Review Article

Genomic selection and its application in animal breeding

Fahar Ibtisham[1] Li Zhang[1] Mei Xiao[1] Lilong An[1*] Muhammad Bilal Ramzan[2]

Aamir Nawab[1] Yi Zhao[1] Guanghui Li[1] YingMei Xu[1]

Abstract

A significant gap exists between animal production and world's population demand. Although conventional breeding methods have been effectual for selection of animal populations on many traits of economic importance, with these methods, the accuracy of breeding value always remains questionable. Simulation and experimental results suggest that breeding values can be predicted with high accuracy by genomic selection for young animals without own performance. Genomic selection is a type of marker-assisted selection in which genetic markers covering the whole genome are used so that all quantitative trait loci are in linkage disequilibrium with at least one marker. The possibility to select animals at an early stage allows defining new breeding strategies aiming at boosting genetic progress while reducing costs. Genomic selection is the future of livestock breeding companies; it improves the genetic gain by decreasing genetic interval and improving reliability. Further research is required to improve the accuracy of genomic estimated value and manage long-term genetic gain. The aim of this review was to provide an overview of the developments of genomic selection and its application in animal breeding.

Keywords: generation interval, genomic breeding, genomic estimated breeding value, genomic selection

[1]*Agricultural College, Guangdong Ocean University, Zhanjiang, Guangdong, China*
[2]*University of Veterinary and Animal Science, Lahore, Punjab, Pakistan*
***Correspondence**: anlilong@126.com*

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Introduction

Production of food requirement is increasing with growing world population. According to Food and Agriculture Organization of the United Nations (FAO) to meet the consumption requirement of world population, food production should be doubled in the next coming years (FAO, 2006). The expected productivity gap could be filled by improving genetic, health and perfection of animal husbandry.

Animal breeding is related to intended human selection based on animal performance record and mostly selection is done based on more than one trait (Ventura et al., 2016). In the absence of molecular knowledge, breeders have effectively used traditional animal breeding methods (TAB) for production of superior animals (Garner et al., 2016). In the TAB method, estimated breeding value (EBV) is based on animal own and family realistic physical character or phenotype, but with these methods animal's production remains questionable due to low reliability. During the past years, animal breeding based on quantitative genetics has remarkably increased animal production. However, the implementation of genetic markers into breeding programmes has been rather limited for technological reasons (Deng et al., 2016). Presently, the availability of dense panels of single nucleotide polymorphism (SNP) markers has offered new opportunities to select the best fit animals for breeding purpose, commonly referred to as genomic selection. The basic concept of such methodology is to use the quantitative trait locus (QTL) linked with a particular phenotypic trait and exploit them for selection purpose. The broad information of dense genetic markers has allowed the estimation of breeding values for young candidates with higher accuracy than before.

The principle of genomic selection is to take advantage of both genotypic and phenotypic data available in reference population to shape prediction equations of the genetic merit of individuals (de Koning, 2016). The reliability of genomic selection is expected with larger reference male or female populations (Azizian et al., 2016). On the other hand, because of the reliable phenotypic information resulting from a large group of daughters, progeny-tested bulls often construct the training set of genomic selection. Using a joint reference population by collecting different data from different populations has been expressed as an efficient method of improving the accuracy of genomic selection (Zhou et al., 2013).

Genomic selection has significantly increased the technical and economic efficiency of animal breeding program (König et al., 2017) and its benefit was first reported for dairy cattle. These expected advantages are generally due to a reduction in the generation interval, increase in the accuracy of EBV and a reduction in costs for progeny testing (Shumbusho et al., 2015). Based on these theoretical findings, genomic selection was rapidly implemented in dairy cattle breeding programs. The first objective of this review was to describe the development of breeding scheme from TAB methods to genomic selection. The second aim was to summarize the application of genomic selection in different farm animals including ruminants, swine and chickens.

Traditional breeding methods

Animal breeding involves the selection of domestic animals with the goal to improve quantitative or qualitative traits in the next generation. A number of breeding methods have been used to improve animals, but the main aim has always been to improve the production of superior animals of desired traits (Plieschke et al., 2016).

Traditionally, animals were selected for breeding purpose based on phenotypic recordings. Thus, traits difficult to be measured such as those later expressed, limited to sex or of low heritability are more difficult to be improved (Calus et al., 2013).

Therefore, best linear unbiased predictions (BLUP), combined individual records and those of relatives into EBV to improve the predictions of performance (Henderson, 1973). The BLUP method increases genetic response to selection by improving the reliability of EBV (Dekkers, 2012). This is so because the method can account for all systematic effects (e.g. batch, sex, production environment, age variation) that are often associated with traits of economic importance in farm animals. In addition, the BLUP method improves the reliability of EBV because in BLUP analysis, all pedigree information is exploited through a numerator relationship matrix to account for changes in additive genetic variance due to inbreeding or assortative mating (Cowling et al., 2015).

Although animal selection based on EBV estimated from phenotype has been very successful, there is still a number of limitations. These mainly relate to the capability to regularly record phenotypic data of selected candidates and/or their close relatives in a timely manner which help to accelerate selection decisions at an early age to reduce generation intervals. Costly phenotype recording for traits difficult to be measured or with low heritability also plays an important role here. Another limitation of TAB is the trait of interest, which is only recorded late in life and only on one sex, requires animals to be sacrificed (meat quality) or exposed to conditions that would hamper the ability to market or export their germplasm (e.g. disease resistance). In addition, these breeding processes remain comparatively slow because of the considerable time required to collect adequate daughter phenotypes to calculate genetic evaluations with high precision.

Marker-assisted selection

The use of genomic information in addition to phenotypic information to increase reliability is known as Marker-Assisted Selection (MAS). The concept of MAS for selection of superior animals was firstly introduced as early as in 1900 (Sax, 1923). Genes controlling specific traits are scattered all over the genome, but pretty few in numbers have large effects with many more genes having gradually smaller effects (Wells et al., 1998) and in MAS, marker genes are used to indicate the presence of desirable genes (Ribaut & Ragot, 2007). MAS depends on identifying association between genetic marker and linked Quantitative traits loci (QTL) (Meuwissen & Goddard, 1996) and the association between marker, while that association depends on distance between marker and target traits (Ron & Weller, 2007). The combination of traditional breeding method with molecular genetic methods is beneficial to the selection response.

With the help of MAS, it becomes possible to recognize the trait of interest which will pass on to the next generation, regardless of environmental condition. This method also helps in identification of the trait with low phenotypic expression like disease resistance. Selection is possible for recessive genes and mutants, in addition to MAS selection, process is faster because an individual's phenotype can be predicted at a very early stage. MAS is profitable compared to TAB for sex-limited traits or traits with poor predictor of breeding value (Hiendleder et al., 2005) and traits that are expressed late in life (Rothschild & Ruvinsky, 2007). MAS could be particularly useful in cross-breeding programmes in which desirable genotypes are introgressed into productive local breeds with overall better breeding values.

Although the MAS technique increases animal production by increasing reliability, it is not timely in animal breeding programs because most traits of interest are governed by a large number of loci. Therefore, it could result in small genetic gain because the use of a limited number of loci can capture only part of the proportion of genetic variance (VanRaden et al., 2009). Moreover, complexity of the calculations involves the estimation of breeding values with incorporation of information molecular markers hampering the use of MAS (Baruch & Weller, 2009).

Development of genomic selection

The MAS method is fruitful for traits with a simple genetic determinism, but delivers unsatisfactory outcomes in many more complex conditions. The two key causes for this low productivity were the limited part of the genetic variance and also the low association between markers and QTL at population level (Boichard et al., 2016). Another limitation of MAS is the expensive cast of genotyping of selection candidates, due to the benefits of MAS in commercial breeding programs being clearly less than expected (Dekkers, 2004).

The success of genomics in animal breeding set in with a new novel approach where the breeding value could be estimated from markers spanning the entire genome (de Koning, 2016). Now parental relationships are no longer vital to make clear similar performances in animals because with the accessibility of low-cost whole-genome SNP panels, analogous performances can now be justified by the reality that animals share the same chromosome fragments (Kemper & Goddard, 2012).

Genomic selection is a type of MAS in which breeding value of animals can be accurately estimated with the help of dense maker map of chromosomes without information about their phenotype or that of close relatives (Rabier et al., 2016). Genomic selection has improved animal production by reducing the generation interval and cost of proving bulls (Konig et al., 2009). The genomic selection is based on the analysis of 10.000 up to 800.000 SNP's (Sonesson et al., 2010). To date, whole genomes of many animals have been sequenced including chicken, horse, sheep, cattle, dog, cat, and rabbit (Fan et al., 2010) (Table 1).

Table 1 Summary of whole-genome sequence information of important animal species with year of completion[1]

Species	Genome Size (Gb)	Year
Cattle (Bos taurus)	2.67	2009
Sheep (*Ovis aries*)	2.61	2008
Goat (Capra hircus),	2.63	2012
Pig (*Sus scrofa*)	2.8	2009
Chicken (*Gallus gallus*)	1.04	2004
Rabbit (*Oryctolagus cuniculus*)	2.73	2009
Dog (*Canis familiaris*)	2.41	2003
Horse (*Equus caballus*)	2.47	2009
Cat (*Felis catus*)	1.64	2006
Turkey (*Meleagris gallopavo*)	1.06	2009
Spotted gar (Lepisosteus oculatus),	0.94	2011
Atlantic salmon (Salmo salar),	2.43	2011
Atlantic cod (Gadus morhua),	0.82	2010

[1]Modified from Stock & Reents (2013)

Principle of genomic selection

The basic principle of genomic selection is the use of marker information for estimation of breeding value without having the information of gene location. The first step of genomic selection is the collation of phenotypic and genotypic information of reference population. For genotypic information, all animals in reference population are genotyped for SNPs of entire genome (Boichard et al., 2016). Although genotyping of large population is expensive, increasing the numbers of animal in reference population will make results more precise (Li et al., 2011). Then, collected phonotypic and genotypic data are used to obtain predictive equation to calculate GEBV (Fernandes Junior et al., 2016). These effects are then applied to candidates for selection with marker genotype information, but without known phenotypes (Figure 1). The precision of GEBV depends on 3 factors: trait heritability (h2), animal number (N) in the reference population, and q parameter (Neves et al., 2014)

Advantages of genomic selection

Genomic selection increases productivity by increasing the rate of genetic gain compared to traditional breeding methods (Table 2).

Table 2 Impact of genomic selection on genetic gain

Animals	Added Genetic gain	References
Pig	23-91%	(Lillehammer et al., 2011)
Dairy sheep	51.7%	(Shumbusho et al., 2013)
Dairy goat	26.2%	(Shumbusho et al., 2013)
Dairy cattle	60 -120%	(Pryce & Daetwyler, 2012)
Layers	60%	(Sitzenstock et al., 2013)
Broilers	20%	(Dekkers et al., 2009)
Meat sheep	17.9%	(Shumbusho et al., 2013)
Beef cattle	15-44%	(Pimentel & Konig, 2012)

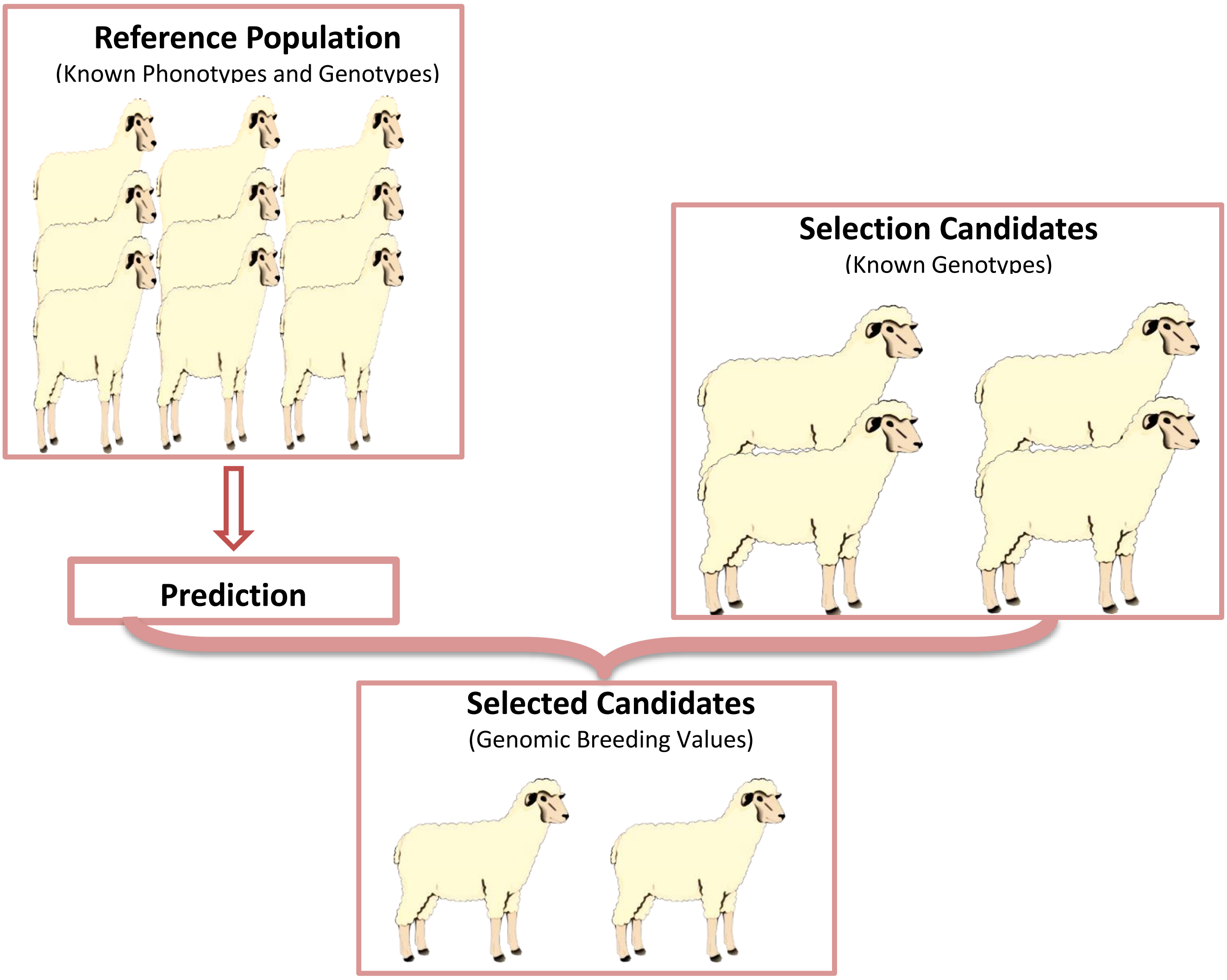

Figure 1 Principle of genomic selection

Genetic gain (ΔG) in animal breeding programs depends upon the intensity of selection (i), accuracy of predictions (r), genetic variance $(\sigma 2g)$ and generation interval (IG): $\Delta G = i * r * \sigma 2g / IG$ (Ibañez-Escriche & Gonzalez-Recio, 2011). Genomic selection increases the rate of genetic gain by decreasing generation interval (Meuwissen & Goddard, 2010) and increasing accuracy of prediction (Hayes et al., 2009). The key benefit of genomic selection is that candidates can be assessed without progeny and phenotypic information. Consequently, selection of animals can be done at very early age, it can even be applied on embryos, thus, genomic selection could increase productivity by reducing generation interval. Moreover, by increasing the size of reference population, selection intensity could increase.

The efficiency of genomic selection for sex-limited (milk yield), low heritable, or poor predictor breeding value traits (fertility) is high compared to traditional selections (Hiendleder et al., 2005). Before the genomic era, genetic improvement depended on huge phonotypic record and thousands of bulls which were progeny tested and used for artificial insemination. However, with the development of genomic selection, progeny testing is no longer necessary, simplifying the selection process and decreasing its cost; due to a strong reduction in generation interval, the yearly genetic trend could be doubled; due to their lower production cost, a much larger number of bulls could be selected and marketed, leading to a better management of genetic resources, limiting inbreeding trends (Henryon et al., 2014). Therefore, whole genomic selection is the effective modern breeding method for production and selection of superior animals.

Implementation of genomic selection in livestock

Animal breeding has had a great influence on the improvement in livestock production. Genetic improvement has played an important role in improving the desired traits' efficiency in livestock, including cattle, sheep, pigs and poultry. The advancement of gene technology allows livestock breeders and commercial livestock product producers to make breeding decisions based on gene marker technology.

- Genomic selection in ruminants

The objective of dense arrays for detection of SNPs has different implications according to the species of interest. In dairy cattle, it has been used to discover markers that will improve the reliability of traits associated with milk production, cow health, and cow conformation. Australia is the leading country in identifying genomic regions associated with milk production (Bolormaa et al., 2010) and several studies have also been completed in the United States, Canada (Wiggans et al., 2009), China (Jiang et al., 2010) and some other countries. Application of genomic estimation has caused significant changes in dairy cattle breeding; the reliability of genomic prediction in dairy cattle exceeds 0.8 for production traits and 0.7 for fertility and other traits (Lund et al., 2011, Wiggans et al., 2011).

Selection is mostly done on the sire side as bulls' semen is distributed via AI for breeding purpose, and with the help of genomic selection elite bulls can be selected at early age. When the accuracy of GEBV for a bull calf at birth is equal to that of conventional breeding values after progeny test, cost reductions in the order of 90% appeared realizable (Schaeffer, 2006). The genotyping of young bull increased the genetic gain and also significantly lowered the cost compared to the genotyping of heifer calves. The lower cost of genomic selection compared to traditional methods has made an incredible impact on the development of dairy industry.

The high reliability and relatively lower cost for genomic prediction from low-density genotyping trailed by imputation has resulted in a very large number of selection candidates being genotyped. To date up to 2 million dairy cattle have been genotyped worldwide (Meuwissen et al., 2016).

Genomic selection could principally benefit more the beef cattle industry paralleled to dairy because beef cattle have long generation interval. Snags of saving phenotype data of satisfactory value and size hamper tradition methods for conventional evaluation, consequently, genomic selection has the efficiency to significantly improve the genetic gain by increasing selection reliability at an early age (Jonas & de Koning, 2015). In beef cattle breeding, selection of indices are often based on a specified market, but adoption is slower primarily due to trait of interest like growth rate, carcass, reproduction, and health that contribute to profitability (Montaldo et al., 2012). Conversely, genomic selection efficiency is still lower in beef cattle compared to dairy cattle possibly due to breed heterogeneity, less advanced structures and breeding programme, predominance of natural service, cross-breeding in commercial herds, as well as effective population size (Johnston et al., 2012).

Reliabilities of genomic prediction in beef cattle have been lower than in dairy cattle (Van Eenennaam et al., 2014). The lower reliability is due to lower quality and quantity of beef cattle population than dairy. In addition, the objective population and validation animals may be less closely related to the reference population in beef cattle than in dairy cattle. Combining data across countries and/or across breeds would possibly increase the accuracy of prediction by solving the problem of small reference populations (de Roos et al., 2009). Better collection of genotypic data and phenotyping might improve the efficiency of genomic selection in beef cattle.

Although whole-genome information exists for small ruminants (Table 1), the likely genetic gain of sheep and goat is smaller than that of cattle (Table 2). A few studies have been done on sheep and most advanced inter flock genetic improvement programmes and genomic research activities have been reported from Australia (Brown et al., 2007). For goats, whole-genome screening has only recently become a possible option, but maybe routine application cannot be expected in the near future. In small ruminants, compared to large ruminants, the breeding organization level is usually lower, with heterogeneous breeding goals but without efficient phenotype recording, so conventional genetic evaluations are more likely to be performed by and within breeding organization than nationally. Genomic selection could suggest new opportunities for small ruminants if a modified description of the dairy cattle organization is followed.

- Genomic selection in swine

Currently, the genomes of more than 20 mammalian species and birds, including human, have been sequenced and in 2009 the genome of pig was added to that list. The key step in pig breeding is the selection of elite boar in nucleus farm, before which boar test recordings generally take place.

Consequently, reduction in generation interval for genetic gain is limited, but genomic selection could still possibly reduce generation interval up to 25% compared to traditional methods (Meuwissen et al., 2016).

Hence, in pig breeding, genetic gain could be increased by improving the accuracy of EBV, particularly for traits which are difficult to improve in traditional methods; single-sex, late-in-life, low heritability, and to measure.

Genomic selection improves litter size in pig (Tusell et al., 2013), but increases pre-weaning mortality in piglet because more number of live piglets than sows are capable of nursing (Andersen et al., 2011). Wide genomic selection made it possible to make selection with high accuracy to increase the number of teats to ensure that sows can nurture all of their piglets (Rohrer & Nonneman, 2017). It is interesting that the use of genomic information could possibly increase the reliability of this trait up to 50% (Lopes et al., 2017).

Post-weaning mortality is another example of a hard to measure trait, with low incidence and heritability, strong environmental influences, but very high economic value (Knap, 2014). With conventional methods, the accuracy of this trait could be increased, but only possible with high mortality incidence. Genomic selection also successfully increased the genetic gain of this trait in pig by increasing the accuracy of EBV up to 50% (Knol et al., 2016). In pigs, cross-breeding is widely used; hence, more effectual selection could be done by using cross-bred pigs as a reference population.

- Genomic selection in poultry

Poultry was firstly sequenced in 2004 (Knol et al., 2016) and then in 2006 the second new build of chicken genome was released, which corrected some of the deficiencies found with the first version (Warren et al., 2017). Chicken breeding programs are in a pyramid form and the larger number of offspring in chicken allows more than double genetic improvement compared to cattle or pigs when using traditional breeding methods (Dekkers, 2007). Some studies showed the possibility to reduce generation interval in layer breeding programs by implementing genomic selection (Wolc et al., 2016).

Breeding of layers for commercial egg production is an international business and is dominated by a few companies. In 2013, Hy-Line Int. performed genomic selection in commercial layers, preceded by 3 years of genomic selection in an experimental line (Wolc et al., 2015). At the end of experiment, birds that were selected based on genomic prediction outperformed those that were submitted to conventional selection for most of the 16 traits that were included in the index used for selection. Other companies also reported genomic selection as a promising alternative to conventional breeding for genetic improvement in layer chickens (Sitzenstock et al., 2013).

Research on the application of genomic selection in broiler breeding was started shortly after the report of chicken genome sequence. However, in broiler the case for genomic selection is not as obvious as in layers because most traits can be recorded on both sexes at an early age. Moreover, in broiler chicken, the improvement in reliability of moderate heritable traits like fertility and egg production can range from 20-45% (Wang et al., 2013), while for highly heritable traits it can be greater than 50% (Wolc et al., 2014).

Conclusion

The demand for high-value protein, lipids, and micronutrients from livestock will probably increase with world population development, thus, more efficient and rapid methods are required to meet the increasing food demand. Although genomic selection is still in its beginning, it is a good tool to increase animal production through improving genetic gain. With the advancement in research and technology, entire genome data of livestock species can be accessed very easily in low price for breeding purpose. Even though in other species, compared to dairy cattle, the implementation of genomic selection is less developed, with research progress, genomic selection will become an efficient tool for the production of elite animals in all livestock species. Further research on the working of genomic selection in breeding programs is definitely privileged, not only for the common good, but also for private breeding companies.

Authors' contributions

Ibtisham conceived the idea, collected information and drafted the manuscript. Zhang, Xiao and An edited the manuscript. Ramzan, Nawab, Zhao, Li and Xu helped with paper writing and data collection.

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บทคัดย่อ

การเลือกจีโนมและการประยุกต์ใช้ในการปรับปรุงพันธุ์สัตว์

ฟาฮาร์ อิบทิชาม[1] ลี้ จาง[1] เหมย เชียว[1] หลี่ลอง อัน[1*] มูฮัมมัด บิลาล ราม[2] อามีร์ นาวาบ[1]
หยี เจา[1] กวงฮวย ลี้[1] หยิงเหมย ชู[1]

การผลิตสัตว์และความต้องการอาหารของประชากรโลกเป็นปัญหาที่สำคัญ โดยทั่วไปวิธีการผลิตสัตว์โดยการผสมพันธุ์ สามารถใช้ในการเลือกประชากรสัตว์ในหลายลักษณะที่มีความสำคัญทางเศรษฐกิจ อย่างไรก็ตามวิธีนี้ยังมีข้อสงสัยถึงความถูกต้องและแม่นยำ การใช้แบบจำลองและการทดลองแสดงให้เห็นว่าคุณค่าการปรับปรุงพันธุ์สามารถให้ผลที่มีความแม่นยำสูง และนำมาใช้ในการคัดเลือกจีโนมสำหรับสัตว์อายุน้อย การคัดเลือกจีโนมเป็นการเลือกเครื่องหมายทางพันธุกรรมที่เป็นตัวแทนทั้งจีโนมเพื่อนำมาใช้บ่งบอกลักษณะเชิงปริมาณ ซึ่งเกี่ยวข้องกับ linkage disequilibrium โดยบอกถึงความเป็นไปได้ที่จะเลือกสัตว์ในช่วงเริ่มต้น เพื่อช่วยให้ได้กลยุทธ์การปรับปรุงพันธุ์ใหม่ ซึ่งมุ่งการส่งเสริมความก้าวหน้าทางพันธุกรรมและลดค่าใช้จ่าย ดังนั้นการเลือกจีโนม จึงสามารถนำมาใช้ในอนาคตในการเพาะพันธุ์ปศุสัตว์ เพื่อเพิ่มผลกำไร โดยการลดช่วงเวลาการปรับปรุงพันธุกรรมและการเพิ่มความน่าเชื่อถือ นอกจากนี้การวิจัยในอนาคตควรมีการประเมินความถูกต้องทางพันธุกรรม และจัดการให้ได้พันธุกรรมที่คงที่ในระยะยาว จุดมุ่งหมายของการบทความนี้เพื่อเสนอภาพรวมของการพัฒนาของการเลือกจีโนมและการประยุกต์ใช้ในการปรับปรุงพันธุ์สัตว์

คำสำคัญ: จีโนมและการผสมพันธ์ ค่าประเมินจีโนมและการผสมพันธุ์ การคัดเลือกจีโนม

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[1] *วิทยาลัยเกษตร มหาวิทยาลัยกวางตุ้งโอเชียน, เมืองจ้านเจียง, มณฑลกวางตุ้ง, สาธารณรัฐประชาชนจีน*

[2] *มหาวิทยาลัยสัตวแพทย์และสัตวศาสตร์, ลาฮอร์, แค้วนปัญจาบ, ประเทศปากีสถาน*

***ผู้รับผิดชอบบทความ** E-mail: anlilong@126.com*