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Selection Methods in Poultry Breeding: From Genetics to Genomics

Vishesh Kumar Saxena and Gautham Kolluri

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Abstract

Scientific and technological advancements have led to great expansion of poultry sector in last few decades. The development of genetically superior stocks capable of higher production, even under adverse climatic conditions, has transformed poultry from rural farming to full-fledged industry within 30–35 years. Increase in production volume and productivity per bird may largely be attributed to the combined crossbred and purebred selection (CCPS). The superior purebred lines were evaluated for their nicking ability by specialized cross-breeding program, and the best nicking male and female lines were used for developing four-way commercial crosses. With advancement in molecular techniques, the DNA marker technology emerged as a finer tool for assessing the genetic variability. Genome-wide scan using microsatellites led to identification of quantitative trait loci (QTL) for their use in marker-assisted selection (MAS). Subsequently, the single nucleotide polymorphisms (SNPs) were discovered as third generation of genetic markers. Recent “next-generation sequencing” technique led to the development of high-density SNP arrays as powerful tool for genetic analysis. Predicting genomic estimate of breeding value (GEBV) of individual using SNPs across the whole genome paved way to conceptualization of “genomic selection” which emerged as the most advanced technology to revolutionize the animal production.

Keywords: quantitative genetics, purelines, microsatellites, SNP, next generation sequencing

1. Introduction

Identifying the superior animals based on performance or phenotype, for breeding, has been practiced since ages. Of course, this practice was followed without the knowledge of underlying

principles of genetics. G.J. Mendel in the year 1866 demonstrated that “factors” (now called genes) are responsible for the inheritance of characters from parent to offspring and “law of heredity” proposed by him, gave the scientific bases for inheritance. Mendelian traits are determined by a single gene and were described as qualitative traits, which follow discontinuous distribution in population and may be subjected to standard genetic analysis. In contrast, the other class of traits exhibits gradual variation following a continuous pattern in population, e.g., body size, milk yield, wool yield, etc. Such traits were described as quantitative traits. Later, Fischer [1] explained the inheritance and variation in quantitative traits as simultaneous segregation of many Mendelian factors (now called genes). The quantitative traits follow multigenic inheritance and each has small allelic and additive effects with substantial environmental influence on phenotype. Mostly, the performance traits are quantitative in nature and controlled by many genes. Therefore, for these quantitative traits, identifying or selecting the superior individuals, different procedures based on theories of quantitative genetics principles were developed. The statistical models and selection theory used in animal breeding are based on the infinitesimal genetic model of quantitative genetics [2]. For quantitative traits the genotype is not able to be observed, it can only be measured through phenotypic value. As a result, specific knowledge of the genetic architecture is not essential for these phenotype-based methods to be effective. The infinitesimal model assumes the trait is affected by a large (infinite) number of unlinked genes with very small and additive effects. But, infinitesimal model has limitations as most of the assumptions of this model are known to be false with regard to the poultry genome [3]. The number of loci in the poultry genome is finite. Directional dominance and linkage may affect the normality of distribution. Economic traits in poultry have considerable genetic nonadditivity. Low-frequency genes with large negative effects have been observed for some fitness traits [4] and many examples of major genes affecting economic traits exist [5, 6].

Expected Breeding Value (EBV) estimated from phenotype has been effective in implementing the selection program and achieving the genetic improvement over the generations. But, a lot of limitations are also being faced *viz.* the ability to accurately and timely recording the phenotypes on candidates and/or their close relatives; the cost of recording the data; and onset of most of the production traits late in life hampers genetic progress per unit time. Heritability estimate of the trait is decisive in deciding the method of selection to be practiced. In long-term selection, the additive genetic variation keeps reducing over the generations resulting in reduced estimation of heritability, and genetic gains in each generation. This necessitates the need of evolving finer tool to assess the genetic variation more accurately, which would help in accurate assessment of the breeding value of the individual. Recent molecular tools may be effectively used for assessing the variations at the genomic level and estimating the breeding values of an individual.

2. Selection methods

The selection and breeding program in poultry has been changing as per the knowledge gained and the needs. In 1940s, the individual poultry flocks were evaluated and after retaining the

selected birds, the surplus culled birds were sold as a terminal product. The concept of two-, three-, or four-way crosses in poultry was adapted from maize improvement program in 1980s, which transformed the poultry breeding for production of the high-yielding modern layer and broiler strains. The purebreds were also replaced by commercial hybrids as terminal cross as well the specialized egg and meat type birds replaced dual type birds. The negative correlations in production and reproduction traits necessitated the need of development specialized male and female lines both in layer stocks and broiler stocks. These specialized lines were developed in meat type stocks [7] and egg type stocks [8]. These specialized male and female lines usually have very different foundation genetic sources [9]. Cornish Game breed was most favored for developing a male line of meat type chicken, whereas developing female lines Plymouth Rock (barred, Columbian, or white) breeds were the most chosen ones for producing commercial broiler across the world. Similarly, for developing brown egg layer male lines, predominantly Rhode Island Red and New Hampshire were used. Plymouth Rock lines were used as female lines. For developing, white shelled egg layers varieties of White Leghorn were used as male and female lines. The modern commercial lines across the world are now a composite of the founding breeds having minor contributions from other suitable breeds [9].

The present poultry breeding, therefore, involves both pure-line selection (PLS) and cross-breeding program. The selection in poultry is therefore combined crossbred and purebred selection (CCPS). Purebred performance and crossbred performance (r_{pc}) are treated as genetically correlated traits assuming the infinitesimal model [10]. Depending on genetic parameters like heritability estimates and correlations, the method such as phenotypic selection primarily followed for improving body weights, whereas for egg production, the index selection (Osborne index) was employed in PLS. The number of traits is now included in selection program, the modern programs, therefore, rely on breeding value estimation with animal model best linear unbiased predictor (BLUP).

i. Pure-line breeding for development of specialized lines:

Specialized sire and dam lines were developed through unique selection program based on different set of traits for sire and dam lines. The dam lines are selected for their reproductive performances, e.g., egg production, egg size, egg weight, shell quality, age at sexual maturity, and hatchability besides juvenile growth. The sire lines are primarily selected for improving the rate of growth, body confirmation, feed conversion ratio, and carcass quality and fertility. Therefore, with the involvement of these specialized lines in the development of commercial broiler stocks thrive toward lowering the cost of production. Crossing of these genetically diverse lines results in gene recombination producing a heterotic effect in progeny for different economic traits. Therefore, intense selection within pure-lines and crossing those genetically diverse lines is the most characteristic feature in broiler breeding program. While practicing the artificial selection, care is taken to minimize the inbreeding, and its related consequences in the population. A control population with the same increment in inbreeding as the selected population may be maintained for comparison and evaluation of the selected population.

- a. *Layers*: for layer, the objectives primarily is “To obtain maximum number of saleable eggs per hen housed at low feed cost per egg or per kg egg mass and the eggs should have optimal internal and external qualities. Stock should have low mortality and high adaptability to different environments.” Layer breeders apply selection to improve over 30 traits important for commercial egg production. Breeders today select for (or at least monitor) the age at sexual maturity, the rate of lay, livability, egg weight, body weight, feed conversion, shell color, shell strength, albumen height, egg inclusions (blood and meat spots), and temperament. The selection strategies to improve egg production include part-time egg production records, persistency of lay, clutch length, FCR/Residual feed consumption (RFC), skeletal problems (majorly osteomalacia and osteoporosis) [11].
- b. *Broilers*: for broilers, selection strategies concentrate on rapid growth and carcass traits. The most practiced strategy for broiler PLS is “selection at commercial weight,” which employs selection at a weight that matches the market weight and the age at selection becomes progressively earlier as growth potential increases. The other two strategies are the selection at a commercial age and multi-stage selection. Different breeding and selection technologies at different period of time were employed for the genetic improvement of poultry (**Table 1**). Breast muscle weight, meat quality, and FCR are major traits; in addition to these, thrust is also being given on skeletal abnormalities, metabolic disorders and welfare. The selection basing on breast area measured through length and width of the breast using a pachymeter along with body weight resulted in a genetic gain of 277% per generation while keeping feed conversion and fertility in the actual levels. The nondestructive means like needle catheters, ultrasonic apparatus etc. were found more accurate for measuring the thickness of the breast muscle. The other non-invasive methods like computed tomography scan (CT scan), magnetic resonance imaging (MRI), and echography are more accurate for measuring the muscle thickness and dimensions of internal organs etc., but these methods are far more expensive [13, 14]. Therefore, among the various non-invasive means, ultrasound offers a viable and advanced solution for breast muscle analysis [15]. In developing or maintaining a strain of broilers, geneticists must consider a balance of characteristics related to growth versus reproduction (**Table 2**).

Utilization of these specialized sire and dam lines in commercial layer and broiler enterprises minimizes the production cost and the gene recombination in these crosses produced a heterotic effect in progeny for different economic traits. While practicing the artificial selection, care is taken to minimize the inbreeding, and its related consequences in the population. A control population with the same increment in inbreeding as the selected population may be maintained for comparison and evaluation of the selected population.

(ii) Combined crossbred and purebred selection

Development of synthetic lines using specialized selection program and their utilization through cross-breeding has been the vital tools for the progress made in poultry production.

Exhaustive literature suggests that including the information recorded on pure as well as crossbreds in selection criterion helps in the improving response to selection in crossbreds

Technique/methodology	Decade
Mass selection	1900
Trap nesting	1930
Hybridization	1940
Artificial insemination	1960
Osborne index in layers	1960
Family feed conversion testing	1970
Selection index	1980
Individual feed conversion testing	1980
BLUP breeding value estimation	1990
DNA markers	2000

c.f: [12].

Table 1. Journey of selection methodology through time.

Growth-related traits	Reproduction
1. Growth rate	1. Egg number
2. Weight-for-age	2. Egg size
3. Feed efficiency	3. Hatchability of fertile eggs
4. Meat (breast) and carcass yield and body conformation	4. Fertility
5. Livability	5. Libido
6. Skeletal integrity	6. Mature weight and age
7. Feathering-cover, rate, and color	7. Aggressiveness (\pm)
8. Adaptation to heat distress	8. Adaptation to heat distress

Table 2. Characteristics most often considered in selecting pure-line breeders [16].

[17–20]. Using the information of both pure as well as crossbreds, the estimated breeding value (EBV) for r_{pc} can be determined, which may also be used as basis for selection [18, 19]; such a selection strategy is known as combined crossbred purebred selection (CCPS). The instance where the selection is based only on the information obtained on pure-line is called as PLS. Genetic correlation between purebred and r_{pc} and heritability of crossbred (h^2_c) are important parameters for optimizing and evaluating crossbreeding systems [21], especially when applying a combined crossbred and purebred selection method to achieve genetic progress in crossbreds [19]. When estimating breeding values for the purebred selection candidates, the information on their crossbred half-sibs can be included in the EBV, which results in a higher accuracy of selection [10]. Bell [22] suggested that r_{pc} is the most reliable indicator of the relative merit of information obtained on purebred versus that received from crossbred when selecting for r_{pc} . When the breeding goal is r_{pc} and the genetic correlation between

purebred and r_{pc} is low, the information coming from crossbred half sibs will dominate the EBVs of selection candidates [10]. Low or negative estimates of r_{pc} indicate the existence of non-additive genetic effect suggesting that reciprocal recurrent selection (RRS) will be more effective. Superiority of CCPS over PLS increases and over crossbred selection (CS) decreases with decreasing r_{pc} .

Wei and van der Werf [19] compared the CCPS was compared with PLS and CS methods. The CCPS was found better than PLS or CS when a fixed number of purebred progeny is tested. However, at very high values of r_{pc} (>0.8) CCPS was worse than PLS. The lesser the estimate of r_{pc} the higher the superiority of CCPS over PLS and decreases over CS. Response of CCPS and CS increase with increasing estimate of h^2_c is (relative to an estimate of purebred heritability). At decreasing values of r_{pc} the difference between actual and optimal response increases but at large r_{pc} values it is small (e.g., for $r_{pc} > 0.7$, the difference between responses is <3%). Furthermore, the expected response has been found to be smaller than the actual response at large values of r_{pc} and $h^2_c > h^2_p$. Finally, for positive values for r_{pc} , the actual response to CCPS is larger than the optimal response to PLS.

The modern commercial poultry strains sustaining the present day production have been developed by crossing the selected parent lines. Crossbreeding exploits both additive and non-additive gene action thereby tends to increase heterozygosity. The resulting crossbreds, therefore, are expected to have uniformity and are least influenced by environmental factors compared to their parent lines. The stocks that complement one another effectively, crossbreeding is the most economical method for combining them.

For the successful crossbreeding program, estimation of crossbreeding parameters and identifying the superior cross combination of lines is essential. A number of experimental design e.g., diallel cross analysis, three-way cross analysis, analysis of double-cross hybrids, line x tester analysis, north Carolina designs, recurrent selection, and RRS have been designed to estimate crossbreeding parameters. Of these diallel or partial diallel cross have been most extensively used for estimation of general and specific combining abilities, which have helped in maximizing the genetic gains through identification of best lines and cross combinations. Systems such as RRS [23] are being widely used for evaluations of purebred and crossbreds. Statistical tools continue to evolve and their improvements have been a hallmark of the continued success of genetics applied to animal breeding [24]. Presently, the most efficient selection method employs the BLUP as a statistical tool. The data from different sources *viz.* individual's phenotype data and family information in a pedigree matrix, may be combined and analyzed.

(iii) Evaluation of crosses under specific climatic conditions ($G \times E$ interactions)

As the phenotype depends on genotype and environment, the environmental effects also need due emphasis while selecting the stocks, and planning the breeding strategy. The ultimate aim of the breeding scheme is to evolve a commercial cross that performs optimally under specific climatic conditions. Therefore, the cross needs to be evaluated under specific climatic condition before releasing it for commercial exploitation.

For a better understanding of $G \times E$, it is important to differentiate microenvironment from macro-environment and also the intrapopulation genotypes from interpopulation genotypes. Diets, ambient temperature, and climatic differences between seasons and regions constitute macro-environments. However, within population, random environmental differences are categorized as micro-environments. Therefore, for deciding breeding strategies particularly between wider ranges of environments, the phenomenon of $G \times E$ interactions is important to be considered. The success of particular cross in a particular environment depends on its ability to adapt and perform in particular environment or climatic zone.

The available evidences for $G \times E$ interactions in performance analysis of modern broilers and various suboptimal conditions emphasize the need for breeding programs aimed at improving the performance under particular environment. The potential importance of $G \times E$ interactions to both the poultry breeder and the producer appears to have been recognized as early as 1936 by Munro. Most of the experiments reported have compared layer and broiler chicken, commercial hybrids, purebreds vs. crossbreds have kept under different rearing and housing systems, climatic conditions etc.

3. Molecular approaches

After discovery of double helical model of DNA, the molecular genetics approaches started making a humble beginning. The advent of the era of molecular genetics in 1970s provided new opportunities to enhance breeding programs through the use of DNA markers associated with traits of interest. Number of type I markers *viz.* RFLPs, ESTs, and SNP and type II markers such as RAPDs, micro- and minisatellites, AFLP, etc. were identified. Because of being highly polymorphic and abundant in the genome, the type II markers are more preferred ones, however, the use of SNPs, the third generation marker is also becoming popular in various genetic applications including.

- i. *QTL identification and genome wide scans*: the genetic control of quantitative traits is expected to be distributed throughout the genome and the numerous regions of the genome, which control the quantitative trait of interest, were described as quantitative trait loci (QTL). These QTLs were identified using specialized experimental crosses, which were specifically developed for the purpose. The identification of QTL and the development of DNA tests were the important steps in the practical application of QTL through marker-assisted selection (MAS) *i.e.*, selection on a combination of information derived from genetic markers associated with QTL and the traditional phenotypic information. Most of these QTL searches were done using 200–350 MS markers and crosses between very diverse breeds, such as heavy meat-type birds and lighter egg-laying varieties or specialized inbred lines [25]. The implementation of MAS in breeding programs was, however, limited for various reasons [26], *viz.* (a) Majority of work on QTL is restricted to experimental crosses having wider linkage disequilibrium rather than original populations undergoing genetic improvement program. (b) The effects identified by QTL analysis are able to explain a limited amount of genetic variation affecting a trait. (c) Due to

the several genetic and non-genetic variations as well as interactions, replication of many associations determined through QTL analysis are difficult to be replicated. And (d) the high-cost of routine genotyping yielding few markers also limits the application of QTL analysis in large breeding operations. Existence of negative correlations between traits of commercial interest also hurdles MAS.

- ii. *Candidate gene approach*: the “candidate genes” are the gene with direct and large effect on the trait of interest. Basing on prior information certain gene (the candidate) may be hypothesized to be responsible for a known major genetic effect. The sequence variations in that gene are identified and then finally various alleles are associated with variation in a trait(s). The genes which are directly associated with production traits like growth hormone (cGH), growth hormone receptor (cGHR), insulin-like growth factor-1 (IGF-1), IGF-1R, TGF betas, myostatin, etc. have been the candidate genes analyzed and molecular markers like SNPs, indel/dels were identified [27–35]. Three physiological candidate genes (i.e., genes for cGH) and gonadotropin-releasing hormone receptor (GnRHR) and neuropeptide Y (NPY) were analyzed to find out their association with egg production, number of double yolk egg, and age at first egg [36, 37]. SNP and deletions were detected in these genes [36–38], and Polymerase chain reaction-restriction length Fragments (PCR-RFLP) was done to determine genotype frequency.
- iii. *High-density SNP genotyping for whole-genome selection*: development of “next-generation” sequencing technologies and high-throughput genotyping platforms has led to the creation of high-density SNP array as a state-of-the-art tool for genetics and genomics analyses of domestic animals. The most promising applications of these arrays in agriculture could be genomic selection for the improvement of economically important traits [39]. Genomic selection is an advanced form of marker-assisted selection (MAS), which concentrates on all markers across the whole genome [40, 41]. It precisely predicts the breeding values of animals by utilizing the information related to the distribution of abundant SNPs across the genome (genomic estimated breeding value, GEBV), with an assumption that abundant SNPs are scattered throughout the genome and there exist LD relationships between SNPs and QTL. The large number of SNPs essentially required for the design and construction of arrays can be obtained through different methods and resources e.g., predicted SNPs generated from genome sequencing and HapMap studies, completing reduced representation library (RRL) sequencing [42, 43] downloading SNP information from dbSNP of NCBI (<http://www.ncbi.nlm.nih.gov/projects/SNP/>) etc. The candidate SNPs for array design should be validated and have high minor allele frequency (MAF) in the testing populations. The two biggest and most competitive SNP chip genotyping platforms are Illumina’s BeadArray based on single-base extension or allele-specific primer extension (<http://www.illumina.com>) and Affymetrix’s GeneChip based on molecular inversion probe hybridization (www.affymetrix.com). Currently, majority commercially released SNP arrays for domestic animals (dog, cattle, horse, pig, and sheep) are constructed using the BeadArray platform with Illumina’s iSelect Infinium technology [39]. Aviagen started developing its first SNP panel for chicken; the chip density increased from 6 K [44], to 12 K [45], 42 K [46], and ultimately to 600 K SNPs [47]. Chicken 60 K SNP array (Illumina Inc., San Diego, CA) [48] was developed using financial assistance from two breeding companies (Cobb-Vantress, and Hendrix

Genetics, the Netherlands), which became proprietary. Heavy restrictions were imposed on its availability to non-academic samples [25]. A second chicken SNP chip (42 K SNP, Illumina Inc.) was subsequently developed completely with private funds [EW Group (Visbeck, Germany), consisting of Aviagen (Huntsville, AL), Hy-Line International (West Des Moines, IA), and Lohmann Tierzucht (Cuxhaven, Germany)]; this was also not available publically [25].

Capitalizing on historical linkage disequilibrium (LD) detected from a genome wide association studies (GWAS), the major QTLs were identified, which utilized to implement MAS. However, the other limitations such as difficulties in detecting and validating QTL and finally the larger proportions of genetic variance for the main quantitative traits of economic importance still remain unexplained, hurdling its application. Several alternate statistical methods have been used in GWAS for determining the association of SNPs with QTL. Single SNP models which employ fitting of each SNP separately as a fixed effect has been most extensively used. The BLUP animal model that accounts for the family structure of the data by fitting a polygenic effect with pedigree-based relationships, found most suitable [49, 50]. Hayes et al. [51] used the mixed linear model methodology to estimate the proportion of genetic variance associated with each genomic region of 50 SNP. The Bayesian methods that have been developed for genomic selection have also been used for GWAS. Several criteria have been used to identify important SNP or genomic regions using these methods current models for genomic selection and GWAS primarily fit additive models but Bayesian variable selection models that fit dominance [52] and even epistatic effects [53] are available or possible. Genomic selection models do not solve the problems of low-accuracy for traits with low heritability and a limited number of records [54]. This is especially advantageous in breeding programs for layers where there is no information available on males before they have records on offspring performances [55]. Application of single step genomic prediction in general leads to increased accuracy of predicted breeding values for both genotyped and non-genotyped individuals in the broiler [56]. An alternative derivation of the single step prediction model based on Bayesian principles were presented by [57]. The main challenge to genomic selection was the high cost of large-scale genotyping due to in large breeding populations and despite the cost of genotyping per SNP is reduced; the overall price per selected candidate that is to be genotyped was relative stable since the density was increasing. The main snag with genomic selection is that, it phenomenally incurs a huge cost for application on the large-scale basis as in involves higher selection candidates. Even though on individual basis SNP cost is reducing, this may not witness the same in overall cost, which is attributed to its relatively high density. Genotyping the animals with a sparse panel comprised of equally spaced markers [58]—the low-density strategies for genomic selection offered a viable solution to the problem.

Author details

Vishesh Kumar Saxena* and Gautham Kolluri

*Address all correspondence to: visheshmeeta@gmail.com

ICAR-CARI, Izatnagar, Uttar Pradesh, India

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