
2. Any variation between the phenotype of F_1(s) and their purebred parents is heterosis (Notter *et al*., 2013).
3. A phenomenon where the immediate descendants of crosses between species or distinct varieties within a species show higher biomass, speed of development, and fertility in comparison to both the parents, is heterosis (Birchler *et al.*, 2010).
4. Hybrid vigour is the production of highly heterozygous offspring as a result of a cross between 2 inbred lines and distinguished by very few recessive deleterious alleles at the homozygous state (Kristensen and Sorensen, 2005).
5. Heterosis is the excellence of crossbreds beyond the average performance of two parents and noticeable across species. This is commonly expressed as mid-parent heterosis (Dickerson, 1973).
6. Heterosis is the result of the pairing of different gametes that stimulates development by whatsoever mechanisms (Shull, 1948).

Heterosis is expressed as $H = \overline{F_1} > MP$ i.e. mean of F_1 progeny ($\overline{F_1}$) exceeds the mean of both the parents (MP).

Classification of Heterosis: Heterosis is classified into four classes as follows-

Hosted@www.ijlr.org DOI 10.5455/ijlr.20190830082035

1. **Based on Origin and Nature (Shahid, 2014)**

a. **Euheterosis or True Heterosis-** It is inherited.

i. **Mutational heterosis:** It is the masking or covering of recessive, harmful, disadvantageous, often deadly and mutant alleles by adaptively superior and advantageous dominant alleles. Moreover, it is regarded as the simplest type of heterosis.

ii. **Balanced heterosis:** The advantages in F_1 over parents originating from balanced gene combinations in F_1 with significant adaptive merits and agricultural utility is balanced heterosis.

b. **Pseudo-Heterosis (also known as luxuriance):** An accidental but exaggerated and un-adaptable expression of transient vigour by immediate descendants of crosses between parents, particularly due to the environment is pseudo-heterosis.

2. **Based on types of estimation (Shahid, 2014)**

a. **Average or relative heterosis:** Average heterosis is the estimation of heterosis over the mean of two parents i.e. mid-parental value. For example, if the average milk yield of parent 1 is 4000 litres and parent 2 is 6000 litres and the average milk yield of offspring is 7000 litres, then the per cent improvement or average heterosis is estimated by subtracting the mean of offspring (7000 litres) with the mean of both the parents (5000 litres) and dividing the resulting value (2000 litres) with the mean of both the parents (5000 litres). The final value (0.4) is then multiplied by 100 to obtain the heterosis in percentage i.e. 40%.

b. **Better parent heterosis or Heterobeltiosis:** Better parent heterosis is the estimation of heterosis over the better parent. For example, if the average milk yield of parent 1 is 4000 litres and parent 2 is 6000 litres and the average milk yield of offspring is 7000 litres, then the per cent improvement or better-parent heterosis is estimated by subtracting the mean of offspring (7000 litres) with the mean of better parent or parent 2 (6000 litres) and dividing the resulting value (1000 litres) with the mean of better parent or parent 2 (6000 litres). The final value (0.16) is then multiplied by 100 to obtain the heterosis in percentage i.e. 16%.

c. **Standard or economic or useful heterosis:** Standard heterosis is the estimation of heterosis over standard commercial hybrid. It is practically useful in plant breeding.

3. **Based on Genetic Components in the Trait (Tomar and Tomar, 2016)**

a. **Direct Component (Individual heterosis):** Any improvement in the merit of an offspring, in contrast to the average of its parents, that is not attributable to maternal, paternal or sex linkage effects is individual heterosis, and this is moreover linked to the effects of an individual's gene. The examples are weaning and yearling weight, carcass traits etc.

b. **Maternal Component (Maternal heterosis):** The excellence or benefits of crossbred mother beyond the average of purebred mothers is maternal heterosis and is particularly linked to the effect of genes in the dam and the environment provided by the dam. The examples are younger age at puberty, increased caving rate, etc.

Hosted@www.ijlr.org DOI 10.5455/ijlr.20190830082035

c. **Paternal Component (Paternal heterosis):** The excellence or benefits of crossbred sire beyond the average of purebred sires is paternal heterosis and is particularly linked to the effect of genes in the sire and the environment provided by the sire. The examples are reduced age at puberty, improved scrotal circumference, sperm concentration, etc.

4. **Based on the Direction of Heterosis (Singh, 2012)**

a. **Positive Heterosis:** An increase in the number or size of cells due to the considerable cell activity or increase in the biological efficiency such as reproductive and production rate or survival ability is called as positive heterosis (Kruse, 1964). An example given by Tomar and Tomar (2016) states that heterosis is positive when parent 1 has better milk yield than parent 2, and their progeny F_1 shows better milk yield than parent 1 i.e. $\overline{F_1} > \overline{P_1}$.

b. **Negative Heterosis:** Heterosis may be negative sometimes for say, reduction in the growth rate or survival rate of crossbreds in comparison to its parents and is called as negative heterosis or hybrid weakness or reverse heterosis. This is uncommon; however, it does occur (Kruse, 1964 and Jones, 1952). It is not always harmful. An example given by Tomar and Tomar (2016) in this context is advantageous in the reproductive life of animals. They stated if parent 2 have lesser age at first calving (AFC) and service period (SP) than parent 1, and their F_1 progeny shows even lesser AFC and SP than parent 2, then heterosis is considered negative and desirable i.e. $\overline{F_1} < \overline{P2}$, i.e. it is the character involved and not the magnitude of mean on which the superiority of parent lies.

Measurement of Heterosis: Per cent heterosis can be calculated by the formula given in Table 1.

Table 1: Formula for measurement of heterosis (Anonymous, 2019a)

S. No.	Types of Heterosis	Formula
1	% Average heterosis	$[(\overline{F_1} - MP) / MP] X 100$
2	% Heterobeltiosis	$[(\overline{F_1} - BP) / BP] X 100$
3	% Standard heterosis	$[(\overline{F_1} - SH) / SH] x 100$
4	Heterosis in F_1^{**}	$\overline{F_1} - MP$
5	Heterosis in F_2	½ Heterosis in F_1^{**}

Where; $\overline{F1}$: Mean of F1 progeny; MP: Mean of 2 parents; BP: Mean of better parent; SH: Mean of standard hybrid

Loss and Maintenance of Heterosis in Later Generations

From the serial no. 5 of the Table 1, it is clearly understood that the F_1 generation exhibits maximum heterosis and it reduces to half in later generations. The reason behind is recombination loss and segregation (Sendros, 2002). However, it is hard to estimate the recombination loss which is caused by separation of favourable genes combination accumulated in parental breeds (Cassell and McAllister, 2009), it is also inferred as unfavourable gene effect in crossbreds due to the breakdown of parental epistatic gene complex (Lidauer *et al*., 2006). In addition to it, segregation is the random separation of pair of alleles encoding the desirable traits in each parental breed during gamete formation.

 DOI 10.5455/ijlr.20190830082035

The losses can be minimized and heterosis can be preserved in the later generations by changing a 2-way cross programme to 3-way cross programme, as no further decline in heterosis is observed in 3rd (F_3) or 4th (F_4) generation with a fact that there should be no inbreeding (Wakchaure *et al*., 2015b). Practically, Hansen (2006) documented the maintenance of heterosis in later generations at the level of 86% in a 3-way cross programme, which when compared to a 2-way cross programme was found maintained at the level of 67%. As stated earlier, hybrid vigour drops to 50% in the F_2 generation in a 2-way cross programme which is however maintained to 100% in the F_2 generation in a 3-way cross programme (i.e. both F_1 and F_2 maintains hybrid vigour at 100%; Pro Cross, 2009).

Reasons for Heterosis

The positive effect of hybrid vigour in F_1 hybrids compared to their inbred lines/ purebred parents were first observed by Darwin (1876) and then described in maize by East (1908) and Shull (1908). Effects of hybrid vigour greatly impact the performances of F_1 hybrids. Three principle genetic mechanisms are proposed to discuss the phenomenon of heterosis. They are dominance, over-dominance and epistasis.

1. **Dominance:** Davenport (1908), Bruce (1910) and Keeble and Pellow (1910) proposed the most widely approved genetic reason for heterosis. It is the covering or hiding of recessive harmful alleles of one parent by the dominant (sometimes partially dominant) advantageous alleles of another parent (Lariepe *et al*., 2012) or it is the aggregation of dominant genes of both the parents in F_1. This is an intra-allelic interaction. In this context, two objections to the dominance hypothesis were also studied and are discussed below (Singh, 2012)-

a. For dominance hypothesis to hold true there should be the production of pure heterotic individuals in F_2 generation with all the dominant genes in the homozygous state. However, such offspring's are never obtained. A possible reason for it is maybe the lineage between the advantageous dominant and disadvantageous recessive genes that do not allow obtaining true-breeding homozygous individuals for all dominant genes in the F_2 generation (Jones, 1917).

b. The F_2 curve in case of dominant heterosis should be skewed towards dominant genes but is always smooth and symmetrical. This objection was removed by Collins in 1921. He said that the traits like yield are governed polygenically and show continuous variation leading to the symmetrical distribution of genes.

2. **Over-dominance:** The term over-dominance was introduced by Hull in 1945 while working with maize crop whereas, the theory was independently suggested by Shull (1908) and East (1908). The theory asserts superiority per se of heterozygous genotype in comparison to the homozygous genotype of either parent at individual loci to be the probable cause of over-dominance heterosis (Lariepe *et al*., 2012). In other words, over-dominance heterosis represents the complementation between alleles diverging from each other or a standard. This is an intra-allelic interaction.

  DOI 10.5455/ijlr.20190830082035

3. **Epistasis:** The theory asserts interaction between 2 different alleles or genes (inter-allelic) at 2 different loci of a chromosome, where the expression of an allele or a gene at one locus suppresses the expression of another allele or gene at another locus. The suppressing gene is called suppressor or epistatic gene and the suppressed gene is called a hypostatic gene.

Factors affecting heterosis: The magnitude of heterosis is affected by four main factors. The factors are:

1. **The adaptability of parents:** Heterosis is well-influenced by the adaptability of parents. It is the crossbred (F_1) that has to perform in an environment and therefore, it becomes necessary for the breeder to cross only those parental breeds that are well acclimatized to that particular environment. A close association has been found between genetic base and adaptability and is considered that "more the adaptability of parents more will be the adaptability of progeny (F_1)" (Singh, 2000).
2. **Heritability:** Heritability exhibits inverse relation with heterosis for a given trait. This can be understood by a given formula i.e. $h^2 = V_G/V_P$ where, h^2 is heritability and V_G and V_P are genetic and phenotypic variance, respectively. V_G can be again partitioned into $V_A + V_D + V_I$ where, V_A, V_D and V_I are additive genetic, dominance and epistatic variance, respectively. V_A is an additive type of gene action whereas, V_D and V_I are the non-additive type of gene action. The additive type of gene actions is heritable whereas the non-additive type of gene actions is non-heritable. Heritability is due to the additive type of gene action and heterosis is due to the non-additive type of gene action. When V_A decreases, V_D and V_I increases, which show that when the additive type of gene action decreases, heritability decreases and non-additive type of gene action increases i.e. heterosis increases. This proves the inverse relation between heritability and heterosis i.e. when heritability is low, heterosis is high (Dubey *et al*., 2019). Large improvements have been observed in low heritable traits for say, reproductive, survival and fitness traits and a maximum of 10% heterosis or improvement has been studied so far. Similarly, 5% heterosis is observed for moderately heritable traits viz. growth and production traits however, very little or no heterosis at all is mentioned for high heritable traits such as carcass traits (Hansen, 2006).
3. **Type of crossbreeding system and number of breeds in the crossbreeding system:** Application of rotational crossbreeding systems such as 3-breed or 4-breed rotational crosses are required to exploit breed differences and heterotic effects (Wakchaure *et al*., 2015b). As discussed earlier, a 3-breed cross claims maintenance of heterosis in later generations at 86% whereas, a 4-breed cross maintains at 93% (Hansen, 2006).
4. **Genetic diversity of parents:** The expression of heterosis increases as degree of relationship or inbreeding between parental lines decrease i.e. cross of diverse and unrelated breeds exhibit higher heterosis. In other words, avoidance of inbreeding by several methods such as; large population size, sex-biased dispersal, extra pair/group copulations or newer methods like artificial insemination etc., to

Hosted@www.ijlr.org DOI 10.5455/ijlr.20190830082035

preserve the higher levels of heterosis and heterozygosity in composite or synthetic breeds is required. Further, frequencies of different alleles at each locus, contributing to a trait also affect heterosis. More the differences more are the heterosis and heterozygosity (Wakchaure *et al*., 2015b).

Utilization of heterosis among livestock: Heterosis is utilized among livestock under the following heads:

1. **Increases the number of progenies at birth:** A research on crossbred cows carried for 12 years revealed production of nearly one more calf (0.82 - 0.97) in comparison to straight bred cows (Cundiff *et al*., 1992). Similar results were obtained when the cross was made between Landrace and Native Nigerian pig which revealed the production of 1.5 more number of piglets per sow at birth (Nwakpu and Onu, 2011).
2. **Improves birth weight of progenies:** Notter (1978) revealed that crossbred lambs experienced 3.2% level of heterosis or improvement in terms of birth weight. Also, calves born to crossbred females show improved birth weight by approximately 1.00 - 2.495 kg than purebred calves at birth (Cundiff *et al*., 1992; Gregory *et al*., 1991). Similar results were obtained for day-old chick of a cross between Naked Neck and Frizzle Feather, where their individual body weight was 4.5g higher than the mean body weight of parental breeds (Nwenya *et al*., 2017).
3. **Enhances survivability of progenies:** Survival ability of F_1 lambs was determined in a study during 2 – 30 and 2 – 60 days of age and found to increase by 8.8 and 14.6%, respectively in comparison to purebred lambs, showing the positive association of heterosis and survival ability (Ferreira *et al*., 2015).
4. **Improves weaning weight of progenies:** Ritchie *et al.* (1999) and Gregory and Cundiff (1980) observed an improvement in crossbred calf weaning weight by 16 – 20% and likewise, crossbred kids of Boer x Etawa grade goats and Boer x Kacang goats experienced improvement in weaning weight by 10.07 – 35%, respectively (Kostaman and Sutama, 2006; Elieser *et al*., 2012).
5. **Improves the weaning rate of crossbreds:** In contrast to straight bred cows, the weaning rate was found to increase by 3.8 – 4.6% in crossbred cows (Cundiff *et al*., 1992).
6. **Improves average feed intake (AFI) and feed conversion ratio (FCR) of crossbreds:** Significantly higher mean AFI (16.40%) and FCR (28.13%) was reported in poultry progenies during the 12th week of study against the mean AFI and FCR of the parental breeds (Nwenya *et al*., 2017).
7. **Improves the average daily gain (ADG) of crossbreds:** Gregory *et al.* (1978) observed the heterotic effect on ADG in crosses of beef breeds and found it 2.20 - 11.73% (originated from original data) higher in comparison to the mean of purebreds. Further, crossbred male kids displayed improvement in ADG by 29.01 - 31.70% in comparison to purebreds (Al-Doori *et al*., 2002). Similarly, against pure strains, crossbred cockerels and pullets displayed 13.00 and 7.00% heavier body weight, respectively at 8 weeks

  DOI 10.5455/ijlr.20190830082035

of age, with further reports of an increase in their adult body weight by 5% (Nordskog and Ghostley, 1953).

8. **Improves body condition score of crossbreds:** An observation of higher body condition score (2.90) in Jersey – Holstein crosses than purebred Holstein cows (2.76) also represents reduced post-partum body weight losses (Heins *et al*., 2008).
9. **Early sexual maturity in crossbreds:** Rhode Island Red and Barred Plymouth Rock crosses are credited for achieving sexual maturity early by 9 days against their parental strains (King and Bruckner, 1952).
10. **Enhances production of crossbreds:** Reports of 477.00 kg more milk yield, 25.3 kg more fat yield and 17.4 kg more protein yield are credited to the North American Holstein Friesian and Jersey crosses (Penasa *et al*., 2010). Likewise, Bunning *et al* (2019) displayed a rise in milk production by 35.15% in tropical cattle. Besides, Rhode Island Red and Barred Plymouth Rock crosses showed progress in 500-day egg production by 19 eggs against their parental strains (King and Bruckner, 1952). A study in Kenya has further revealed better milk production in crossbred goats (2.6 lit./day) than indigenous goats (0.3 lit./day) (Ahuya *et al*., 2019).
11. **Better hatchability of total eggs set:** An increase in hatchability of total eggs set by 5.7% against the purebred strains is reported by Nordskog and Ghostley (1953).
12. **Improves fertility of crossbreds:** Improvement in fertility was seen in tropical cattle with 12.02% heterosis (Bunning *et al*., 2019).
13. **Improves services per conception:** Crossbred boars of crosses between Duroc, Landrace, Spot and Yorkshire revealed 1.22 services per conception against 1.41 for purebreds (Johnson, 1981).
14. **Enhances conception rate in crossbreds:** A non-significant but 8% higher result was obtained in crossbred boars against purebreds (Wilson *et al*., 1977). Similarly, crossbred lambs and ewes displayed better conception rate with 2.60 and 8.70% heterotic effects, respectively against the mean of purebreds (Notter, 1978).
15. **Reduces calving interval in crossbreds:** F_1 crosses of North American Holstein Friesian with Montbeliarde exhibits a beneficial decline in calving interval by 10.2 days than the mean of parental breeds (Penasa *et al*., 2010).
16. **Improves calving rate in crossbreds:** Cundiff and Gregory (1999) reported percentage improvement in calving rate of the crossbred calf and crossbred cow by 3.2 and 3.5 with 4.4% individual and 3.7% maternal heterosis, respectively as compared to the average of purebreds.
17. **Improves the health of crossbreds:** Improvement in health was seen in tropical cattle with 31.84% heterosis (Bunning *et al*., 2019). On the contrary, van Raden and Sanders (2003) presented certain unfavourable effects on the udder health possibly due to more milk production potential of crossbreds and associated increased stress on the udder. However, in the proceedings of "10th World Congress on

  DOI 10.5455/ijlr.20190830082035

Genetics Applied to Livestock Production", non-significant changes in the udder health of crossbreds were measured by somatic cell score (Norberg, 2014).

18. **Improves body measurements of crossbreds:** Significant heterosis was reported by Reddy *et al* (1959) in swine where he reflected an improvement in body length, heart girth and flank girth by 1.12, 2.21 and 3.46%, respectively in F_1 cross in comparison to the average of parental breeds (Landrace and Poland).
19. **Improves carcass traits of crossbreds:** Improvement in carcass traits *viz.*, hot carcass weight, cold carcass weight, rib eye area and fat thickness were observed in crossbred male kids by 6.38 – 9.03%, 2.18 – 7.84%, 4.54% and -7.89 – -9.21%, respectively in comparison to purebreds (Al-Doori *et al*., 2002).
20. **Higher economic efficiency in the dairy farm:** Holstein Friesian (HF) and Jersey cross provided higher economic returns than the purebred HF and Jersey cows (Lopez-Villalobos, 1998). It was also observed that a two-breed rotation between Ayrshire and Holstein produced 3.2% more profitability than the straightbred cows (McAllister *et al*., 1994).
21. **Increases longevity of crossbreds:** Heterosis has increased the longevity of cows by 0.99 - 1.3 years (Cundiff *et al*., 1992). It was further observed that crossbred dogs lived 1.2 years longer than the purebreds (O'Neill *et al*., 2013).

Limitations of heterosis: The limitations of heterosis are given below (Wakchaure *et al*., 2015a; Anonymous, 2019b; Anonymous, 2019c) -

1. Heterosis requires maintenance of two or more pure breeds to obtain the crossbreds. This requires higher initial investment and maintenance expenditures.
2. As stated earlier, the heterotic effect deteriorates beyond F_1 generation in two-breed crosses and is negligible or less for high heritable traits.
3. Sometimes F_1 crosses are vulnerable to diseases.
4. Superior performance observed in crossbred animals is not transmitted to progeny upon mating as favourable gene combinations are either rearranged or lost when crossbred animals are mated together.

Conclusion

The low performances of indigenous animals have brought concerns in the minds of geneticists. To improve the performances of indigenous animals some genetic interventions are required and in this context, the scientists have been focusing on the varying forms of crossbreeding between pure breeds to exploit heterosis or non-additive gene actions, however, it should be used in judicial manner considering the government policies, socio-economic status of the owner of livestock, ethics and cultural values of livestock in different societies or regions of the country. Researchers, in the future, need to emphasize on the fact that maximum improvement is seen in low heritable traits as heterosis shares inverse relationship with the heritability of traits and it is futile to crossbreed animals for improvement in high heritable traits. Besides, it is advised to

  DOI 10.5455/ijlr.20190830082035

include more number of breeds in a cross to maintain heterosis at the subsequent generations. Moreover, studies are required at the level of F_2, F_3 generations and so on to develop more purified progenies that can perform better than their F_1 generation counterparts.

References

1. Ahuya, C.O., Okeyo, A.M. and Murithi, F.M. (2019). Productivity of cross-bred goats under smallholder production systems in the Eastern highlands of Kenya. United Kingdom Department for International Development. U.K. https://bit.ly/2Xpugdm. Accessed on 19 June, 2019. 54-60 pp.
2. Al-Doori, M.K., AL-Rawi, A.A. and AL-Kass, J.E. (2002). Effect of crossbreeding of local goat with Damascus of Sannen on the average daily gain and carcass traits. *Information Processing in Agriculture Journal of Agriculture Research, 12*(1): 77.
3. Anonymous. (2019a). Types of heterosis. Theagricos. https://bit.ly/2V0t0br. Accessed on 5 May, 2019.
4. Anonymous. (2019b). Plant breeding methods: Advantage and disadvantage. Slideshare. https://bit.ly/2VpbTAt. Accessed on 13 May, 2019.
5. Anonymous. (2019c). Developing and implementing a genetic improvement programme. Iowa State University, Ames. https://bit.ly/2PYwBps. Accessed on 13 May, 2019.
6. Birchler, J.A., Yao, H., Chudalayandi, S., Vaiman, D. and Veitia, R.A. (2010). Heterosis. *The Plant Cell, 22*: 2105-2112.
7. Bruce, A.B. (1910). The Mendelian theory of heredity and the augmentation of vigor. Science, 32: 627–628.
8. Bunning, H., Wall, E., Chagunda, M.G., Banos, G. and Simm, G. (2019). Heterosis in cattle crossbreeding schemes in tropical regions: Meta-analysis of effects of breed combination, trait type, and climate on level of heterosis. *Journal of Animal Science*, *97*(1): 29-34.
9. Cassell, B. and McAllister, J. (2009). Dairy crossbreeding research: Results from current projects. Virginia Cooperative Extension. 404-494.
10. Collins, G.N. (1921). Dominance and vigor of first-generation hybrids. Am. Nat., 55: 116–133.
11. Cundiff, L.V. and Gregory, K.E. (1999). What is systematic crossbreeding? Proc. NCBA Cattleman's College, Charlotte, NC, February 1999.
12. Cundiff, L.V., Nunez-Dominguez, R., Dickerson, G.E., Gregory, K.E. and Koch, R.M. (1992). Heterosis for lifetime production in Hereford, Angus, Shorthorn, and crossbred cows. *Journal of Animal Science, 70*(8): 2397.
13. Darwin, C.R. (1876). The effects of cross and self-fertilization in the vegetable kingdom (London: John Murray).
14. Davenport, C.B. (1908). Degeneration, albinism and inbreeding. Science, 28(718): 454-455.
15. Dickerson, G.E. (1973). Inbreeding and heterosis in animals. *Journal of Animal Science*, 54–77.
16. Dubey, A., Jain, A., Gadpaylae, R., Bara, D.K., Yadav, A., Kumar, V. and Sahu, J. (2019) Importance and utilization of non-additive genetic variance in farm animals. *Journal of Entomology and Zoology Studies, 7*(3): 1561-1564.
17. East, E. (1908). Inbreeding in corn. In: Reports of the Connecticut Agricultural Experiment Station for Years 1907–1908. Connecticut Agricultural Experiment Station, New Haven, CT. 419-428.
18. Elieser, S., Sumadi., Budisatria, G.S. and Subandriyo. (2012). Productivity comparison between Boer and Kacang goat dam. *Tropical Animal Health and Production*, *37*(1): 15–21.
19. Ferreira, V.C., Rosa, G.J.M., Berger, Y.M. and Thomas, D.L. (2015). Survival in crossbred lambs: Breed and heterosis effects. *Journal of Animal Science*, *93*: 912-919.
20. Gregory, K.E. and Cundiff, L.V. (1980). Crossbreeding in beef cattle: Evaluation of systems. *Journal of Animal Science*, *51*: 1224-1242.

 DOI 10.5455/ijlr.20190830082035

21. Gregory, K.E., Cundiff, L.V. and. Koch, R.M. (1991). Breed effects and heterosis in advanced generations of composite populations for birth weight, birth date, dystocia, and survival as traits of dam in beef cattle. *Journal of Animal Science, 69*(9): 3574-3589.
22. Gregory, K.E., Cundiff, L.V., Koch, R.M., Laster, D.B. and Smith, G.M. (1978). Heterosis and breed maternal and transmitted effects in beef cattle. I. Preweaning traits. *Journal of Animal Science, 47*(5): 1031-1041.
23. Hansen, L.B. (2006). Monitoring the worldwide genetic supply for dairy cattle with emphasis on managing crossbreeding and inbreeding. *In*: Proceedings of the 8th World Congress of Genetics Applied to Livestock Production, Belo Horizonte, Brasil, 01-01.
24. Heins, B.J., Hansen, L.B., Seykora, A.J., Johnson, D.G., Linn, J.G., Romano, J.E. and Hazel, A.R. (2008). Crossbreds of Jersey Holstein compared with pure Holsteins for production, fertility, and body and udder measurements during first lactation. *Journal of Dairy Science, 91*(3): 1270–1278.
25. Hull, F.H. (1945). Recurrent selection for specific combining ability in corn. J. Am. Soc. Agron. 37: 134–145.
26. Johnson, R.K. (1981). Crossbreeding in swine: Experimental results. *Journal of Animal Science, 52*(4): 906-923.
27. Jones, D.F. (1917). Dominance of linked factors as a means of accounting for heterosis. *Proceedings of the National Academy of Sciences of the United States of America, 3*(4): 310-312.
28. Jones, D.F. (1952). Plasmagenes and chromogenes in heterosis. Heterosis. Iowa State College Press, Ames, Iowa.
29. Keeble, F. and Pellow, C. (1910). The mode of inheritance of stature and time of flowering in peas (Pisum sativum). J. Genet., 1: 47–56.
30. King, S.C. and Bruckner, J.H. (1952). A comparative analysis of purebred and crossbred poultry. *Poultry Science, 31*(6): 1030-1036.
31. Kostaman, T. and Sutama, I. (2006). Korelasi bobot badan induk dengan lama bunting, litter size, dan bobot lahir anak kambing Peranakan Etawah. *Seminar Nasional Teknologi Peternakan dan Vete-riner*, 522–527 pp.
32. Kristensen, T.N., and Sorensen, A.C. (2005). Inbreeding—lessons from animal breeding, evolutionary biology and conservation genetics. *Animal Science, 80*(2): 121–133.
33. Kruse, R. (1964). Genetic basis of heterosis. *NACTA Journal, 8*(1): 6-9, 12-13.
34. Lariepe, A., Mangin, B., Jasson, S., Combes, V., Dumas, F., Jamin, P. and Gallais, A. (2012). The genetic basis of heterosis: Multiparental quantitative trait loci mapping reveals contrasted levels of apparent overdominance among traits of agronomical interest in maize (*Zea mays* L.). *Genetics, 190*(2): 795-811.
35. Lidauer, M., Mantysaari, E.A., Stranden, I., Poso, J., Pedersen, J., Nielsen, U.S., Johansson. K., Eriksson, J.A., Madsen, P. and Aamand, G.P. Random heterosis and recombination loss effects in a multibreed evaluation for Nordic Red dairy cattle. Advances in Statistical Genetics, 8th WCGALP, Belo Horizonte, Brazil, 2006.
36. Lippman, Z.B. and Zamir, D. (2006). Heterosis: Revisiting the magic. *Trends in Genetics, 23*(2): 60-66.
37. Lopez-Villalobos, N. (1998). Effects of crossbreeding and selection on the productivity and profitability of the New Zealand industry. PhD thesis, Massey University, Palmerston North, New Zealand.
38. McAllister, A.J., Lee, A.J., Batra, T.R., Lin, C.Y., Roy, G.L., Vesely, J.A., Wauthy, J.M. and Winter, K.A. (1994). The influence of additive and non-additive gene action on lifetime yields and profitability of dairy cattle. *Journal of Dairy Science, 77*(8): 2400-2414.
39. Norberg, E., Sorensen, L.H., Byskov, K. and Kargo, M. (2014). Heterosis and breed effects for milk production, udder health and fertility in Danish herds applying systematic crossbreeding. *In:*

DOI 10.5455/ijlr.20190830082035

Proceedings, 10th World Congress of Genetics Applied to Livestock Production, Vancouver, BC, Canada, August 17-22, 2014.

40. Nordskog, A.W. and Ghostley, F.J. (1953). Heterosis in poultry: 1. Strain crossing and crossbreeding compared with closed flock breeding. Department of Poultry Husbandry, Iowa State College, Ames, Iowa. 704-715 pp.
41. Notter, D.R., Scherf, B. and Hoffmann, I. (2013). *Breeding of Animals. Encyclopedia of Biodiversity. 2nd Edn.*, Elsevier, New York.
42. Notter, G. (1978). Breed utilization for meat production in sheep. *Animal Breeding Abstracts*, *46*: 131-143.
43. Nwakpu, P.E. and Onu, P.N. (2011). Heterosis for litter size traits in native by two exotic inbred pig crosses. *Agriculture and Biology Journal of North America, 2*(10): 1340-1346.
44. Nwenya, J.M.I., Nwakpu, E.P., Nwose, R.N. and Ogbuagu, K.P. (2017). Performance and heterosis of indigenous chicken crossbreed (Naked Neck x Frizzled Feather) in the humid tropics. *Journal of Poultry Research, 14*(2): 07-11.
45. O'Neill, D.G., Church, D.B., McGreevy, P.D., Thomson, P.C. and Brodbelt, D.C. (2013). Longevity and mortality of owned dogs in England. *The Veterinary Journal, 198*(3): 638–43.
46. Penasa, M., Lopez-Villalobos, N., Evans, R.D., Cromie, A.R., Dal Zotto, R. and Cassandro, M. (2010). Crossbreeding effects on milk yield traits and calving interval in spring-calving dairy cows. *Journal of Animal Breeding Genetics*, *127*(4): 300-307.
47. Pro Cross. (2009). Retrieved October 9, 2010, from Creative Genetics: http://www.creativegeneticsofca.com/procross.htm
48. Reddy, V.B., Lasley, J.F. and Tribble, L.F. (1959). Heritabilities and heterosis of some economic traits in swine. Research Bulletin 689, Agricultural Experiment Station, University of Missouri, Columbia, Missouri. 01-27 pp.
49. Ritchie, H., Banks, D., Buskirk, D. and Cowley, J. (1999). Crossbreeding systems for beef cattle. Michigan State University Extension Bulletin, E-2701.
50. Sendros, D. (2002). *Genetic factors affecting milk production, growth and reproductive traits in Bos taurus x Bos indicus crosses in Ethiopia.* PhD Thesis. Faculty of Natural and Agricultural Sciences, Department of Animal, Wildlife and Grassland Sciences. University of Free State, Bloemfontein, South Africa.
51. Shahid, M. (2014). Heterosis: Outbreeding and hybrid vigour. https://bit.ly/2Vh2Ki4. Accessed on 5 May, 2019.
52. Shull, G.H. (1908). The composition of a field of maize. Am. Breeders Assoc. Rep. 4: 296–301.
53. Shull, G.H. (1948). What is "Heterosis"? *Genetics, 33*(5): 439-446.
54. Singh, P. (2000). *Essentials of Plant Breeding: 10. Heterosis and Hybrid Varieties*. Kalyani Publishers, New Delhi, India. 178-195 pp.
55. Singh, P. (2012). *Quantitative genetics at a glance.* Kalyani Publishers, New Delhi, India, 69-78 pp.
56. Tomar, A.K. and Tomar, S.S. (2016). *Genetics of Livestock Population.* Daya Publishing House, New Delhi, India.
57. van Raden, P.M. and Sanders, A.H. (2003). Economic merit of crossbred and purebred US dairy cattle. *Journal of Dairy Science*, *86*(3): 1036–1044.
58. Wakchaure, R., Ganguly, S., Para, P.A., Praveen, P.K., Kumar, A. and Sharma, S. (2015a). Development of crossbred cattle in India: *A review. International Journal of Emerging Technology and Advanced Engineering*, *5*(10): 75-77.
59. Wakchaure, R., Ganguly, S., Praveen, P.K., Sharma, S., Kumar, A., Mahajan, T. and Qadri, K. (2015b). Importance of heterosis in animals: A review. *International Journal of Advanced Engineering Technology and Innovative Science. 1*(1): 1-5.
60. Wilson, E.R., Johnson, R.K. and Wettemann, R.P. (1977). Reproductive and testicular characteristics of purebred and crossbred boars. *Journal of Animal Science, 44*(6): 939.

DOI 10.5455/ijlr.20190830082035