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Genome-wide association studies: In-depth mining of variants for quantitative traits in livestock: A review

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Abstract
In recent years, genome-wide association studies (GWAS) have become a powerful approach for investigating the genetic underpinnings of complex phenotypic traits. In contrast to Mendelian disorders, which result from a single variant, quantitative traits are shaped by numerous genetic variants in interaction with environmental influences. A genome-wide association study (GWAS) is a method that entails thorough scanning of genetic markers throughout an individual's complete genome to identify those linked to specific traits. Advances in high-throughput sequencing technologies have enabled the detection of genomic regions, QTLs, and genes that account for these associations and their impact on the phenotype in question. These advancements have significantly enhanced the understanding of genetic mechanisms underlying complex traits, driving progress in domestic animal breeding and genetics research.

Keywords: GWAS, Phenomics, SNP, QTL, Quantitative traits

1. Introduction
Quantitative or polygenic traits are governed by numerous genes in conjunction with environmental factors. The majority of economically important traits in livestock breeding fall into this category, driving substantial efforts to study them for instance, to predict breeding values for selection candidates or to locate the responsible genes or chromosomal regions. During the 1990s, quantitative trait locus (QTL) mapping relied mainly on microsatellite markers (Lipkin *et al*., 1998) [32]. Nowadays, whole-genome sequencing technologies facilitate the detection of genetic variations, providing a thorough insight into an organism's genetic composition. Genome-wide association studies (GWAS) leverage these variations across the entire genome, together with phenotypic data, to pinpoint genomic regions genuinely linked to the trait of interest (Stranger *et al*., 2011) [57]. As compared to traditional QTL mapping strategies, GWAS covers the major advantages both in the power to detect causal variants with modest effects and indicating the narrower genomic regions that harbor causal variants (Zhang *et al*., 2012) [70]. Compared to conventional QTL mapping approaches, GWAS offers key advantages in both detecting causal variants with moderate effects and pinpointing narrower genomic regions containing those variants (Ikram *et al*., 2010) [22].
The basic principle of GWAS relies on the assumption that a strong association between the genetic variants and the economic trait of interest can be detected because the SNPs are in linkage disequilibrium (LD) with the QTL (Korte and Farlow, 2013) [25]. Zhang *et al*. (2012) [70] has stated that the high density of SNP marker chips used in GWAS is extremely effective in the identification of strong candidate regions harbouring casual mutation through Linkage Disequilibrium. With advances in molecular genetics and reduced genotyping costs, GWAS has become practical across most livestock species. The availability of commercial SNP chips such as those for cattle (50,000 SNPs: Illumina BovineSNP50 BeadChip; 777K HD), dogs (22,362 SNPs: Illumina CanineSNP20 BeadChip), sheep (56,000 SNPs), pigs (60,000 SNPs: Illumina PorcineSNP60 BeadChip), horses (54,602 SNPs: Illumina EquineSNP50 BeadChip), and chickens (60,000 SNPs: Illumina ChickenSNP60 BeadChip) has greatly accelerated

genome-wide association studies in recent years (Zhang *et al*., 2012) [70].

GWAS in Identifying Novel Variant-Trait Associations

GWAS have successfully pinpointed numerous loci associated with a wide array of complex traits in livestock, such as milk yield, fat and protein content, somatic cell count, growth rate, meat quality and yield, sensory panel scores, calving ease, and egg production (Sharma *et al*., 2015) [54]. Usually, variations in breed-specific genetic architectures, combined with the polygenic basis of complex traits, lead to the identification of distinct genomic regions and genes linked to the same trait across different breeds of the same species. (Ma and Zhou, 2021) [37]. GWAS has proven to be an effective approach for identifying genes linked to diverse phenotypes and for clarifying the underlying mechanisms of complex traits (Table 1). In cattle, GWAS has identified novel SNPs associated with milk yield, milk fat content, milk fat composition, milk protein composition, body conformation traits (Yu *et al*., 2023) [67], reproductive traits (Gangwar *et al*., 2025) [15]. In goat and sheep, GWAS has revealed novel loci and genes for litter size (Mahmoudi *et al*., 2022) [40], body conformation traits (Moaeen-ud-Din *et al*., 2022) [43], and feed efficiency traits (Zhang *et al*., 2025). In pigs, variants linked to growth rate, feed efficiency, intramuscular fat, meat quality, and reproductive traits have been identified with the aid of GWAS (Lan *et al*., 2023) [26]. Likewise, in poultry various workers have identified loci associated with various economic traits including growth traits, body size traits, egg production traits, eggshell quality, and disease resistance, such as resistance to Marek's disease.

GWAS can lead to the discovery of novel biological pathways and mechanisms

GWAS loci frequently highlight genes with unknown functions or those not previously suspected to be involved (Hirschhorn, 2009) [18], and experimental follow-up of these loci can uncover novel biological mechanisms underlying disease (Visscher *et al*., 2017) [61]. Palombo *et al*. (2018) [48] employed a gene-centric approach and pathway meta-analysis, identifying not only established genes linked to quantitative trait loci for milk fatty acid components-such as FASN, SCD, and DGAT1-but also additional significant candidate genes, including those with functional roles in lipid metabolism pathways (Table 2).

GWAS are important to investigate low-frequency and rare variants

Currently, most GWAS are performed using data obtained by SNP arrays. Originally designed to capture common genetic variation, genome-wide SNP arrays have evolved significantly to include higher variant density and a broader spectrum of allele frequencies (Table 3). Studies using exome-focused custom arrays have successfully identified rare and low-frequency coding variants associated with various complex traits, such as blood lipid levels, hematological parameters, blood pressure, height, BMI, and type 2 diabetes (T2DM), (Tam *et al.*, 2019) [59].

GWAS can study genetic variants other than single-nucleotide variants (SNVs)

GWAS are mainly designed to assess single nucleotide variants (SNVs) for associations with complex diseases and traits. Nevertheless, they can also detect other types of genetic variants that influence disease susceptibility. For example, GWAS have associated rare (Bochukova *et al*., 2010) [3] and common copy number variants (D′ Angelo, and Koiffmann, 2012) [8] with BMI and obesity, among several other common traits and diseases (Table 4).

Limitations of GWAS

GWAS explain only a modest fraction of the missing heritability

GWAS have uncovered an unprecedented array of genetic variants linked to common diseases and traits, yet these variants explain only a modest fraction of the estimated heritability for most complex traits (Manolio *et al*., 2009) [41]. Several explanations for the missing heritability have been suggested (Eichler *et al*., 2010) [12]. One likely reason is that SNPs with modest effects go undetected because they fail to meet the strict significance threshold.

GWAS do not necessarily pinpoint causal variants and genes

Genetic mapping is a double-edged sword: while linkage disequilibrium enables the initial detection of a locus through correlated variants, it complicates pinpointing the true causal variant(s). Most association signals occur in non-coding genomic regions, where biological interpretation is particularly difficult (Hindorff *et al*., 2009) [17]. Therefore, after conducting a GWAS, further steps are typically necessary to pinpoint the causal variants and their target genes, such as re-sequencing and fine-mapping in multi-ethnic or admixed populations, methodological advancements, functional analyses, or evolutionary genetic studies (Thurner *et al*., 2018) [60].

GWAS based on SNP arrays depends on pre-existing genetic variant reference panels

A drawback of SNP array-based GWAS is their reliance on the comprehensiveness of prior sequencing studies and reference panels used to design genotyping arrays and impute untyped variants. This issue has been mitigated by the advent of next-generation high-density arrays, which incorporate sequencing data from more diverse populations to enhance genomic coverage across species and breeds (Hoffmann *et al*., 2011) [19]. However, advanced sequencing methods like reduced-representation sequencing (RRS) techniques-including Genotyping-by-Sequencing (GBS) and double-digest Restriction-site Associated DNA sequencing (ddRAD-seq)-have emerged as versatile, unbiased alternatives that bypass the requirement for prior knowledge of genetic variants (Magbanua *et al*., 2025) [39].

GWAS are significantly constrained by an stringent multiple-testing correction

A key limitation of genome-wide approaches is the requirement for a stringent significance threshold to adjust for multiple testing. In GWAS, this is typically achieved through Bonferroni correction, which sets the genome-wide false-positive rate at 5% by assuming approximately 1 million independent tests for common variants. Consequently, standard GWAS lack sufficient power to capture all SNP-based heritability, as association signals must surpass this strict threshold to be deemed significant (Dudbridge *et al*., 2008) [11].

Large population studies are essential for detecting associations

Adequate sample size with sufficient statistical power is crucial for the success of genetic association studies aimed at identifying causal genes in complex human diseases.

Genome-wide association studies, in particular, demand substantially larger sample sizes to attain the necessary statistical power (Hong *et al*., 2012) [20].

Conclusion

GWAS has proven to be an excellent tool for identifying genes linked to diverse phenotypes and for unravelling the mechanisms underlying complex traits. These findings have offered unprecedented insights into the role of common variants in complex traits, shed light on genome function, and created new opportunities for developing therapeutic interventions. Looking ahead, deeper exploration of epistasis (gene-gene interactions), gene-environment interactions, and copy number variants is expected to yield further understanding of complex disorders in humans and animals.

Table Caption

Table 1, traits for which variants identified through Genome-Wide Association Studies

Table 2, biological pathways and networks identified through GWAS

Table 3, rare genetic variants associated with economically important traits in livestock and poultry species through GWAS

Table 4, other variants other than SNVs associated with traits identified by GWAS.

Table 1: Traits for which variants identified through GWAS

S. No.	Traits	Species	References
1.	Visual Score	Cattle	Machado *et al*., 2022 [38]
2.	Young stock survival	Cattle	Cai *et al*., 2023 [7]
3.	Meat Quality (Water holding capacity and pH)	Sheep	Revelo *et al*., 2023 [51]
4.	Body size traits	Sheep	Liu *et al*., 2024 [68]
5.	Resilience traits	Sheep	Argyriadou *et al*., 2023 [1]
6.	Health and production traits	Sheep	Kaseja *et al*., 2023 [24]
7.	Litter size	Goat	Mahmoudi *et al*., 2022 [40]
8.	Reproductive traits	Cattle	Gangwar *et al*., 2025 [15]
9.	Growth and body conformation traits	Goat	Moaeen-ud-Din *et al*., 2022 [43]; Yang *et al*., 2024 [68]
10.	Growth and reproductive traits	Goat	Shangguan *et al*., 2024 [53]
11.	Body measurements and reproductive traits	Pigs	Lan *et al*., 2023 [26]
12.	Feed efficiency traits	Sheep	Zhang *et al*., 2025 [69]
13.	Body conformation traits	Cattle	Yu *et al*., 2023 [67]
14.	Growth traits	Pigs	Zeng *et al*., 2024 [68]
15.	Feed efficiency traits	Pigs	Fu *et al*., 2020 [14]
16.	Loin muscle area	Pigs	Zhenyu *et al*., 2025 [72]
17.	Teat number	Pig	Li *et al*., 2023
18.	Immune traits	Pig	Dauben *et al*., 2021 [9]
19.	Bone mineral density	Pig	Nan *et al*., 2020 [45]
20.	Average daily gain, backfat thickness, eye muscle area	Pig	Park, 2024 [49]
21.	Growth and Egg traits	Poultry	Liao *et al*., 2016 [31]
22.	Body composition and structural soundness traits	Pig	Fan *et al*., 2011 [13]
23.	Fatty acid metabolic traits	Pig	Zhang *et al*., 2016 [71]
24.	Litter traits	Pig	Wu *et al*., 2018 [64]
25.	Hyperpigmentation	Broiler	Zhou *et al*., 2022 [73]
26.	Body weight, Growth traits, Body size traits	Poultry	Dou *et al*., 2022 [10]
27.	Serum Biochemical Indicators	Chicken	Song *et al*., 2023 [56]
28.	Milk production, milk fatty acid	Cattle	Atashi *et al*., 2023 [2]
29.	Somatic cell, Body conformation	Cattle	Wang *et al*., 2022 [73]
30.	Milk protein and milk minerals	Cattle	Singh *et al*., 2022 [55]

Table 2: Biological pathways and networks identified through GWAS

S. No.	Species	Biological pathway and Network	Genes involved	References
1.	Cattle	Lipid biosynthetic process, regulation of lipid metabolism, developmental growth, multicellular organism growth	*PPARG, FABP4, ACACA, FASN*	Naserkheil *et al*., 2020 [46]
2.	Cattle	GABAergic synapse pathway, non-alcoholic fatty liver disease (NAFLD) pathway	*GABRA2, GABRB1, MTOR, PIK3R1*	Sanchez *et al*., 2017 [52]
3.	Cattle	Ion/cation transmembrane transporter activity, neuronal signalling, hormone signalling, signal sequence binding (casein micelle formation)	*GFI1B, ZNF407, NR5A1*	Pegolo *et al*., 2018 [50]
4.	Pigs	Bone and cartilage development, muscle growth, insulin signalling	*CHCHD3, BMP2, HOXA2, HOXA10*	Fan *et al*., 2011 [13]
5.	Cashmere goat	Wnt signaling, BMP signaling (cashmere development)	*PDGFRA, WNT5A, PPP2R1A, BMPR2, BMPR1A, SMAD1*	Liu *et al*., 2022
6.	Chickens	Regulation of autophagy pathway	*ATG5, ATG7, LC3*	Zhang *et al*., 2014
7.	Cattle	Steroid metabolism, signal transduction	*HSD17B3, SHC3, IGFBP2*	Bolormaa *et al*., 2011 [4]
8.	Pig	Calcium signalling, transcription factor activity, immune regulation	*COX10, C2C12, mtND4L*	Yu *et al*., 2024 [53]
9.	Pigs	Lipid metabolism, glycerolipid metabolism, PPAR signalling	*PLIN2, LPL, FASN, SCD*	Zhang *et al*., 2016 [71]
10.	Chickens	Immune response, cytokine-cytokine receptor interaction	*IL6, CXCL12, TNFSF10*	Borodin *et al*., 2020 [5]
11.	Goats	Calcium signaling, extracellular matrix organization	*CACNA1C, COL1A1, ITGB5*	Mucha *et al*., 2018 [44]

Table 3: Rare genetic variants associated with economically important traits in livestock and poultry species through GWAS

S. No.	Species	Rare variants in genes	Traits associated	References
1.	Cattle	rs110066139 (*SLC2A2*), rs109326954 (*FGF2*)	Milk fat yield	Liu *et al*., 2020
2.	Pig	rs80815129 (*PLIN2*), rs319647833 (*SCD*)	Backfat thickness	Zhang *et al*., 2016 [71]
3.	Chickens	rs315964677 (*IL6*), rs317219876 (*CXCL12*)	Marek's disease resistance	Li *et al*., 2021
4.	Goat	rs660693523 (*DGAT1*), rs670258914 (*LPL*)	Milk fat content	Martin *et al*., 2017 [42]
5.	Cattle and Pig	rs43705173 (*CYP2E1*), rs80893456 (*IRF2*)	Methane emissions, gut microbial composition	Wen *et al*., 2023
6.	Chickens	rs314672189 (*KRT5*), rs316543210 (*WNT7A*)	Feather pecking behaviour	Lutz *et al*., 2020
7.	Goats	rs668124567 (*CACNA1C*), rs671893456 (*COL1A1*)	Milk yield	Mucha *et al*., 2018 [44]
8.	Pigs	rs319256789 (*MC4R*), rs80845678 (*LEPR*)	Feed efficiency, growth rate	Onteru *et al*., 2013 [47]
9.	Chickens	rs317891234 (*GHR*), rs315789012 (*IGF1*)	Growth rate, body weight	Boschiero *et al*., 2018 [6]

Table 4: Other variants other than SNVs associated with traits identified by GWAS

S. No.	Species	Genetic variants type	Traits associated	References
1.	Cattle	CNVs (CNV150 on Chr26: 25,719,640-26,013,587, CNV151 overlapping *ELF3*)	Feed intake (RFI, DMI), milk quality, female fertility	Zhou *et al*., 2018 [64]
2.	Pig	CNVs (34 homozygous CNVs: 27 deletions, 7 duplications, overlapping exonic regions), Haplotypes	Growth patterns, fertility, metabolic function	Liu *et al*., 2025 [30]
3.	Cattle	CNVs (1755 CNVRs: 9171 deletions, 4101 duplications, covering 2.8% autosomes)	Milk yield, somatic cell score, fertility	Lee *et al*., 2020 [27]
4.	Pigs	Structural Variants (123,151 SVs: deletions, duplications, insertions, mobile element insertions), Haplotypes	Carcass traits, skeletal traits, meat quality	Zong *et al*., 2023 [75]
5.	Goats	Haplotypes (*CCSER1)*	Milk fat content, coat colour	Martin *et al*., 2017 [42]
6.	Chickens	Indels (1-125 bp insertions/deletions in *IGF1*), Haplotypes (growth-related regions)	Growth rate, body weight	Boschiero *et al*., 2018 [6]
7.	Chickens	CNVs (Chr8: 10,250,123-10,350,789, overlapping *IL6A*	Marek's disease resistance	Li *et al*., 2021

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