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Semiu Folaniyi Bello

Raman Akinyanju Lawal

The Jackson Laboratory, raman.lawal@jax.org

Adeniyi Charles Adeola

Qinghua Nie

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The study of selection signature and its applications on identification of candidate genes using whole genome sequencing data in chicken—a review

Semiu Folaniyi Bello,^{*,†,‡} Raman Akinyanju Lawal,[§] Adeniyi Charles Adeola,[#] and Qinghua Nie^{®*,†,1}

^{*}Department of Animal Genetics, Breeding and Reproduction, College of Animal Science, South China Agricultural University, Guangzhou 510642, Guangdong, China; [†]Guangdong Provincial Key Lab of Agro-Animal Genomics and Molecular Breeding and Key Lab of Chicken Genetics, Breeding and Reproduction, Ministry of Agriculture, Guangzhou 510642, Guangdong, China; [‡]Agriculture Research Group, Organization of African Academic Doctors (OAAD), Langata, Nairobi, Kenya; [§]The Jackson Laboratory, Bar Harbor, ME 04609, USA; and [#]Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, 650223 Yunnan, China

ABSTRACT Chicken is a major source of protein for the increasing human population and is useful for research purposes. There are almost 1,600 distinct regional breeds of chicken across the globe, among which a large body of genetic and phenotypic variations has been accumulated due to extensive natural and artificial selection. Moreover, natural selection is a crucial force for animal domestication. Several approaches have been adopted to detect selection signatures in different breeds of chicken using whole genome sequencing (WGS) data including integrated haplotype score (iHS), cross-populated extend haplotype homozygosity test (XP-EHH), fixation index (F_{ST}), cross-population composite likelihood ratio (XP-CLR), nucleotide

diversity (P_i), and others. In addition, gene enrichment analyses are utilized to determine KEGG pathways and gene ontology (GO) terms related to traits of interest in chicken. Herein, we review different studies that have adopted diverse approaches to detect selection signatures in different breeds of chicken. This review systematically summarizes different findings on selection signatures and related candidate genes in chickens. Future studies could combine different selection signatures approaches to strengthen the quality of the results thereby providing more affirmative inference. This would further aid in deciphering the importance of selection in chicken conservation for the increasing human population.

Key words: chicken, domestication, selection signature, genes, conservation

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INTRODUCTION

Domestication of Chicken

Studies have reported where and how chicken domestication from the jungle fowl species occurred. Most of these studies have either reported the Red jungle fowl (RJF) (*Gallus gallus*) as the dominant ancestor of domestic chicken based on mitochondrial DNA (Fumihito et al., 1994, 1996) or its domestication was from the RJF (*Gallus gallus*) in the south and Southeast Asia based on whole genome sequencing (WGS) analyses

(Sawai et al., 2010; Tixier-Boichard et al., 2011; Peters et al., 2015; Mohamed et al., 2017; Lawal et al., 2018, 2020; Wang et al., 2020b). It was reported that *Gallus sonneratii* also contributed to the genetic makeup of domestic chickens (Tixier-Boichard et al., 2011). Moreover, it was reported that RJF was domesticated (approximately 800–5,400 BC) in Asia and has spread across the world (Xiang et al., 2014; Peters et al., 2016). Considering the maternal perspective, subhaplogroup C1 and haplogroups A revealed the recent expansion of domestic chicken in northern China (Huang et al., 2018), and they have developmentally adapted to different local environments which include aridness, high altitude, and harsh African conditions (for instance poor nutrition, resistance to diseases, heat stresses, etc.) (Wang et al., 2015; Elbeltagy et al., 2019; Walugembe et al., 2019). The genus *Gallus* comprises 3 other wild species namely the Gray jungle fowl *G. sonneratii* with body plumage on a gray background (found in

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¹Corresponding author: nqinghua@scau.edu.cn

Southwest India), La Fayette's or Ceylon jungle fowl *G. lafayettii* whose morphology resembles RJF (in Sri Lanka), and the Green jungle fowl *G. varius* (in Southeast Asia widespread to Java and neighboring island) that have contributed to the genetic background of the domestic chicken (Sawai et al., 2010; Lawal et al., 2020). The white and yellow skin phenotypes have been shown to have ancestral origins linked to the RJF (*Gallus gallus*) and Gray jungle fowl (*G. sonneratii*), respectively (Eriksson et al., 2008).

There is significant genome divergence in these chickens due to the effect of environmental pressures and artificial selection thereby contributing substantial evolutionary force to both phenotypic and genotypic differentiation (Li et al., 2019). Interestingly, natural selection (specifically extreme environmental conditions) is an important force in determining the genome heterogeneity of chicken and other poultry species during their domestication (Zhu et al., 2021b). The occurrence of selection pressures could affect the genome structure and strand signatures at particular positions of the genome which include widespread linkage disequilibrium (LD), increased allele frequencies, similar genotypes, and dropped local diversity (Nielsen, 2005; Qanbari and Simianer, 2014). Moreover, positions that are close to regions under selection are mostly affected by background selection and genetic hitchhiking (Smith and Haigh, 1974).

Usefulness of Domestic Chicken

Domestic chickens (*Gallus gallus domesticus*) are the most prevalent birds (Lawler, 2014), and are raised for several reasons which include meat and egg production, religion, and recreational activity (i.e., cock fighting) in some geographical areas (Rostamzadeh Mahdabi et al., 2021). Chickens serve as one of the major sources of animal proteins (meat and egg) consumed by humans (FAO, 2019). Interestingly, over 65 billion poultry birds are raised per annum by the commercial sector to meet the demands for meat (Bennett et al., 2018) while above 80 million metric tons of eggs are produced per year for human consumption across the world (Lawal et al., 2020). In addition, chickens are used in studies related to bacterial and viral diseases, and genetic diseases associated with humans (Dodgson and Romanov, 2004; Burt, 2007), useful for essential research models in development, physiology, and aging (Deist et al., 2018; Zhang et al., 2018a,b), and also serve as a source of living provisions during journeys (Peters, 2014). The genetic differences of indigenous chicken breeds are important resource for breeding and understudying the degree of genetic diversity which is essential for the conservation of potential traits and molecular breeding (Blackburn, 2006; Toro et al., 2009; Lyimo et al., 2014). Several phenotypic attributes affect adaptation to abiotic and biotic pressures, physiology, morphology, fitness, body size,

plumage, flying ability, behavior, skin color, and egg production (West and Zhou, 1988; Kim et al., 2019; Li et al., 2020a).

USE OF WHOLE GENOME SEQUENCING TO IDENTIFY SELECTION SIGNATURE

WGS involves the usage of next-generation sequencing technology to understand the genomic potentials (i.e., genetic variants; single nucleotide polymorphisms (SNPs), insertion/deletion polymorphism (indels), structural variations (SVs), copy number variations (CNVs), presence/absence variation (PAV), quantitative trait locus (QTL) analysis, and marker-assisted selection) in different organisms (Ng and Kirkness, 2010; Wang et al., 2021). WGS is cost-effective and efficient. WGS offers the chance to comprehend the benefit and capacity of genomes (Zhao and Grant, 2011).

WGS could be high-density SNP chips or massively parallel sequencing adopted to detect region of selection signatures in an organism (Elferink et al., 2012). The availability of WGS data enables the detection of adaptation and evolution at novel opinion (Horscroft et al., 2019). In addition, WGS is utilized to understudy the disparity in phenotypic traits and chemical composition that are related to genomic differences in organisms (Huang et al., 2009). WGS involves the pooling of DNA samples and provides comprehensive genomic data to accurately detect selection signatures at a moderately low cost, especially for nonmodel organisms (Schlötterer et al., 2014). However, WGS at sufficient depths is quite expensive to reveal genomic information of several individuals for a large population, and this necessitates the need to sequence some individuals as a representative of the whole population (Schlötterer et al., 2014; Lou et al., 2021). A previous study that first utilized pooled genome sequencing revealed assumed selective sweeps under profound artificial selection in both broiler and layer chickens (Rubin et al., 2010). Different studies have adopted WGS to reveal selection signatures in poultry species including chicken (Luo et al., 2020; Cho et al., 2022), duck (Gu et al., 2020b; Zhu et al., 2021a), quail (Bouquin et al., 2021), geese (Wen et al., 2023), ruminant animals such as goats (Sun et al., 2022), sheep (Li et al., 2020b), and cattle (Maiorano et al., 2022), pig (Wang et al., 2022b), etc.

SELECTION SIGNATURE

The selection signature is the distinctive genetic pattern abandoned in the genomic areas subdued to selection (Nielsen, 2005; Jensen et al., 2016). This regional reduction in genetic variation (i.e., up or down) of the selected important mutation is influenced by the swift disposition of the mutation over multiple generations (Saravanan et al., 2020). The process by which essential mutations amplify in number in a population and cause

a reduction in irregularity in the related autonomous sites is known as selective sweep or hitchhiking effect or genetic drift (Smith and Haigh, 1974; Fay and Wu, 2000). There are 3 types of signatures of selection which include positive, negative, and balancing selection (Horscroft et al., 2019). However, the determination of positive signatures of selection is one of the major interests of researchers as it could provide pertinent information about the impact of selection on adaptive, productive, and morphological features (Rostamzadeh Mahdabi et al., 2021). Also, it serves as a means to identify genes and utilize crucial variations that cause selective advantage in a specific population (Zhao et al., 2015). The positive selection might enable an increase in the specific allele distribution in the population while it is expected that negatively selected alleles and alleles with balancing selection should lead to a decrease and fairly stable frequency, respectively when considered in a population provided there is a constant environment (Horscroft et al., 2019). Nevertheless, genetic drift occurs when alleles lead to fixation (possession or complete loss of allele) due to random selection (Honnay, 2013), and this phenomenon is an inconsistent factor when investigating for signatures of selection (Andrews, 2010).

Approaches in the Detection of Selection Signatures

Different methods such as allele frequency spectrum, reduced local variability, LD, and phenotype features have been adopted to detect the selection of signatures (Qanbari and Simianer, 2014). In a recent report, the advantages and constraints of the site frequency spectrum (SFS), LD, reduced local variability, single site population differentiation, and haplotype-based differentiation methods were highlighted in detail (Saravanan et al., 2020). However, this report lacks detailed information on selection signatures in chicken. Herein, we review different studies on selection signatures and their applications in identifying candidate genes in domestication and different traits in diverse breeds of chicken using analyses from whole genome data.

With the recent advancement of high throughput sequencing techniques such as WGS, there is a huge opportunity to determine selection signatures at the genome level. Subsequently, different statistical tests have been developed to investigate imperative selection signatures considering different models (i.e., demographic or selection) (Vitti et al., 2013; José De Simoni Gouveia et al., 2014). As reported by Ma et al. (2015), unique important variants under selection pressure would produce distinct signatures in the particular region of the genome (i.e., extreme (high or low) frequencies of allele spectrum, excess homozygous genotypes, long haplotype with high frequency or extreme local population differentiation) (Ma et al., 2015). Different methods have their attributes, for instance, integrated haplotype score (iHS) is sensitive to the continuing or incomplete selection signatures, and the cross-

population extend haplotype homozygosity test (XP-EHH) is accurate at evaluating the selection signatures close to fixation (Sabeti et al., 2002), and could also detect regions with selection genomics within a small sample size (Pickrell et al., 2009) while fixation index (F_{ST}) is an outlier approach used in the identification of genomic regions involved in speciation (Kozma et al., 2019). It has been reported that F_{ST} , nucleotide diversity (π), and XP-EHH are mostly used in positive natural selection analyses (Xu et al., 2021). In addition, F_{ST} (Weir and Cockerham, 1984), cross-population composite likelihood ratio (XP-CLR) (Chen et al., 2010), and nucleotide diversity (Π) have been utilized to detect positive selection in chicken (Gu et al., 2020a).

Different studies have adopted several approaches to detect selection signatures in different poultry species such as ducks (Zhang et al., 2018a,b; Xu et al., 2019; Wang et al., 2020b; Feng et al., 2021), Helmeted Guinea fowl (Vignal et al., 2019; Shen et al., 2021), racing pigeons (Gazda et al., 2018), turkey (Durosaro et al., 2022), quail (Morris et al., 2020), geese (Wang et al., 2017; Ren et al., 2021; Liu et al., 2021), and chickens (Weng et al., 2020; Luo et al., 2020).

Detection of Selection Signature and Candidate Genes Related to Several Traits in Different Breeds of Chicken

The changes that occurred at the genetic level can trigger local adaptation when individuals from a specific population have important fitness traits, including morphology camouflage ability, innate immune responses, and fetal viability (Savolainen et al., 2013). Interestingly, these changes could lead to genetic and phenotypic population segregation and difference in genetic structure over a while (Savolainen et al., 2013).

Different studies have adopted WGS data to study the genetic configuration and economic features under positive selection. Table 1 shows our critical reviews on traits considered, prominent genomic regions, number of SNPs identified, number of insertion/deletion (Indels), number of SV, CNV, SNP density in a chromosome, number of associated SNPs and Indels, methods adopted to determine selection signature, genes linked to a trait of interest (chromosome position), enriched KEGG and GO of the identified candidate genes in different breeds of chickens.

Domestication and Genetic Diversity A recent study identified selection signatures in 2 Iranian indigenous chicken ecotypes namely the Lari fighting and the Khazak or creeper (short-leg) chickens using whole-genome resequencing data (Rostamzadeh Mahdabi et al., 2021). Based on the findings, 342 candidate genes were similar in both ecotypes of which 225 were protein-coding genes. In the Khazak ecotype, few of the genes were revealed to play a function related to reproduction (*ELF3*, *ESR1*, and *CALCR*), immune traits (*DOCK2*, *LCP2*, *PTPN2*, and *IL1RAPL1*), and abdominal fat deposition

Table 1. Different studies on selection signature and identification of candidate genes using WGS in chicken.

Breeds of chicken used	Trait (s) considered	Prominent genomic regions	Number of SNPs identified	Number of insertion/deletion (INDELS) identified	Number of structural variations (SV), copy number variants (CNV) identified	SNP density in chromosomes	Number of associated SNPs and INDELS	Methods adopted	Selection signature	Gene (s) linked to trait of interest (chromosome position)	Enriched KEGG (most enriched)	Enriched gene ontology (GO) (most enriched)	References
Baicheng You	Feather color	Chromosomes 1, 7 and 13	18.37 million	2.61 million	Not reported	Not reported	Not reported	XP-CLR	934 genes (black vs. lavender), 3,620 genes (black vs. yellow), 989 genes (yellow vs. lavender), 685 genes (black vs. yellow + lavender), 836 genes (lavender vs. black + yellow), and 820 genes (yellow vs. black + lavender).	<i>EGR1- black plumage</i> <i>RAB17, MLPH, and SOX5- lavender plumage.</i> <i>GRM5- yellow plumage</i>	Not reported	Not reported	(Wang et al., 2022a)
Guangxi Yellow, Hetian, Huaixiang, Huanglang, Huiyang bearded, Jiangban, Ningdu Yellow, Wenchang, Wulua Yellow, Zhengyang Yellow	Feather color	Intergenic and intronic regions	16,817,111	1,289,024 Deletions (785,806) Insertions (503,218)	95,918 (CNVs) Intrachromosomal (65%), deletion (26%)	Not reported	Not reported	Locus specific branch length statistics (LSBL) and $\theta\pi$ -ratio	268 analytical window within 1% of LSBL test π -ratio test (370 windows) 366 PSGs (LSBL), 504 PSGs (π -ratio test)	28 PSGs were common (<i>RALY, LGR4, RYR2, RYR3, SLC23A2, SLC2A14 BCDO2</i> (chr 24: 6,110,301 -6,130,965) (along with its flanking genes: IL18 and PTS)	Not reported	Vitamin transport activity (<i>SLC23A2 and SLC2A14</i>)	(Huang et al., 2020)
Rhode Island White hens	Eggshell qualities	Protein coding regions	7,450,661 SNPs in the LES group and 7,588,813 SNPs in the NES group. Although, only 3,671,919 (484,857 and 563,437 unique SNPs in the LES and NES groups, respectively) protein coding regions	508,035 Indels 67,925 and 76,319 indels were unique to LES and NES groups, respectively. More of the indels were identified in intronic and intergenic regions	Not reported	Lowest in sex chromosomes (Z and W) Highest in chromosomes 16 and LEC64	1,755 (nonsynonymous variations) and 19 frame shift indels detected in 427 DEGs	Not reported	Not reported	<i>OC-116, LTF and SPP1</i> Almost 64 DEGs (located at 15QTL regions) were associated with eggshell strength 36DEGs located at 3 QTL region were associated with eggshell thickness	Calcium signaling pathway, focal adhesion, extracellular matrix (ECM)-receptor interaction, vascular smooth muscle contraction	Calcium ion transport	(Zhang et al., 2015)
F ₂ chickens (broiler cocks × fat line with abdominal fat content) and Baier layer dams (Chinese native breed)	Bone traits	Chromosomes 1, 4 and 27	2,028,112	Not reported	Not reported	Not reported	Not reported	Combination of F _{ST} and $\theta\pi$ -ratios statistics	Using femur and shank traits on 34 Chr. during either natural or artificial selections, potential genes in selection regions of LShL (354), HShL (361), LShW (179), HShW (456), LFeL (334), HFeL (438), LFeW (148), and HFeW (386) were identified.	21 potential genes including <i>LRCH1, RBL1, FMOX3A, MLNR, CAB39L, FOXO1, LHFP, TRPC4, POSTN, SMAD9, RBP1, PPARGC1A, SLIT2, NCAPG, NKX3-2, CPZ, SPOP, NGFR, SOST, ZNF652, and HOXB3</i> might regulate bone growth and development	Calcium signaling	Embryonic skeletal system development	(Li et al., 2021)
Tibetan chickens breed Shigatse (SH), Nyemo (NM), Dazge (DZ), Nyingchi (LZ), Lhasa white (LW)	Environmental adaptations	Candidate regions on GGA5 and GGAS	Number of SNPs contained in the ROHs are between the studied populations, and SH population contained the maximum number (22,386) located on CGA1	Not reported	Not reported	Not reported	Not reported	integrated haplotype score (iHS)	The genomic region ranges from 0.03Mb to 1.13Mb of GGAS, and enclosed 6 top 0.1% ROH islands across the 5 populations. SNPs of 1, 1, 8 and 2 enclosed selection signature in SH, NM, LZ and LW, respectively	<i>AMY2A, NTNG1 and VAV3</i>	Not reported	Positive regulation of synapse assembly, positive regulation of I-kappaB kinase/NF-kappaB signaling, osteoblast differentiation, cellular response to amino acid stimulus, cell adhesion and endodermal cell differentiation	(Yuan et al., 2022)
Eight chicken breeds Laitwu Black, Langya, Shouguang, Luxi mini, Jining Bairei, Wenshang Barred, Luxi gamecock, recessive white	Breed features	28 Chromosomes	22,082,777 11,209,417 SNPs were retained for analyses	Not reported	Not reported	Not reported	Not reported	F _{ST}	540 genomic regions in the F _{ST} analyses	58 genes related to the various characteristics <i>TSHR- circadian rhythm</i> <i>ADGRL3- aggression</i> <i>RAC1 and EPB41L1- Body size and skeletal development</i> <i>GRM5- feather color</i> <i>TSHR, ANK2, SPIRE2 and PSMD7- Reproduction-related genes</i> <i>MGA1AC, PPP1CB, RAC1, EPB41L1- Body size</i> <i>ACMO, ADGRL3 and VSTM2A</i> related to morphology and behavior	Not reported	Not reported	(Wang et al., 2022c)

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Table 1 (Continued)

Breeds of chicken used	Trait (s) considered	Prominent genomic regions	Number of SNPs identified	Number of insertion/deletion (INDELs) identified	Number of structural variations (SV), copy number variants (CNV) identified	SNP density in chromosomes	Number of associated SNPs and INDELs	Methods adopted	Selection signature	Gene (s) linked to trait of interest (chromosome position)	Enriched KEGG (most enriched)	Enriched gene ontology (GO) (most enriched)	References
Iranian native chickens from Isfahan (highland with altitude= 2087m) and Mazandaran (low land with altitude= 54m)	Adaptive features associated with hypoxia	Chromosome 29 (In female) Chromosome 2 (In male)	20 million (single nucleotide variant (SNV), multi nucleotide variant (MNV), insertion, deletion and replacement)	Not reported	Not reported	Not reported	Not reported	F _{ST}	Based on extremely high F _{ST} (top 5%), 95 biological categories and 858 candidate genes were reported considering different databases	<i>COX3</i> (affected cell respiration in adaptation to hypoxia) <i>MIR6644-2</i> (involves in hypoxia and adaptation to high altitude by regulating development of embryo) <i>DCLRE1C</i> , <i>ATAD2</i> , <i>MRE11A</i> , <i>DDIAS</i> , <i>PRIM2</i> , <i>DNASE</i> , <i>MMS22L</i> , <i>TRAT1</i> , <i>BMX</i> , <i>CXCR4</i> , <i>PSMD13</i> , <i>COX7A2</i> , <i>MTOR</i> , <i>ME3</i> , <i>MICU3</i> , <i>HCCS</i>	Not reported	5'-3' exodeoxycytidine activity and histone binding (female) DNA repair (male)	(Kharrati-Koopae et al., 2019)
Domestic chickens (tropical and temperate regions in Asia) (northern China, Indonesia, Sri Lanka, Thailand)	Tolerance to heat in tropical and temperate regions in Asia	Intergenic and intronic regions	Approximately 12.99 million biallelic SNPs	Not reported	Not reported	Not reported	Not reported	F _{ST} and π -ratio	F _{ST} and π -ratio revealed 301 and 389 PSGs, respectively in tropical region	<i>FABP2</i> , <i>RAMP3</i> , <i>SUGCT</i> , and <i>TSHD</i> and vascular smooth muscle contractility (<i>CAMK2</i>)	Sphingosine N-acyltransferase activity and thyroid-stimulating hormone receptor activity	Metabolism and vascular smooth muscle contractility	(Guo et al., 2022)
Brazilian, Sri Lankan and Egyptian chickens	Different environmental factors	Chromosomes 2, 3 and 8	Chromosomes 2 (25.25–25.35 Mb; 25.35–25.45 Mb) and 26.15–26.25 Mb) with 38, 40, and 45 SNPs respectively), 3 (111.25–111.35 Mb-4SNPs) and 8 (650–750 Kb-44SNPs)	Not reported	Not reported	Not reported	Not reported	F _{ST} and hapFLK	Eight significant regions on chromosomes 1 (1.71–2.72 Mb; 43.05–46.79 Mb), 2 (38.74–38.96 Mb), 3 (102.39–103.09 Mb), 4 (71.24–71.34 Mb), 5 (28.61–29.14 Mb), 10 (14.06–14.09 Mb), and 11 (18.79–20.20 Mb) in Egyptian breeds, chromosomes 1 (34.44–34.53 Mb) and 4 (61.18–62.15 Mb) in Sri Lankan	<i>TLR3</i> , <i>SOCS2</i> , <i>EOMES</i> , <i>NFAT5</i> (within regions of selection), <i>TLR3</i> and <i>NFKB1</i> (Chr. 4), <i>SNRPB</i> , <i>MIRPL42</i> and <i>ACSF3</i> (Chr. 1 and 11), <i>CYP4V2</i> (Chr. 4)	Not reported	Immune system	(Walugembe et al., 2019)
Two Iranian breeds (Lari and Khazak)	Diversity and adaption	Not reported	Approximately 11.9 million	Not reported	Not reported	Not reported	Not reported	F _{ST} , hapFLK, ROH, and composite likelihood ratio (CLR)	Most significant CLR value in i. the Lari ecotype (98.56) was observed on chromosome 2 (27.6 and 27.8 Mb contains DGKB (diacylglycerol kinase beta) gene ii. Khazak ecotype (124.43) was observed on chromosome 1 between 117.6 and 117.8 Mb	342 candidate genes for both ecotypes (225- protein coding genes) Growth- <i>DCN</i> , <i>MEOX2</i> , <i>CACNB1</i> reproduction- <i>ESR1</i> , <i>CALCR</i> disease resistance- <i>SIPRI</i> , <i>ALPK1</i> , <i>MHC-B</i> , behavior pattern- <i>AGMO</i> , <i>GNAO1</i> , <i>PSENI</i> , morphological traits- <i>IHH</i> and <i>NHEJ1</i>	Immune response, Toll-like receptor 3 signaling	Epithelial cell proliferation, cell proliferation, Golgi organization, cell differentiation	(Rostanzadeh Mahdabi et al., 2021)
Xichuan black-bone	Black skin	Intergenic	5,062,529 SNPs (247,054 homozygous SNP)	830,606 InDels (372,903 insertions and 457,703 deletions)	1,279 CNVs, 11,433 SVs	Not reported	Not reported	F _{ST}	one sweep found on chromosome 20 displayed a high F _{ST} value (obvious genetic differentiation between the 2 populations considered)	1,469 candidate genes within these sweeps were associated with black-skin <i>SLC45A2</i> , <i>SLMO2</i> , <i>ATP5c</i> , <i>EDN3</i> long noncoding RNA (TCONS-00054154)	Neuroactive ligand-receptor interaction, Jak-STAT signaling pathway, mTOR signaling pathway	Vesicle membrane, synaptic membrane, receptor complex, microtubule, cytoplasmic vesicle membrane	(Li et al., 2020a)
Yeosan Ogye black	Local adaptation traits, such as egg development, immune system	With a threshold of the top 0.5% outliers of windows	18,902,359 bi-allelic SNPs	1,862,730	Not reported	Not reported	Not reported	cross-population composite likelihood ratio test (XP-CLR) and cross-population extended haplotype homozygosity test (XP-EHH)	Strong selection signature for OGYE at <i>SPP1</i> , <i>RNASEL</i> , and <i>TLR4</i> genes	293 candidate genes Egg development - <i>SPP1</i> , <i>HSP90AA1</i> , <i>P2RX4</i> Determination of the innate immune response <i>RNASEL</i> , <i>BHPI1</i> , <i>TLR1</i> , <i>NFKB1A</i> , <i>DYNC1H1</i>	NOD-like receptor signaling pathway, cytosolic DNA-sensing pathway, Toll-like receptor signaling pathway, necroptosis	Not reported	(Cho et al., 2022)

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Table 1 (Continued)

Breeds of chicken used	Trait (s) considered	Prominent genomic regions	Number of SNPs identified	Number of insertion/deletion (INDELs) identified	Number of structural variations (SV), copy number variants (CNV) identified	SNP density in chromosomes	Number of associated SNPs and INDELs	Methods adopted	Selection signature	Gene (s) linked to trait of interest (chromosome position)	Enriched KEGG (most enriched)	Enriched gene ontology (GO) (most enriched)	References
North American Araucana	Laying eggs with blue eggshells, characteristic ear-tuffs, a pea comb, and runplumlessness.	21 chromosomes (1–20, 26, and 28)	9.17 million 203 (top discriminatory SNPs)	Not reported	Not reported	Not reported	Not reported	The creeping window method	8 strong selective sweeps in NAA at several regions	<i>SLCO1B3</i> (blue eggshell color), <i>ENS-CALG00000019276</i> , <i>TSNARE1</i> , <i>SMADI</i> , <i>MMAA</i> , <i>ENS-CALG00000043141</i> , <i>ENSGALG00-000028322</i> , <i>ZNF827</i> , <i>SEC24D</i> , <i>METTL14</i> , <i>STX2</i> , <i>RF02271</i> , <i>ADGRD1</i> , <i>MYH1D</i> , <i>MYH1F</i>	Not reported	Vesicle trafficking, Cell adhesion,	(Noorani et al., 2019)
Paternal broiler line	Performance traits	Macro chromosomes	9,914,904	793,603	Not reported	Not reported	Not reported	ROH and F_{ST}	Windows with F_{ST} values equal or higher than 0.3-candidate selection signatures. About 72.8% of the 1,941 cROH overlapped with QTL regions ($n = 2,617$). Overlap of 60.1% of the 178 F_{ST} SNP windows and 68.2% of the 154 F_{ST} INDEL windows with QTL regions ($n = 107$ and 105, respectively)	<i>APOB</i> , <i>IGF1</i> , <i>IGFBP2</i> , <i>POMC</i> , <i>PPARG</i> , <i>ZNF423</i>	Not reported	Skeletal muscle, matrilin proteins, adipose tissue, hyperglycemia, diabetes, Salmonella infections and tyrosine	(Almeida et al., 2019)
Domestic (Male Silkie and male TCC L2)	Phenotypic diversity	intronic and intergenic regions Coding region	6,021,032 5,385,458 and 5,142,622 (male Silkie and TCC L2, respectively)	5,776,404 635,574 and 633,782 (male Silkie and TCC L2, respectively)	8,839 CNVs for Silkie relative to L2	Not reported	Not reported	H_{ROH}	10-kb sliding with at least 10 homozygous SNP sites in every 0.5 kb step. 509 genes were identified	<i>MX</i> , <i>POMC</i> , <i>Ovocalycin-32</i> , <i>GnRHRR</i> , <i>ACAN</i> , <i>iNOS</i> , <i>CCL4</i> , <i>PRDM1</i> , <i>MBL2</i> , <i>LIP1</i>	Not reported	Selection sweep region-GTPase regulator activity, Glycoprotein biosynthetic process, Nucleoside binding, regulation of cell adhesion Silkie- Muscle contraction, response to radiation, adult behavior, cell death	(Fan et al., 2013)
Chantecler	Cold tolerance	Intergenic (50.3%) and intronic (33.8%) regions	4,681,038	Not reported	Not reported	Not reported	Not reported	Fst, nucleotide diversity (π), and XP-EHH were adopted	310 genes with significantly higher Fst CA-to-ME values (top 1%) were identified as candidate PSCs in the CA Chickens However, 24 PSCs in the CA chickens involved in fat metabolism, including <i>ME3</i> , <i>TBX15</i> , <i>LRP2</i> , <i>PPARG</i> , <i>PNPLA2</i> , and <i>CERS6</i>	<i>ME3</i> (fat metabolism) and <i>ZNF536</i> (nervous system) in cold adaptation	Not reported	Neuronal development or migration, lipid metabolism, hair bundle morphogenesis, vasoconstriction and vasodilation, developmental processes, kidney development, skin pigmentation, and circadian rhythm	(Xu et al., 2021)
Native chickens from China (Niya and 15 other indigenous)	Hot arid and harsh environments	123 regions (21 chromosomes)	161,322 SNPs located within the coding region of the chicken genome	Not reported	Not reported	Not reported	Not reported	a sliding-window approach (40 kb windows sliding in 20 kb steps) $\log_2 \theta_{\pi}$ ratio, F_{ST} and XP-CLR were used	Total of 32.4 Mb genomic regions (3.07% of the genome, containing 436 genes, 24 chromosomes, the average length is 67.2 kb) with strong selective sweep signals in Niya chicken 8.67 Mb genomic regions (0.81% of the genome, containing 407 genes, 26 chromosomes, the average length is 24.9 kb) with strong selective sweep signals in Niya using XP-CLR analysis	Circulatory system and blood vessel development- <i>BVES</i> , <i>SMYD1</i> , <i>IL18</i> , <i>PDGFRA</i> , <i>NRP1</i> , <i>CORIN</i>), Central nervous system development- <i>SM2</i> , <i>NALCN</i> Apoptosis- <i>CLPTM1L</i> , <i>APP</i> , <i>CRADD</i> , <i>PARK2</i> Response to stimuli- <i>AHR</i> , <i>ESRRG</i> , <i>FAS</i> , <i>UBE4B</i> Fatty acid metabolism- <i>FABP1</i>	P53 signaling pathway	Regulation of ARF protein signal transduction, Axon terminus, Amino acid transmembrane transporter activity	(Gu et al., 2020a)

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Table 1 (Continued)

Breeds of chicken used	Trait (s) considered	Prominent genomic regions	Number of SNPs identified	Number of insertion/deletion (INDELS) identified	Number of structural variations (SV), copy number variants (CNV) identified	SNP density in chromosomes	Number of associated SNPs and INDELS	Methods adopted	Selection signature	Gene (s) linked to trait of interest (chromosome position)	Enriched KEGG (most enriched)	Enriched gene ontology (GO) (most enriched)	References
Tibetan chickens from Sri Lankan (SL) and Saudi Arabian (SA)	Adaptations to Tropical Climates	Intronic followed by intergenic regions	10.69 million	2.09 million	Not reported	Not reported	Not reported	F _{ST} , θ_{pi} , XP-CLR and XP-EHH methods were adopted	942 PSGs in SA breed and 923 PSGs in SL breed (4 methods) and 150 of them were found in both SA and SL breeds	12 PSGs (<i>ADCY1, CACNA1C, CAMK2D, PACRC, PARR2, PRKCH, SDHD, SIRT1, WNT7B, TBXAS1, IL18, and VPS13C</i>)	Adrenergic signaling in Cardiomyocytes, GαRH signaling pathway, Calcium signaling pathway, Neuroactive ligand-receptor Interaction	Regulation of blood circulation, regulation of blood vessel diameter, regulation of systemic arterial blood pressure by hormone	(Tan et al., 2020)
Brazilian Chicken	Fat deposition	22 unique QTLs	371,786 SNPs from the autosomal chromosomes	Not reported	Not reported	541 SNPs/Mbp	Not reported	Comparison of PCGs against selection signature regions detected in a previous study using CrossMap tool	Four PCGs overlapped with selection signature regions. One PCG (CRY1) was located 1.5 kb from a selection signature region	<i>IL6, PLA2G1B, SELM, DOK5, HTR2A, GDF3</i>	Insulin receptor signaling pathway	Response to insulin, lipid storage, glucose homeostasis, regulation of lipid kinase activity, fat cell differentiation, insulin and triglycerides levels	(Moreira et al., 2018)
10 phenotypic diverse breeds	Pattern of genetic diversity and selection	Z chromosome than in any of the autosomes total size of 27.36–38.00 Mb, corresponding to 2.61 to 3.63% of the genome (337–645/breed)	5.27–9.59 million 1,398–4,716 specific SNPs were detected for each breed	Not reported	Not reported	Not reported	Not reported	θ_{pi} , F _{ST} and Tajima's D value	74 genes that had strong selective sweep signals (shared by more than 5 chicken breeds) Five genes (CH25H, PANK1, LIPA, SLC16A12 and IFT5) in an 80-kb region (18.86–18.94 Mb) of chromosome 6 (at least 5 of the domestic population). Strongest sweep of $r_{2F_{ST}}$ score of 9.67 related to body weight in Muchuan black-boned fowl. Selected region for laying characters that enclosed <i>KIF18A</i> 22 genes that are mainly located on chromosome 11 for black skin and bone Five genes under selection in all Tibetan chickens in a small region (40 kb) of chromosome 23	<i>LIPA, IFT5, SLC16A12</i> (All located on chromosome 6) <i>Silky feather- CACNA2D1, GRMs, PDE7B, NECAB2, CAMK2D, SLC38A8, PDSS2, ZBTB43, NFATC3, ASCC3.</i> <i>Black skin and bones- AEBP2, CHMP2B, PLEKHA5, PIT-1, MC1R and TUBB3</i> High altitude adaptation- <i>TRIT1, HPCAL4, NT5C1A, LOC19677, HEYL</i>	Aromatic compound biosynthesis, muscle cell development, muscle contraction, GαRH (Gonadotropin-releasing hormone) signaling and MAPK (mitogen-activated protein kinase) signaling etc.	Energy metabolism, body size maintenance and digestion	(Li et al., 2019)
Gyeongbuk Araucana	Origin and genetic characteristics	Z chromosome is a highly conserved region	7,124,664	2,254,900 Indels in mapped regions.	16,342,621 SNVs in mapped regions	Not reported	Not reported	log10 (θ_{pi} ratio and F _{ST})	223 genes as a positive signature of the each statistic (log10 (θ_{pi} ratio) > 3.378, F _{ST} > 0.387).	<i>MYLK2, BCL2L1, GSS, SCARA3, ERBB4</i>	Not reported	Response to oxidative stress	(Jeong et al., 2016)
3 domestic (DC) breeds (Ethiopian, Saudi Arabia, Sri Lankan) and Red jungle fowl (RJC)	Unique adaptation and production to local environments	Autosomes	Approximately 6 million (i.e., 6 SNPs/kb excluding multi-allelic sites) Although, Red jungle fowl5 and red jungle fowl koon had ≥7 million SNPs. 11.05 million shared between DC and RF. 5.4 and 3.8 million unique to DC and RJC, respectively. Novel SNPs were 1.76 (Ethiopian), 1.03 (Saudi Arabian), and 2.33 million (Sri Lankan)	Not reported	Not reported	Not reported	Not reported	Pool heterozygosity approach	434 out of 90,170 windows (genome wide threshold ≤-4 led to 190 candidate sweep regions in RJC. 89,443 windows analyzed, only 247 windows passed the threshold in Ethiopian DC with 84 candidate sweep regions. 87,646 windows but only 565 passed the threshold with 212 candidate sweep regions in Saudi Arabian. 89,701 windows revealed but only 299 passed the threshold with 127 candidate sweep regions in Sri Lankan. Only 2 common sweep regions in all DC and RJC. 4 candidate genome regions under positive selection in all DC but not RJC.	<i>TSHR</i> - metabolic regulation and reproduction process and <i>GTF2A1</i> - for ovarian tumor. Both at chromosome 5. In Ethiopian chicken, <i>HRH1</i> and <i>AGTR1</i> genes were identified. <i>KCNMA1</i> gene was revealed in genomes of Saudi Arabian and Sri Lankan DC along with RJC. This gene is associated with hypoxia response challenge and regulation of smooth muscle contraction. <i>ADAM9</i> was identified in RJC and this gene plays a key function in development of cardiorespiratory system. <i>NT5C1A</i> was identified in RJC and Sri Lankan. This gene is important for regulation of levels of heart adenosine during hypoxia and ischemia.	Blood circulation, regulation of heart contraction, regulation of muscle system process, regulation of muscle adaptation, and regulation of cardiac muscle contraction	RJC- Progesterone-mediated oocyte maturation, Purine metabolism, vascular smooth muscle contraction. In Ethiopian DC- Neuroactive ligand-receptor interaction, Calcium signaling pathway, Adrenergic signaling in Cardiomyocytes In Saudi Arabian DC- Toll-like receptor signaling pathway, vascular smooth muscle contraction Sri Lankan DC- Adrenergic signaling in Cardiomyocytes and Calcium signaling pathway	(Lawal et al., 2018)

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Table 1 (Continued)

Breeds of chicken used	Trait (s) considered	Prominent genomic regions	Number of SNPs identified	Number of insertion/deletion (INDELs) identified	Number of structural variations (SV), copy number variants (CNV) identified	SNP density in chromosomes	Number of associated SNPs and INDELs	Methods adopted	Selection signature	Gene (s) linked to trait of interest (chromosome position)	Enriched KEGG (most enriched)	Enriched gene ontology (GO) (most enriched)	References
Pengxian Yellow (PYC)	Domestication	Intergenic (57%) Intronic (38%)	12.97 Mb PYC and RJF held 6.25 Mb and 6.72 Mb of SNPs, respectively	Not reported	Not reported	~1 per 180 bp	Not reported	θ_{π} and F_{ST}	several regions with strong selection signals, containing 497 protein-coding genes.	Digestion- <i>ABCG5</i> , <i>ABCG8</i> , <i>ADLB1</i> muscle development and growth- <i>SMPD3</i> , <i>NELL1</i> , <i>BICC1</i> Reduced immune function- <i>CD86</i> , <i>MTA3</i> <i>CTNND2</i> is involved in the evolutionary changes in domestic chickens <i>VATI</i> - regulate mitochondrial fusion <i>TSHR</i> , <i>INSR</i> <i>TBC1D1</i>	Wnt signaling pathway	Negative regulation of digestive system process, regulation of digestive system process, muscle organ development, muscle cell development, nervous system development, Retinal dysplasia, Micro-cornea	(Yin et al., 2019)
Populations containing Red jungle fowl, broilers and layers	Domestication	Not reported	>7,000,000	Not reported	Not reported	Not reported	Not reported	allele counts at SNP positions to identify signatures of selection in sliding 40-kb windows	The sweep region showed almost complete fixation over a 40-kb region	<i>TBC1D1</i>	Not reported	Not reported	(Rubin et al., 2010)
Dulong (DLC)	Adaptation	Intergenic (53.51%) Intronic (41.33%)	18,262,807	Not reported	Not reported	Not reported	Not reported	F_{ST}	494 candidate genes (i.e., 469-DLC and 29-RJFs) by F_{ST} , using a 40-kb window with a 10-kb step among DLCs and RJFs genome	Resistance to disease- <i>PAIP1</i> , <i>MIPOL1</i> , <i>TLE1</i> High-altitude and high humidity adaptation- <i>FGF10</i> , <i>RICTOR</i> , <i>NFIB</i> Egg production- <i>KIF18A</i> , <i>ADAMTSL1</i> , <i>NNT</i> , <i>AGTPBP1</i> Aggressiveness- <i>CHRNA7</i> , <i>BDNF</i> , <i>GDNF</i> , <i>FGF2</i> , <i>PRMT7</i> Small body size- <i>FAM19A5</i> , Vision- <i>HCF1</i>	Not reported	Response to growth factor, developmental growth, developmental growth involved in morphogenesis, proteoglycan metabolic process, antral ovarian follicle growth	(Wang et al., 2020)
Domestic and Red jungle fowl chickens	Origin and domestication	Not reported	> more than 33.4 million bi-allelic	Not reported	Not reported	Not reported	Not reported	LSBL statistics and π -ratios	Genes under selection were identified based on Z-transforming score ≥ 3.3 signal of selection are associated with development of nervous system, muscle and bone as well as regulation of growth, metabolism and reproduction	Regulation of embryonic development and skeletogenesis- <i>FGFR1</i> (fibroblast growth factor receptor 1), <i>MYC-1</i> , <i>ERBB4</i> , and <i>BMPs</i> Reproductive processes- <i>GNRH-1</i> , <i>KIF18A</i> , <i>TSHR</i>	Crest development	Not reported	(Wang et al., 2020d)

(*ELOVL2* and *MAOA*). In the study, genes related to energy homeostasis (*AGRP*), behavioral traits (*AGMO* and *PSEN1*), muscle development (*HDAC9*), wound healing (*MMP13*), and Immune (*APBB1IP*) in Lari chickens were identified (Rostamzadeh Mahdabi et al., 2021). In the consensus, ROH regions that overlapped with the F_{ST} windows, genes related to immune responses were detected. These genes include the *SIPR1* gene which plays a crucial role in inflammatory responses to infection with the Newcastle disease virus (Li et al., 2016a) and *ALPK1* (alpha-kinase genes) which is an important gene for innate responses to invasive bacteria and influenza virus (Ryzhakov et al., 2018). In the Lari population, the *AGMO* gene was identified across the consensus region (Rostamzadeh Mahdabi et al., 2021). Interestingly, a strong selective sweep for *AGMO* in behavioral patterns was revealed in Chinese gamecock chickens (Luo et al., 2020). In our previous study, aggressive behavior was progressively conserved during chicken domestication (Li et al., 2016b). More so, *GNAO1* gene was detected in the cROH region on chromosome 11 of Lari chickens (Rostamzadeh Mahdabi et al., 2021). The aggressive behavior of the Xishuangbanna fighting chicken is caused by the *GNAO1* gene and under selection in that population (Guo et al., 2016). *PSEN1* (presenilin 1) located on chromosome 5 was detected in the Khazak ecotype. It has been reported that the *PSEN1* gene might contribute to feather pecking behavior in chickens (Wysocki et al., 2013). Further validation studies such as functional analysis and scanning replicated populations could be utilized to better understand the roles of these genes in chickens as this would be useful for the conservation of chickens for such traits.

A previous study examined the genetic basis of phenotypic diversity between 2 domestic chickens (i.e., a male Silkie and a male TCC L2) (Fan et al., 2013). The study revealed 27,852 nonsynonymous SNPs located in 13,537 genes. Moreover, 509 genes were detected in the putative selective sweeps (Fan et al., 2013). Interestingly, 46 out of these 509 genes were identified in a previous study (Rubin et al., 2010). It has been reported that *IGF1*, *PMCH*, *ARID4B*, *ROBO2*, *SLC6A12*, *OSGIN1*, *TBC1D1*, *ANK2*, and *TSHR* displayed intensely selective sweeps in all domestic or commercial breeds (Rubin et al., 2010). *IGF1* and *HMGA2* are related to body weight gains in Silkie chicken (Tang et al., 2010; Song et al., 2011). In addition, *IGF1*, *TSHR*, *PMCH*, and *TBC1D1* are correlated with appetite, metabolic regulation, and growth in the broiler (Rubin et al., 2010). *TSHR* mutation could control reproduction by regulating photoperiod (Yoshimura et al., 2003). It was suggested that *TSHR* could be an important gene for domestication in chickens where all individuals of domestic breeds possess the same mutant allele. However, there is a need to further investigate this.

The genetic diversity of 10 phenotypically different breeds of chicken was investigated (Li et al., 2019). The genome-wide analysis revealed that sex chromosomes have less genetic diversity and are under strong selection

than autosomes during domestication and local adaptation. The genomic regions harbored 337 to 645 genes per breed with strong selective sweep signals in each breed. Most of the genes identified with strong selective sweep are important for reproduction, immunity, behavior, metabolism, and growth. In addition, 74 genes including *CH25H*, *PANK1*, *LIPA*, *SLC16A12*, and *IFIT5* had a strong selective sweep in a 80-kb region (18.86–18.94 Mb) of chromosome 6 and were shared by more than 5 chicken breeds (Li et al., 2019). Altogether, *LIPA*, *SLC16A12*, and *IFIT5* could be regarded as major genetic contributors to chicken domestication. Further, eleven SNPs located in coding regions were revealed to possess extreme differences in allele frequencies between Tibetan chickens and other domestic chickens. However, only 3 genes which include *PKD2L1*, *EVI5*, and *ZDHHC9* had nonsynonymous mutations. There is a need to further investigate whether *ZDHHC9* is involved in adaptation to high altitude.

The origin and genetic characteristics of Gyeongbuk Araucana “a newly developed blue egg-laying chicken breed” were investigated (Jeong et al., 2016). 223 genes were identified as positive signatures. Moreover, most of the selected regions were located on the Z chromosome. Among the significant genes including *MYLK2*, is essential in cardiac muscle tissue morphogenesis and fast-twitch skeletal muscle fiber contraction which are necessary for response to quick bursts like flight (Al Madhoun et al., 2011). In addition, *BCL2L1*, *GSS*, *SCARA3*, and *ERBB4* genes related to feedback to oxidative stress were identified (Martindale and Holbrook, 2002).

The WGS of Pengxian Yellow Chickens (PYC) was done to detect genomic regions with strong selective sweeps (Yin et al., 2019). Different regions with 497 protein-coding genes were detected under strong selection signals. These genes include *ABCG5*, *ABCG8*, and *ADRB1* important for digestion, *SMPD3*, *NELL1*, and *BICC1* involved in muscle growth and development, and *CD86* and *MTA3* which reduced immune function. In addition, numerous genes with highly strong selection signals related to the loss of visual ability of the domestic chickens were identified (Yin et al., 2019). Although only *CTNND2* was associated with retinal development at this strong selection signal. *CTNND2* was reported to be strongly related to myopia in humans (Li et al., 2011). The genetic changes in PYC during domestication would be valuable to promote the genetic resource for the utilization of chickens.

Adaptation to Different Environmental Conditions

One of the recent study determined the genomic regions associated with environmental adaptations of 4 Tibetan native chickens [Shigatse (SH), Nyemo (NM), Dagze (DZ), and Nyingchi (LZ)] along with Lhasa white (LW) chicken breed due to their partial inclusion in the conservation plans (Yuan et al., 2022). Interestingly, the genomic region containing common QTLs in GGA8 ranged from 0.03 Mb to 1.13 Mb was revealed. In the SH, NM, LZ, and LW populations, there were 1, 1, 8, and 2 SNPs with selection signatures, respectively (Yuan et al., 2022). Further exploration of the GGA8

region unveiled only 3 genes (*AMY2A*, *NTNG1*, and *VAV3*). *AMY2A* participates in carbohydrate and glycogen metabolism thereby influencing feed intake efficiency, growth, and carcass traits in chickens (Zhang et al., 2021). In addition, the selection of *AMY2A* was reported for energy availability, response to thermal stress, and metabolism in African chickens (Elbeltagy et al., 2019). Could the expression of *AMY2A* be responsible for environmental adaptation in Tibetan chickens? This needs to be examined in future studies. *NTNG1* plays an important role in axon and neurite growth (Yamagishi et al., 2021). Additionally, *NTNG1* was significantly expressed in chicken hepatocellular cell line in reflex to stress (Sun et al., 2015). In a previous finding, *VAV3* was identified as a candidate gene related to highland adaptation in Ethiopian sheep (Edea et al., 2019), and also plays an important function in the homeostasis of the cardiovascular system (Sauzeau et al., 2006) thereby suggesting the adaptive role of *VAV3* to the high altitude of Tibetan native chicken.

The adaptive variants responsible for high altitude adaptation in Iranian native chickens (i.e., lowland and highland) were investigated (Kharrati-Koopae et al., 2019). Selection signature analysis disclosed differential variants that are adaptive in response to hypoxia and are not due to other evolutionary pressures. Interestingly, 50 variants were detected in mitochondrial DNA (mtDNA) for the highland and lowland chickens (Kharrati-Koopae et al., 2019). *COX3* gene was associated with high altitude. *COX3* is involved in cell respiration and hypoxia adaptation. In a previous study, the relationship between MT-CO3 (mitochondrially encoded cytochrome c oxidase subunit III) and high-altitude adaptation in Tibetan chickens was examined (Sun et al., 2013b). *MIR6644-2* was predicted as a candidate gene involved in high-altitude adaptations (Kharrati-Koopae et al., 2019), which might influence the adaptation process to hypoxia by the control of embryo growth. *MIR6644-2* plays a key function in gastrulation (an important step in embryonic development) in chickens (Shao et al., 2012). Although, the relationship between the *MIR6644-2* gene and adaptation to high altitude is yet to be investigated. Further scientific question to be explored is that could the expression of the *MIR6644-2* gene influence the adaptation to high-altitude in different breeds of chickens?

Harsh environmental situations are major bottlenecks in livestock production. The ability of an animal to survive under extreme environmental factors might be in response to natural selection and artificial production traits that often times might leave selection signatures in the genome (Walugembe et al., 2019). The detection of selection signatures that might be included in the adaptation of indigenous chickens from 2 different climatic regions (i.e., Sri Lanka—Tropical and Egypt—Arid) and in nonindigenous chickens that migrated to the tropical state of Sao Paulo Brazil was investigated (Walugembe et al., 2019). In Egyptian breeds, 8 prominent regions were detected as strong selection signatures on chromosome 1, and 3 genes including Suppressor of

cytokine signaling 2 (*SOCS2*), Eomesodermin (*EOMES*), and nuclear factor of activated T-cells 5 (*NFAT5*) related to the immune system were found within these regions. *SOCS2* is essential in the control of different biological processes that regulate development, immune function, growth, and homeostasis (Rico-Bautista et al., 2006), and might influence breast meat yield during heat stress (Van Goor et al., 2015). *EOMES* assists in the functions of cytotoxic innate lymphocytes which include the natural killer (NK cells) that contribute to early defense against pathogens (Zhang et al., 2018c). The previous finding has shown the importance of TLR-induced *NFAT5L*-regulated genes including *TNF- α* serve a major role in inflammatory responses (Tellechea et al., 2018). Although, 2 regions located on chromosomes 1 and 4 were detected as strong selection signals in Sri Lankan chickens (Walugembe et al., 2019). One (*GRIP1*) and 18 genes (including Toll-like receptor 3 (*TLR3*) and nuclear factor kappa B subunit (*NFKB1*) genes involved in the immune system were found within chromosomes 1 and 4, respectively. *TLR3* could identify and attach to double-stranded RNA intermediates that are secreted by viral replication (Iqbal et al., 2005). *NFKB1* proteins play a key role in several processes such as growth, survival, development, and different pathological conditions (Morgan and Liu, 2011). Considering the regions under selection, hapFLK analyses unveiled genes related to production traits in Egypt and Sri Lanka chickens. *SNRPF*, *MRPL42*, and *ACSF3* located on chromosomes 1 and 11 were found in the Egypt populations while *MTNR1A* and *CYP4V2* on chromosome 4 were found in Sri Lanka populations (Walugembe et al., 2019). *MRPL42* is crucial in transcription, DNA synthesis, and RNA processing and translation (Van Goor et al., 2015). *ACSF3* is an important gene for egg-laying performance in chickens (Tian et al., 2018). In a previous study, *CYP4V2* was identified on chromosome 4 of the region under selection for fat deposition in chicken (Claire D'Andre et al., 2013). In the Brazilian breeds, no strong selection signals were detected. However, 2 regions with strong signals were revealed across 2 Brazilian breeds with Asian ancestry (i.e., Cochinchina and Brahma on chromosomes 1 and 14), and 3 genes namely *SOX5*, *MIR6608-2*, and *MIR6608-1* were detected within the selection signature on chromosome 1 only. However, the functions of these genes on the 2 Brazilian chicken breeds have not been examined (Walugembe et al., 2019). Could their functions affect the selection of Brazilian chicken breeds? This needs to be elucidated by further studies.

The response to acute thermal has been tremendously studied in commercial chickens due to its serious consequences on poultry production across the globe (Nawab et al., 2018). A recent study on genomic analyses revealed several selective regions and genes responsible for adaptation to hot arid and harsh environments of the Niya (NY) chicken breed (Gu et al., 2020a). In the findings, a total of 8.67 MB genomic regions encompassing 407 genes and 26 chromosomes were identified as strong selective regions in NYs. Although, 672 putative

genes were obtained by combining 3 different statistical analyses ($\log_2 \theta\pi$, F_{ST} , and XP-CLR) and only 171 genes were common in the 3 statistics. Numerous genes associated with development of blood vessel, heart, circulatory and cardiovascular systems were found in NYs (Gu et al., 2020a). These genes including *BVES* plays an important function in the regulation of heart rate (Froese et al., 2012). *SMYD1* is important in angiogenesis (Ye et al., 2016), and selective signals of *IL18* and *NRP1* are essential in the adaptation studies in East African vs. North-African chickens (Elbeltagy et al., 2019). *CORIN* controls blood pressure and volume in humans (Chen et al., 2015). The functions of *FABP1* are numerous which include serving as a mediator for the catabolism or anabolism of lipid metabolic pathways and controlling FA-responsive gene transcriptions (Wang et al., 2019). *FABP1* might be crucial in the maintenance of lipid metabolism and normal growth in NYs due to adaptation to the hot arid environment.

Genomic analyses revealed regions of genetic adaptations to tropical climates in chickens (Tian et al., 2020). 24.18 Mb and 15.59 Mb containing 723 and 464 positively selected genes (PSGs) were detected in Saudi Arabian (SA; adapted to hot and arid environments) and Sri Lankan breeds (SL; tropical area), respectively using modified population-branch statistic (PBS) method (Tian et al., 2020). In addition, 376 and 396 PSGs were identified using XP-CLR, 233 and 305 from $\log_2(\theta\pi)$ ratio, and 383 and 267 from XPEHH in SA and SL breeds, respectively. 942 and 923 PSGs were obtained in SA and SL breeds, respectively after combining the 4 methods. In the study, 12 PSGs including *ADCY1*, *CACNA1C*, *CAMK2D*, *PACRG*, *PARK2*, *PRKCH*, *SDHD*, *SIRT1*, *WNT7B*, *TBXAS1*, *IL18*, and *VPS13C* were discovered to exhibit crucial roles in chicken adaptations to both tropical desert and tropical monsoon island climates (Tian et al., 2020). *EPAS1* was discovered as a significant PSG involved in the cellular response to hypoxia. In a previous study, intron 5 of *EPAS1* enclosed a significant SNP related to erythrocyte abundance to positively impact adaptation to hypoxia (Yi et al., 2010). In the SA breed, the advantageous mutations of *TLR7* and *ZC3HAV1* could hinder the replication of viruses in a cell through immune adaptation to defend against zoonotic diseases in chickens (Tian et al., 2020).

The selection signature analysis of Yeonsan Ogye (OGYE) black chicken “A Korean native chicken breed” was done (Cho et al., 2022). Based on their genome-wide selection analysis, local adaptation traits including egg development that assist in fetal viability and the innate response were identified. *SPP1*, *P2RX4*, and *HSP90AA1* genes were detected under the selection signature for OGYE chicken (Cho et al., 2022). Previous studies have revealed the important roles of *SPP1* and *P2RX4* genes in bone and eggshell (Jonchère et al., 2010; Wesseliuss et al., 2012). The heat shock proteins including *HSP90AA1* serve as a major defense against heat stress (Causton et al., 2001). Further, a positive selection signature of OGYE to the innate immune system was

detected. *RMASEL*, *HSP90AA1*, *BRIP1*, and *TLR4* genes were identified as related to the innate immune system (Cho et al., 2022). *RMASEL* enhances the protective response against viral infection via the induction of other immune-related genes (Chakrabarti et al., 2015) and *TLR4* plays a crucial function in innate and adaptive immune responses (Akira and Takeda, 2004). Based on the findings, it was proposed that OGYE expanded environmental pressures and possesses a strong innate immune system. Although, there is a need to further check if OGYE could be considered as a potential chicken breed in other environments aside from Korea.

Chickens have migrated across the world and have acclimatized to different local environments including hot and temperate conditions (Wang et al., 2015). The adaptive mechanism of 3 indigenous Chinese chicken breeds from temperate regions and 5 indigenous chicken breeds from tropical zones was examined (Guo et al., 2022). Based on the study, *CAMK2D* showed a positive selection in tropical chickens. *CAMK2* gene plays a crucial function in the control of vascular smooth muscle contractility (Rokolya and Singer, 2000). The body temperature is affected by the balance between relaxation and contraction (Tian et al., 2020). It was suggested that positively selected *CAMK2D* could be an important gene to maintain body temperature for chickens from tropical regions to respond to heat stress (Guo et al., 2022). In addition, *FABP2*, *RAMP3*, *SUGCT*, and *TSHR* were found (Guo et al., 2022). These genes are also important in metabolism and energy production which are essential activities necessary for adaptation to hot environments (Tian et al., 2020). Moreover, it was reported that chicken adaptation to high ambient temperature conditions in tropical climates might be regulated by the variation of the *TSHR* (41020238:G>A) (Guo et al., 2022). Nevertheless, the molecular approach and networks of *TSHR* (41020238:G>A) in the regulation of heat stress response in chickens require further investigation.

Another study examined the genome-wide scan for selective footprints and genes related to cold tolerance in Chantecler (CA) chickens (Xu et al., 2021). Of the 36 PSGs were reliable in the CA chickens. Further, haplotype and nonsynonymous mutation analyses were performed to find which of the 36 PSGs common in the 3 methods adopted (F_{st} , π -ratio, and XPEHH) in the CA group were most probably linked to cold adaptation. A strong selective sweep spanning a 250 kb region (190,090,000–190,340,000 bp) on chromosome 1, which exhibited high $F_{st}CA$ -to-ME, π -RatioME/CA, and XPEHHCA-to-ME values were revealed (Xu et al., 2021). Five PSGs that include *PRCP*, *FAM181B*, *PRSS23*, *DDIAS*, and *ME3* might be associated with adaptation to cold in CA chickens were detected in this region (Xu et al., 2021). *ME3* was found associated with fat deposition and might probably play an essential function in cold adaptation in CA chickens (Xu et al., 2021). In previous reports, *PRCP* and *FAM181B* might be involved in adaptation to cold by controlling the nervous system and angiogenesis (Hagedorn, 2011; Marks

et al., 2016). Further, *ZNF536* found on chromosome 11 showed a strong positive selection in CA chickens (Xu et al., 2021). *ZNF536* is crucial in the development of forebrain neurons involved in social behavior and stress (Thyme et al., 2019). The authors claimed *ME3* and *ZNF536* are more steady PSGs that might be involved in cold adaptation (Xu et al., 2021). However, functional studies are necessary to examine their importance in CA chicken cold adaptation, as this would provide a molecular foundation for poultry breeding.

Feather and Skin Color Feather and skin color are important traits in chickens. Wang et al. revealed candidate genes associated with 3 different feather colors (i.e., black, lavender, and yellow feathers) in Baicheng You chickens (Wang et al., 2022a). In the study, XP-CLR statistical method was adopted to unveil the region of selection signatures. Further, the *EGR1* gene that overlapped at chromosome 13: 18,940,001–18,980,000 bp was detected in black plumage chickens. It was hypothesized that variation at loci T1297C (Ser433Phe) in *EGR1* could be related to the synthesis of eumelanin. *SOX5*, *RAB17*, and *MLPH* genes were harbored at chromosomes 1 (65,940,001–65,980,000 bp), 7 (4,800,001–4,840,000 bp), and 7 (4,820,001–4,860,000 bp), respectively, in lavender plumage color (Wang et al., 2022a). Interestingly, *MLPH* and *RAB17* have been reported to be related to the lavender phenotype (Roulin and Ducrest, 2013) and *SOX5* is important in melanocyte lineage by controlling the processes of transcription factor *SOX10* (Yue et al., 2022). *GRM5* was identified at chromosome 1 (18,240,001–18,280,000 bp in the yellow feather color of the Baicheng You chicken (Wang et al., 2022a). In a previous report, *GRM5* was revealed as a candidate gene that might be responsible for plumage color in Polverara chicken (Mastrangelo et al., 2020).

A recent investigation ascertained the genetic structure and selection signatures for color in 10 traditional Chinese yellow-feathered chicken breeds (YFCs), beta-carotene dioxygenase 2 (*BCDO2*), RALY heterogeneous nuclear ribonucleoprotein (*RALY*), leucine-rich repeat-containing G protein-coupled receptor 4 (*LGR4*), solute carrier family 23 member 2 (*SLC23A2*), and solute carrier family 2 member 14 (*SLC2A14*) were identified as the major candidate genes under selection for the determination of color pigmentation in the YFCs (Huang et al., 2020). The *BCDO2* gene is a historic yellow color gene in chickens (Gao et al., 2017). A known epistatic relationship exists between *RALY*, *ASIP*, and *MC1R* (Nazari-Ghadikolaei et al., 2018), thereby suggesting that *RALY* might be an important gene in the pigmentation of chicken. *SLC23A2* belongs to the solute carrier family (SLC) and plays a significant factor in the transportation of ascorbic acid which is an essential metabolite for survival (Eck et al., 2017). Moreover, it was reported that deficiency of this vitamin was associated with neonatal jaundice and yellow chromophore in eye lenses of human and humanized mouse models (Fan et al., 2006; Ayyappan et al., 2015). Part of the question yet unanswered revolves around the influence of the expression of

SLC23A2 on the conservation and breed selection of chicken for color trait?

To identify candidate genes contributing to black skin in Xichuan black-bone chicken using genomic and transcriptomic data, it was revealed that *EDN3* might be related to ncRNA *LOC101747896* to induce black skin color during melanogenesis (Li et al., 2020a). *EDN3* is an important gene in dermal melanin which is located on chromosome 20 in the fibromelanosis (**Fm**) region and could result in excessive accumulation of black pigment in chickens (Dorshorst et al., 2011; Sohn et al., 2018). In our previous study, we found out that *END3* mutation could cause black skin in Silkies chicken (Gao et al., 2016). In addition, *EDN3* improves the proliferation, survival, and differentiation of melanocytes (Hutt, 1930; Shinomiya et al., 2012), and the distinctiveness in *EDN3* copy number coincides with black and white pigmentation of chicken skin (Han et al., 2014).

WGS of 3 domesticated chicken breeds (i.e., White Leghorn, Korean domestic, and Araucana) was done (Oh et al., 2016). Based on the findings, approximately 4 kb insert within *SLCO1B3* responsible for blue eggshell color was identified. The variants related to Korean domestic and Araucana chickens were similar and showed similar morphology in terms of feather coloring patterns (Oh et al., 2016). In addition, the whole genome resequencing of the chicken genome revealed a similar pattern along with 240 SNVs within the *SLCO1B3* region (chr1: 65,319,423–65,319,424) of Araucana, although this is observed in the genome of other breeds (Oh et al., 2016). Previous findings have linked blue eggshells to ectopic expression of *SLCO1B3* in uterine shell glands with an EAV-HP insertion in the 5' flanking region of the gene (chr1: 65,220,675), which might be responsible for blue eggshells in Araucana chickens (Wang et al., 2013; Noorai et al., 2019).

Eggshell Qualities In a study to reveal major genes and mutations affecting chicken eggshell qualities, the integration of transcriptome and genome resequencing was done using 49 wk old Rhode Island White hens (*Gallus gallus*) classified into 2 groups namely low eggshell strength (**LES**) and normal eggshell strength (**NES**) (Zhang et al., 2015). In the study, nearly 64 DEGs were found on the 15 QTL regions that are associated with eggshell strength while 36 DEGs were found on 3 QTL regions that are correlated with eggshell thickness. Although, only *CACNA1D*, *GNA11*, and *OXTR* were found in the calcium signaling pathway (Zhang et al., 2015). However, the role of these genes are yet to be deeply investigated in chickens.

Bone Traits To elucidate the genetic configuration which is crucial for bone traits in chickens, Li et al. adopted the integration of a genome-wide association study and selection signature analysis (Li et al., 2021). According to the findings, all detected top SNPs for the bone traits under consideration were distributed on chromosomes 1, 4, and 27 (Li et al., 2021). GWAS and selection signature analysis comapped 166 specific candidate genes including *ZNF652* which plays an essential function in the bone growth of chickens (Wang et al.,

2020a), *LHFP* serves as a major controller of osteoblast activity and bone mass in mice (Mesner et al., 2019), *SAMD9* regulates the transcription of BMP signaling (Tsukamoto et al., 2014), *SLIT2* could inhibit osteoclastogenesis and bone resorption (Park et al., 2019), and *CPZ* regulates Wnt signaling and controls the growth of skeletal elements in the chicken (Moeller et al., 2003) were identified. However, the importance of these genes has not been extensively studied in chickens.

Residual Feed Intake Feed efficiency is an important criterion in poultry production to maximize production costs and enhance profitability (Marchesi et al., 2021). In a previous study, whole genome resequencing was adopted to determine the genomic variants responsible for residual feed intake (RFI) in Beijing-You (a local breed) and Cobb (a commercial breed) chickens (Liu et al., 2018). In the study, the most significant SNPs were found enriched on GGA1, GGA2, GGA4, and GGAZ. However, after filtering, only 6,288 SNPs including 85 synonymous and 27 missense mutations were identified as candidate SNPs for RFI traits in Beijing-You chickens (Liu et al., 2018). In Cobb chickens, 575 SNPs including 10 synonymous and 2 missense mutations were annotated to 448 genes (Liu et al., 2018). However, out of the 192 SNPs selected, only 46 SNPs were significantly correlated with RFI in Cobb chickens. Interestingly, 127 enriched genes were found common in both breeds considered. Based on gene enrichment analysis, organismal development physiological processes were enriched in both breeds. The differentially expressed genes that might be major genes responsible for RFI include *NOS1*, *PHKG1*, *NEU3*, and *PIP5K1B* in Beijing-You and *CDC42*, *CSK*, *PIK3R3*, *CAMK4*, and *PLCB4* in Cobb (Liu et al., 2018).

Fat Deposition and Production Traits The accumulation of fat harms poultry production by reducing feed efficiency and subsequently leads to the high costs of egg and meat production (Jennen et al., 2004). The integration of GWAS and genome sequencing revealed selection signature regions and candidate genes of fat deposition in chickens (Moreira et al., 2018). Based on the 22 QTLs identified, 14 positional candidate genes (PCGs) associated with fat deposition were selected. Although, 4 PCGs (*CHST11*, *NR4A2*, *GPD2*, and *INSR*) that overlapped with selection signature regions have been previously reported (Boschiero et al., 2018). *CHST11* is related to lipid metabolism (Tasdelen et al., 2013), and *INSR* is essential for insulin signaling (Rubin et al., 2010). *NR4A2* enhances retinoid synthesis (Volakakis et al., 2009; Han and Cao, 2012), and retinoid is known for their crucial function in lipid metabolism (Bonet et al., 2012). The expression of *GPD2* might affect glucose homeostasis and gluconeogenesis (Madiraju et al., 2014). There was an overlap of *NR4A2* and *GPD2* with one selection signature region suggesting the tendency of selection to affect the frequency of their SNPs in chicken (Moreira et al., 2018). In addition, *NR4A2* was reported as a strong candidate gene for a fat deposition because it was found within a QTL related to carcass fat content traits and under-selection in the founder lines (Moreira et al., 2018).

A previous study identified selection signatures and genes annotated in regions that might be responsible for performance traits in a paternal broiler line (i.e., a cross-bred between Cornish and White Plymouth Rock breeds) (Almeida et al., 2019). In the findings, common genes annotated in F_{ST} and cROH regions are important in biological processes involved in economic traits in chickens. Genes including *ACTC1*, *MYO6*, *MYO1B*, *MYO7A*, *VCL*, *MYO1E*, and others were annotated in the selection signatures and involved in structural constituents, cell differentiation, and development of muscle tissues (Izpisúa-Belmonte et al., 1991; Boschiero et al., 2018). Moreover, selection signatures revealed regions involved in lipid metabolism and adipose tissue development enclosing *ATPR2*, *APOB*, *PPARG*, *ZNF423*, *IGFBP2*, *ADCY2*, *AKAP6*, *SCARB1*, and *PLA2R1* genes (Zhang et al., 2006; Sun et al., 2014; Boschiero et al., 2018). Renaudeau et al. (2012) revealed that stress response is very crucial for behavior, regulation of immune and cardiovascular systems, and metabolic rates in livestock production. The selection signatures identified with ROH analysis display genes such as *MRTO4*, *MYH9*, *ELP2*, *ACE*, *CACNAIC*, *MOCOS*, *MYH9*, *NSUN2*, *PAX5*, *BAG1*, *HSPA8*, *TRPM8*, and *PQLC2* responsible for controlling responses to stressor conditions (Sun et al., 2015; Fleming et al., 2016; Marchesi et al., 2018).

The regions of selection signature in 10 traditional Chinese yellow-feathered chicken breeds (YFCs) revealed that *RYR2* and *RYR3*, *IL-18*, *FBXO5*, *COL1A2*, *COL4A2*, *COL6A1*, *COL6A2*, *COL4A1*, and *COL23A1*, *GDF8*, *HSPA5*, and *SHISA9* are crucial factors of meat quality in chicken (Huang et al., 2020). *RYR* plays an important role in skeletal muscle and the development of pale, soft, and exudative meat in poultry birds (Paião et al., 2013). A previous study reported that *COL1A2* is an important gene for meat quality traits in chickens (Sun et al., 2013a). The identified genes provide bedrock information for a better understanding of the meat characteristics of YFCs.

In a previous study to detect signatures of selection in Dulong chicken “a dual purpose breed providing meat and egg” (Wang et al., 2020c). *KIF18A*, *ADAMTSL1*, and *AGTPBP1* genes were detected in one of the regions of selection signatures. *KIF18A* is essential for mitotic advancement during germline development, *ADAMTSL1* was highly expressed in a growing ovary and *AGTPBP1* is an important gene for testis growth and development in chicken (Carré et al., 2011; Czéchanski et al., 2015; Zhang et al., 2017).

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Chicken remains the major source of protein across the globe. The detection of selection signatures in chickens is very crucial to aid conservation and improve molecular breeding programs. Different statistical approaches have utilized WGS data to reveal regions of

positive selection signatures in different breeds of chicken. In addition, candidate genes related to the traits of interest at specific regions were revealed through gene enrichment analysis. The accuracy of the selection signatures detected depends largely on the approaches adopted. The reviewed studies adopted one or more approaches in the detection of selection signatures. Thus, in our opinion, these perspectives would be essential to improve research related to selection signatures and identification of candidate genes in chicken;

- i. Selection signatures of different breeds of chicken along with their adaptive traits considering different environmental factors could be done,
- ii. Adoption of different approaches to detect selection signatures in different breeds of chicken considering several traits would strengthen the quality of the results thereby providing better affirmative inferences, and
- iii. Functional studies to deeply understand the importance of the candidate genes on discussed traits would enhance breed selection in chicken thereby providing foundational information for breeding program of traits essential for the improvement of poultry production.

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DISCLOSURES

The authors declare that they have no competing interests relevant to this publication.

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