SPECIAL ISSUE ARTICLE

Whole-genome sequencing reveals the artificial selection and local environmental adaptability of pigeons (*Columba livia*)

Haobin Hou[1,2] 🆔 | Xiaoliang Wang[1,2] | Weixing Ding[1] | Changfeng Xiao[1,2] | Xia Cai[1,2] | Wenwei Lv[2] | Yingying Tu[2] | Weimin Zhao[3] | Junfeng Yao[1,2] | Changsuo Yang[1,2]

[1]Shanghai Academy of Agricultural Sciences, Shanghai, China

[2]National Poultry Engineer Research Center, Shanghai, China

[3]Shanghai Jinhuang Pigeon Company, Shanghai, China

Correspondence
Junfeng Yao and Changsuo Yang, Shanghai Academy of Agricultural Sciences, Shanghai, China.
Emails: yaobison1983@163.com (J.Y.); yangchangsuo@189.cn (C.Y.)

Funding information
Shanghai Agriculture Applied Technology Development Program, China (Grant No., Grant/Award Number: 2018-02-08-00-12-F01546); SAAS Program for Excellent Research Team No. 2017, Grant/Award Number: (B-03)

Abstract

To meet human needs, domestic pigeons (*Columba livia*) with various phenotypes have been bred to provide genetic material for our research on artificial selection and local environmental adaptation. Seven pigeon breeds were resequenced and can be divided into commercial varieties (Euro-pigeon, Shiqi, Shen King, Taishen, and Silver King), ornamental varieties (High Fliers), and local varieties (Tarim pigeon). Phylogenetic analysis based on population resequencing showed that one group contained local breeds and ornamental pigeons from China, whereas all commercial varieties were clustered together. It is revealed that the traditional Chinese ornamental pigeon is a branch of Tarim pigeon. Runs of homozygosity (ROH) and linkage disequilibrium (LD) analyses revealed significant differences in the genetic diversity of the three types of pigeons. Genome sweep analysis revealed that the selected genes of commercial breeds were related to body size, reproduction, and plumage color. The genomic imprinting genes left by the ornamental pigeon breeds were mostly related to special human facial features and muscular dystrophy. The Tarim pigeon has evolved genes related to chemical ion transport, photoreceptors, oxidative stress, organ development, and olfaction in order to adapt to local environmental stress. This research provides a molecular basis for pigeon genetic resource evaluation and genetic improvement and suggests that the understanding of adaptive evolution should integrate the effects of various natural environmental characteristics.

KEYWORDS
artificial selection, genome sweep, local environmental adaptability, pigeon, whole-genome sequences

1 | INTRODUCTION

Charles Darwin wrote in *The Variation of Animals and Plants under Domestication* that pigeons with diverse phenotypes are derived from the domestication and artificial selection of rock pigeons (Darwin, 1868). Modern genomic technology has verified this and provided evidence of origins in the Middle East (Shapiro et al., 2013). Archeological evidence suggests that humans exploited rock

Hou, Wang and Ding contributed equally to this work.

pigeons as food for >67 thousand years (Blasco et al., 2014). Human-mediated selection can accelerate changes in animal morphological characteristics (Sendell-Price et al., 2020), especially important economic traits (Ghoreishifar et al., 2020). Given the human need for food, showing, communication, and competition, breeders or pigeon enthusiasts have bred >350 pigeon breeds (Price, 2002). According to the classification of pigeons, breeds can be divided into four categories, including production, ornamental, competition, and experimental. The diversity of pigeon breeds offers an animal model for the study of genetics (George et al., 2020; Stringham et al., 2012), domestication (Shapiro et al., 2013), neurology (Belekhova et al., 2009; Cnotka et al., 2008; Rehk et al., 2007), and behavior (Sasaki et al., 2018). Additionally, there have been advances in understanding of the evolution, development, and genetics of intraspecific variations (Domyan & Shapiro, 2016a). Research associated with pigeon genetics generally has two main subfields: 1) analysis of the genetic mechanism of quality traits, especially the crest (Shapiro et al., 2013; Vickrey et al., 2015), foot feather (Boer et al., 2019; Domyan et al., 2016b), and plumage color (Domyan et al., 2014; Vickrey et al., 2018) and 2) analysis of quantitative traits, including determination of which homing ability in racing pigeons is a complex trait related to endurance, speed, survivability, and positioning ability, as well as navigational experience (Julia et al., 2017). Moreover, genes involved in the positively selected formation of neuromuscular junctions and the central nervous system in carrier pigeons have been identified (Caspermeyer, 2018; Gazda et al., 2018; Shao et al., 2020).

Moreover, study of adaptive genetic evolution mechanisms in relation to extreme or severe environments has increased in recent years, including the adaptability of humans and animals to high-altitude hypoxia (Beall, 2006; X. Liu et al., 2019; Wei et al., 2016), severe cold (Fumagalli et al., 2015; Ghoreishifar et al., 2020), strong ultraviolet radiation (Bertolini et al., 2018; Flori et al., 2019; L. Yu et al., 2016), and hot and dry climates (Kim et al., 2016). F_{ST} & θ_π ratio has been proved to be a very effective method for detecting and selecting and eliminating areas, especially when mining functional areas closely related to the living environment, it can often get a strong selection signal (Ababaikeri et al., 2020; Chen et al., 2016; Liu et al., 2020; Qiu et al., 2015). This method identified a large number of genes related to artificial selection or economic traits in other domestic animals (Li et al., 2013, 2014; Zhang et al., ,2018, 2020). F_{ST} is suitable for the detection of selection signals between two populations and can detect the regions where the genome is differentiated (gene frequency). The principle of θ_π analysis is based on the heterozygosity, and the selected regions tend to decrease in nucleotide polymorphism. That is to say, the genomic region has both the differentiation of the genotype frequency and the reduction in nucleotide polymorphism, and it is considered that the region has been selected. These research strategies allow identification of the local environmental adaptability of pigeons and offer new insights into adaption to harsh environment and climate.

The Tarim pigeon (i.e., the Yarkant pigeon and the Kashgar pigeon) was bred over thousands of years by residents of the Yarkant River and Tarim River basins in the western part of the Tarim Basin in Xinjiang through natural breeding and domestication of feral pigeons (Liang Yayan, 2019). This breed is well-adapted to the extreme local climate (Mainuer Slamu, 2017; Tan Rui, 2011), which is a typical warm-temperate, continental, arid climate. The main climatic characteristics are dry heat, severe cold, and strong solar radiation, with large daily and annual temperature ranges (Abdul Rexiti Aji, 2002). Because of the pursuit of economic benefits, modern large-scale pigeon breeding enterprises mostly choose commercial pigeon varieties for production, such as King pigeons (Ye et al., 2018) and Euro-pigeons (Pomianowski et al., 2009), which have the advantages of a white carcass, large size, and high fecundity.

Here, we generated the whole-genome sequences of 52 pigeons from seven breeds, including one local breed, one high-flying breed, and five commercial meat-types, by selective sweep and performing combined calculations for the F_{ST} and log$_2$(θ_π ratio) values. We observed strong selection markers near genes known to be artificially selected for plumage color, growth, and development in other animals. Importantly, we discovered genetic pathways related to local environmental adaptability in the Tarim pigeon.

2 | MATERIALS AND METHODS

2.1 | Pigeons

The five commercial meat breeds included seven Euro-pigeons (EU; Shanghai Jinhuang Pigeon Industry Co., Ltd.), eight Silver Kings, seven Shiqi, eight Shen Kings, and eight Taishen self-distinguishing male and female pigeons (WK, SQ, SK, and TS; Shenzhen Tianxiang Da Pigeon Co., Ltd). Six high fliers (HF) were from Shanghai Jinhuang Pigeon Industry Co., Ltd., and eight Tarim pigeons (TR) were from Mushi Township, Shufu County, Kashgar, Xinjiang (Figure 1). Pigeons used in this study were approved by the Ethics and Animal Welfare Committee of Shanghai Academy of Agricultural Sciences (No. SAASPZ0521012). For each pigeon, genomic DNA was extracted from blood samples using a Tiangen DNA extraction kit, and sequencing was performed on an Illumina HiSeq PE150 systems (Illumina, Carlsbad, CA, USA).

2.2 | Alignment against the reference genome

High-quality sequencing data were aligned with the reference genome (https://www.ncbi.nlm.nih.gov/genome/10719?genome_assembly_id=39619) using BWA software (parameter: mem-t4-k32-m) (Li & Durbin, 2009), and the results were analyzed using SAMTOOLS (parameter: rmdup) (Li et al., 2009).

2.3 | SNP detection and annotation

We used SAMtools to detect population SNPs (Li et al., 2009) and a Bayesian model to detect polymorphic sites in the population.
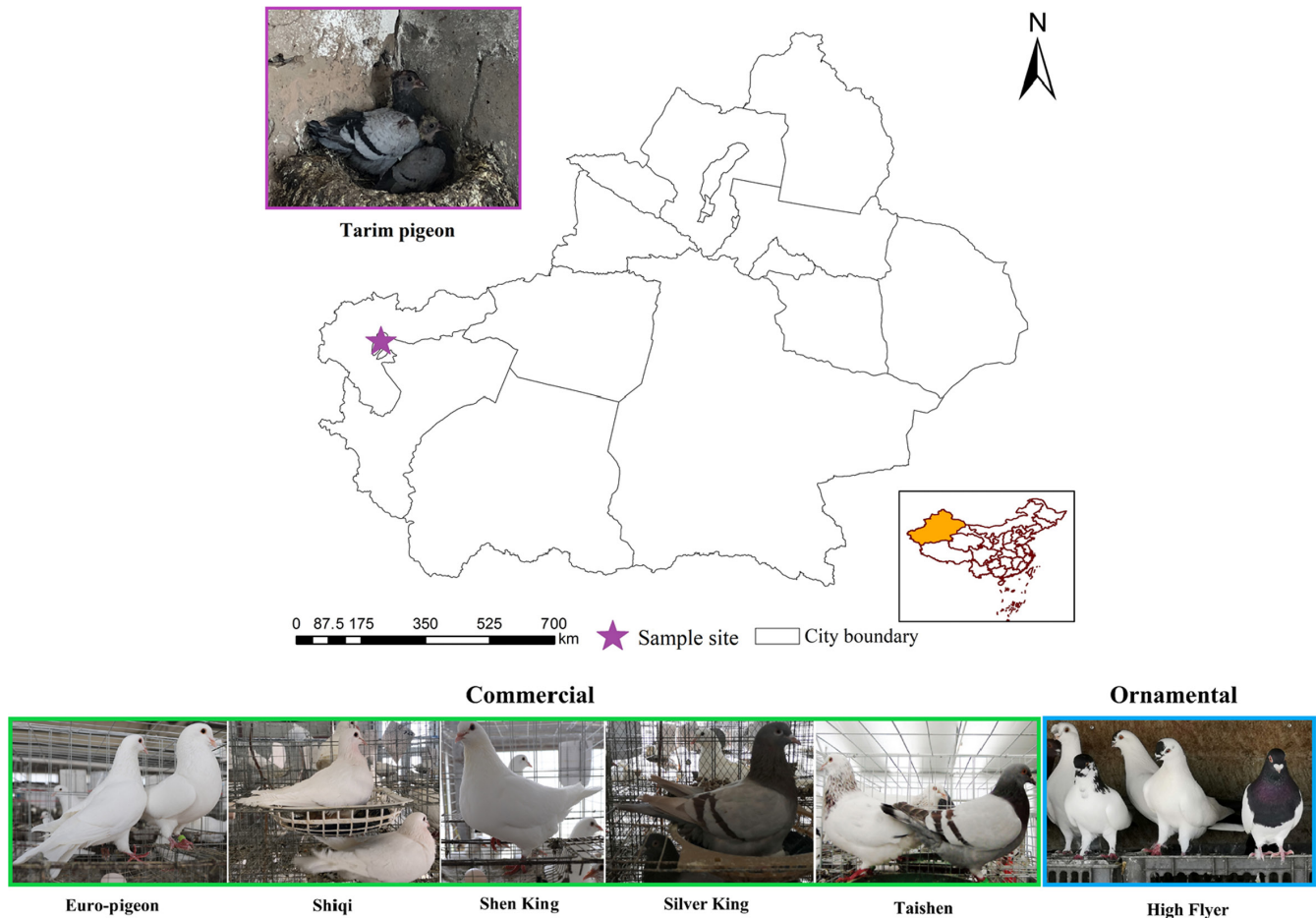
FIGURE 1 Phenotype of the seven pigeon breeds and geographical origins of local breeds

High-quality SNPs were obtained by filtering and screening as follows:

1. Q20 quality control (filter SNPs with quality values with a sequencing error rate >1%).
2. SNP sites separated by at least 5 bp.
3. SNP coverage depth ranging from 1-, 3-, or 5-fold the average depth.

ANNOVAR software was used to annotate the SNP results (Wang et al., 2010).

2.4 | Analysis of genetic background in the population

The distance matrix was calculated using TreeBeST software (v.1.9.2; http://treesoft.sourceforge.net/treebest.shtml), and phylogenetic trees were constructed using the neighbor-joining (NJ) method. The bootstrap values were obtained after 1,000 calculations. We used EIGENSOFT (v5.0; https://www.hsph.harvard.edu/alkes-price/software/) for principal component analysis on an individual scale for the 52 pigeons (Patterson et al., 2006). Use PLINK to analyze

population structure, create PLINK input file—Ped file, and then use FRAPPE v1.1 to estimate individual admixture (Tang et al., 2005).

2.5 | Analyses of regions of homozygosity (ROHs) and linkage disequilibrium (LD)

Regions of homozygosity for each pigeon breed were identified using PLINK (v.1.07) (Purcell et al., 2007). The parameters of ROH analysis are as follows (plink -- file result -- allow extra chr -- homozyg SNP 100 -- homozyg kb 500 -- homozyg density 50 -- homozyg gap 1000 -- homozyg window SNP 50 -- homozyg window het 2 -- homozyg window missing 5 -- out roh; rm *. Nosex). Based on the detected ROHs, the genomic inbreeding coefficient (F_{ROH}) of pigeons was calculated (McQuillan et al., 2008):

$$F_{ROH} = \frac{L_{ROH}}{L_{AUTO}}$$

Among them, L_{ROH} represents the total length of ROH fragment on autosomal, and L_{AUTO} is the total length of autosome.

To evaluate LD decay, the squared correlation (r^2) between any two loci was calculated using Haploview (v.4.2) (Barrett et al., 2005).

LD analysis parameters are as follows (-n –dprime-minMAF 0.05). The average r^2 value was calculated for pairwise markers in a 500-kb window and averaged across the whole genome.

2.6 | Genome-wide selective-sweep test

F_{ST} and θ_π have proven effective for detecting selective elimination regions, especially when mining functional regions closely related to the living environment, when strong selection signals can be obtained. We calculated the genome-wide distribution of F_{ST} values (Weir & Cockerham, 1984) and θ_π ratios among the seven pigeon breeds, using a sliding-window approach (40-kb windows with 20-kb increments). The θ_π ratios were $\log_2(\theta_\pi$ ratio) transformed. We considered the windows with the top 5% values for the F_{ST} and $\log_2(\theta_\pi$ ratio) simultaneously as candidate outliers under strong selective sweeps (Li et al., 2013) (Table S1). F_{ST} and $\log_2(\theta_\pi$ ratio) joint analysis including TR. VS. EU, TR. VS. SQ, and TR. VS. SK revealed the genomic region imprint of three commercial white feather pigeon breeds. TR. VS. TS was used to analyze the selection of TS, and TR. VS. WK was used to reveal the selection of WK. The other six varieties were used as controls to detect the selection signal of HF. Five commercial meat pigeon breeds were used as control to study the adaptive selection of Tarim pigeon. Furthermore, the overlap information of a selected signal was obtained using the "vennDiagram" package in R (https://www.omicstudio.cn/tool/6).

2.7 | Candidate gene analysis

We compared F_{ST} and $\log_2(\theta_\pi$ ratio) values of the selective genomic regions with those at the whole-genome scale for TR pigeons. Overlaps of candidate genes were identified in extreme environments. Gene Ontology (GO) analysis was performed using R packages (GOseq and topGO), and Kyoto Encyclopedia of Genes and Genomes (KEGG) analysis was performed using Kobas software (http://kobas.cbi.pku.edu.cn/kobas3/).

3 | RESULTS

3.1 | Genome sequencing and mapping

After filtering the sequencing data, high-quality clean data were obtained. The data of 52 samples were statistically analyzed (Table S2), including sequencing data output, sequencing error rate, Q20 content (%), Q30 content (%), and GC content (%). The total amount of sequencing data is 491.6 Gb, and the clean data are 490.7 Gb. The genome size is 1107989085 bp, the average mapping rate of population samples is 97.5%, the average sequencing depth of genome is 7.85, and the average coverage 1X is 98.4% (Table S3). Finally, a total of 5,673,290 SNPs with high quality were obtained (Table S4), and 26,640 genes were annotated (Table S5).

3.2 | Population genetics

Neighbor-joining tree analysis supported two of the separate clusters, including Chinese breeds and commercial breeds (Figure 2a). PCA results revealed strong clustering of seven pigeon breeds into three genetic groups, with HF and TR clustered in a group, EU, SK, WK, and SQ clustered together, and TS separated into a single group (Figure 2b). ADMIXTURE analysis confirmed that three ancestral groups were formed (Figure 2c).

The genomic variations [average ROHs, mean ROH size, and the inbreeding coefficient (F_{ROH})] for the seven pigeon groups showed congruent patterns. Chinese HF breeds showed an extreme inbreeding coefficient (F_{ROH}) and exhibited the most ROHs (96) and the largest ROH size (76,829.6 kb), whereas the greatest genomic variations were observed in the TR breed from Kashgar in Xinjiang (Figure 3a, Table S6). The TR and SK pigeon breeds showed an overall high level of genetic diversity and rapid LD decay, whereas the HF breeds, as a Chinese traditional pet pigeon, exhibited lower genetic diversity and slower LD decay (Figure 3b).

3.3 | Selective-sweep signals in commercial pigeon breeds

3.3.1 | Plumage color

Using WK as the control group, 303, 181, and 190 gene regions were identified by F_{ST} and $\log_2(\theta_\pi$ ratio) analyses in EU, SQ, and SK, respectively (Table S7). Furthermore, nine genes were identified by overlap analysis, among which EDNRB was associated with white plumage color (Figure 4a and b, Table S8). With white pigeons and TR pigeons as the control group, a total of 118 overlaps were identified in TS pigeons (Table S9), among which genes enriched for the KEGG pathway melanogenesis (ID: clv04916) included AHCY, ASIP, WNT6, and WNT10A. When compared with the HF pigeons, ASIP was identified as related to feather color with WK. Other genes related to WK plumage color included CREB1 and SLC45A1.

3.3.2 | Production

Compared with the TR pigeon, 21 genes in the white-feathered meat pigeon were identified as related to body size according to overlap analysis, including 7 definite named genes (EDNRB, PLPPR5, RBFOX1, IGFBP1, TNS3, ADCY8, and LCORL) (Figure 4c and d, Table S10). Additionally, LCORL was identified in TS pigeons, whereas TNS3 and IGFBP1 genes were identified in WK pigeons. We speculated that these three genes are related to body size traits of commercial pigeon breeds. Selective signal analysis revealed that RAMP3, KIAA0556, VAMP3, and GSG1L play key roles in WK reproduction. Compared with the TR pigeons of all commercial meat pigeon breeds, overlap analysis identified four genes (Table S11), with RBFOX1 shared between breeds and related to human neuronal development (Fogel et al., 2012).
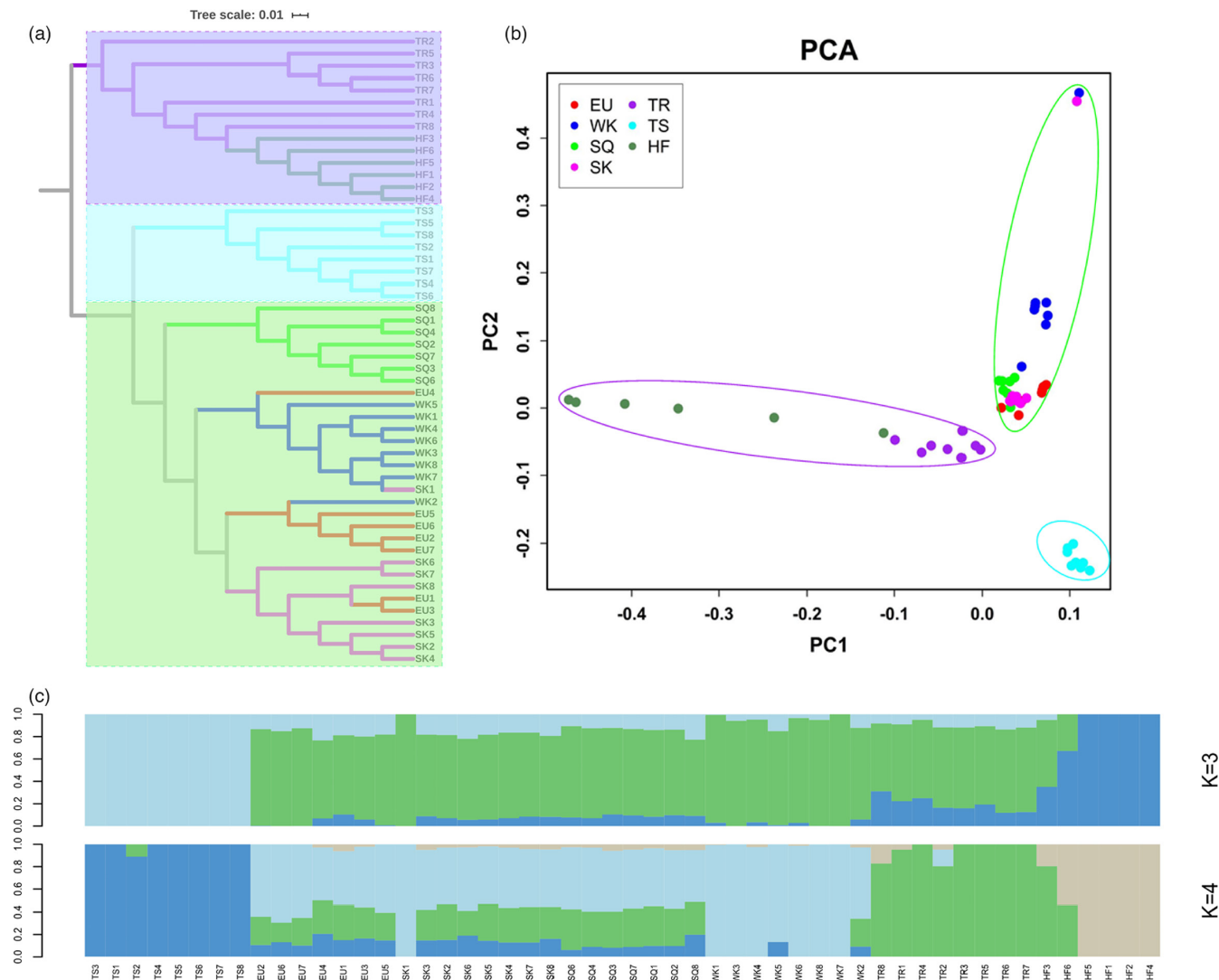
FIGURE 2 (a) NJ phylogenetic tree for the seven pigeon breeds. European pigeon (EU); Silver King (WK); Shiqi (SQ); Shen King (SK); Tarim pigeon (TR); Taishen (TS); High Flier (HF). (b) Two‑ dimensional PCA plot of pigeon breeds. (c) Genetic structure of pigeon breeds according to ADMIXTURE, with K = 3, 4

3.4 | Selective-sweep signals in High Fliers

The HF are a highly cultivated breed with a breeding history of >300 years in China. Selection signals and overlap analysis revealed that 73 gene regions received strong artificial selection or showed the lowest genetic diversity (Table S12), with all of these genes annotated in the human phenotype ontology database (http://www. webgestalt.org/). HPO enrichment analysis revealed their association with facial features and muscular dystrophy (Tables 1, S13). Genes associated with pigment deposition included *MC1R*.

3.5 | Selective-sweep signals in Tarim pigeons

Rapidly evolving adaptive genes related to environmental stress were used as the windows to identify the top 5% (F_{ST} and the $\log_2(\theta_\pi$

ratio)) of genes as the candidate outliers of strong selective sweeps (Figure 5a). Compared with the five commercial varieties, positive selection genes were identified in TR, including 422, 389, 422, 253, and 336 genes related to adaptability (Table S14). Additionally, 47 gene regions were identified by overlap analysis (Figure 5b, Table S15), and GO analysis revealed significant enrichment of 22 candidate genes embedded in the selective regions (169 GO terms; $p < 0.05$) (Tables S16, S17), including organ development (GO:0048513, $p = 0.001$), potassium channel inhibitor activity (GO:0019870, $p = 0.003$), cellular response to chemical stimulus (GO:0070887, $p = 0.003$), reproductive structure development (GO:0048608, $p = 0.02$), and blue light photoreceptor activity (GO:0009882, $p = 0.02$) (Figure 5c). These enriched genes were related to adaptability, including strong solar radiation, large diurnal range, and alkaline water. According to the selected regions, the enrichment pathways were mainly related to abiotic factors (physical and chemical environments), as
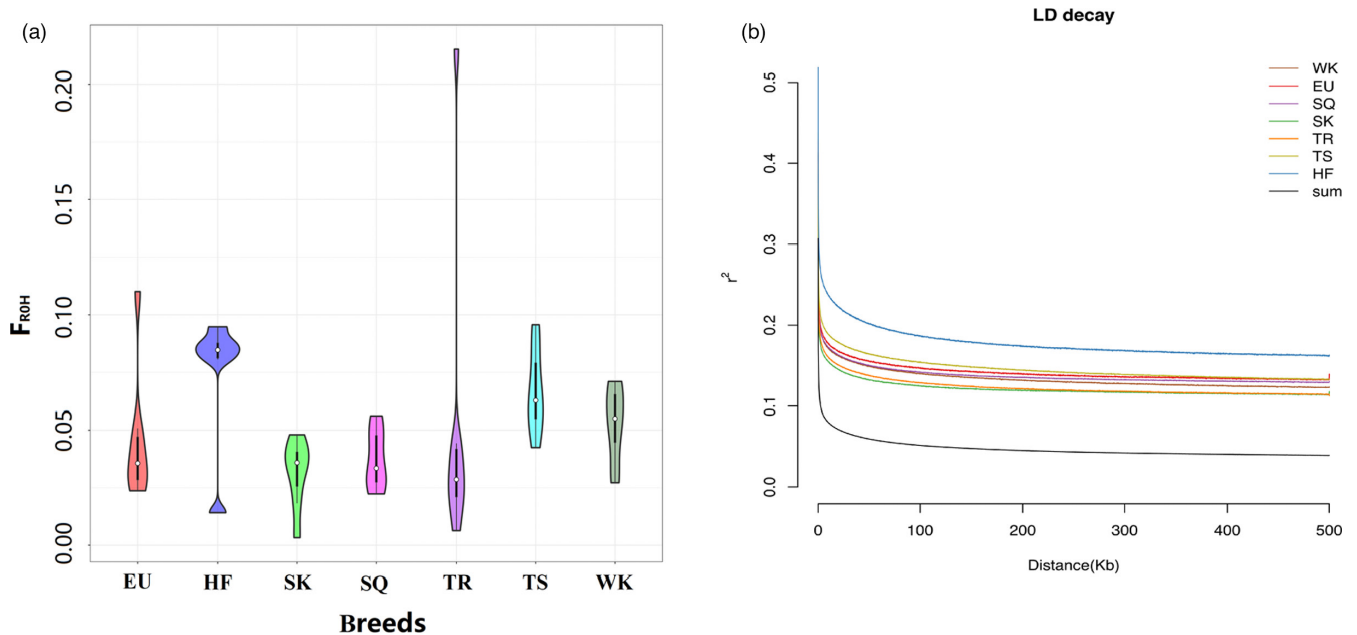
FIGURE 3 (a) Analysis of the F_{ROH} of the seven pigeon breeds. (b) LD decay of the seven pigeon populations, as measured by r^2

well as organ development and olfactory and visual systems. The KEGG pathways enriched by the selected genes of TR include Adipocytokine Signaling Pathway (ID: clv04920, $p = 0.03$) and Insulin Signaling Pathway (ID: clv04910) (Table S18, Figure S1). Both pathways involve *PPARGC1A* gene, which plays a key role in adaptive thermogenesis.

4 | DISCUSSION

The genetic architecture plays a fundamental role in the origin and maintenance of local adaptation with gene flow (Tigano & Friesen, 2016). Here, phylogenetic tree mainly includes two branches: one for commercial pigeons and mostly introduced and cultivated varieties; and the other comprises TR and HF pigeons, indicating that traditional Chinese ornamental pigeons might originate from local breeds. The results of ROH analysis of the high-flying pigeon breed revealed their being highly inbred. The artificial high-intensity and continuous selection requires that this group maintain specific morphological characteristics for breeding, such as a short beak and lightweight. Meat pigeon breeds can provide humans with high-quality protein sources, mainly including meat and egg products. Artificial selection targets mainly focus on body size and fertility, and large-scale cages are often used. These pigeon genetic resources provided a more extensive phenotypic basis for research purposes. The results are mainly classified into two categories: economic traits and local environmental adaptability. Economic traits mainly include feather color, body size, fecundity, and ornamental traits, whereas environmental adaptability abiotic factors include physical environment (light, temperature, etc.) and chemical environment (water, food, air, etc.).

4.1 | Economic traits

4.1.1 | Genes related to plumage color

Compared with colored feather pigeons, white feather pigeons have better carcass appearance after slaughtering, so they occupy the mainstream market in the world. Comparative analysis between white-feathered pigeons and other colored pigeons revealed that the *EDNRB* gene region showed a strong selection signal. This gene is widely reported as related to mammalian skin, coat, and iris pigmentation, including several human syndromes with eye-color defects and heterochromia (Issa et al., 2017; Morimoto et al., 2018), iris pigmentation, heterochromia patterns, and coat color in pigs (Moscatelli et al., 2020; Wilkinson et al., 2013). Additionally, a missense mutation in *EDNRB* causes lethal white foal syndrome in horses (Metallinos et al., 1998; Santschi et al., 1998). In birds, only sporadic reports of this gene variation have been associated with feather color of quails (Miwa et al., 2006, 2007). Pigeons with white plumage usually have dark brown iris color. The results of selective signal scanning suggested that *EDNRB* might play a key role in pigeon feather and iris color.

As a monotypic bird, the sex identification of pigeons is difficult in the commercial production of meat pigeons. TS pigeons are one of the a few breeds in which males and females can be identified by feather color. For almond-colored pigeons with sex-linked, copy number variation analysis identified a genomic region that include *MLANA* (Bruders et al., 2020). Moreover, homozygous almond males (ZSt/ZSt) develop severe eye defects and often lack plumage pigmentation, suggesting that higher dosage of the mutant allele is deleterious (Bruders et al., 2020). In this study, the genomic region controlling pigment deposition in TS, which includes *AHCY*,
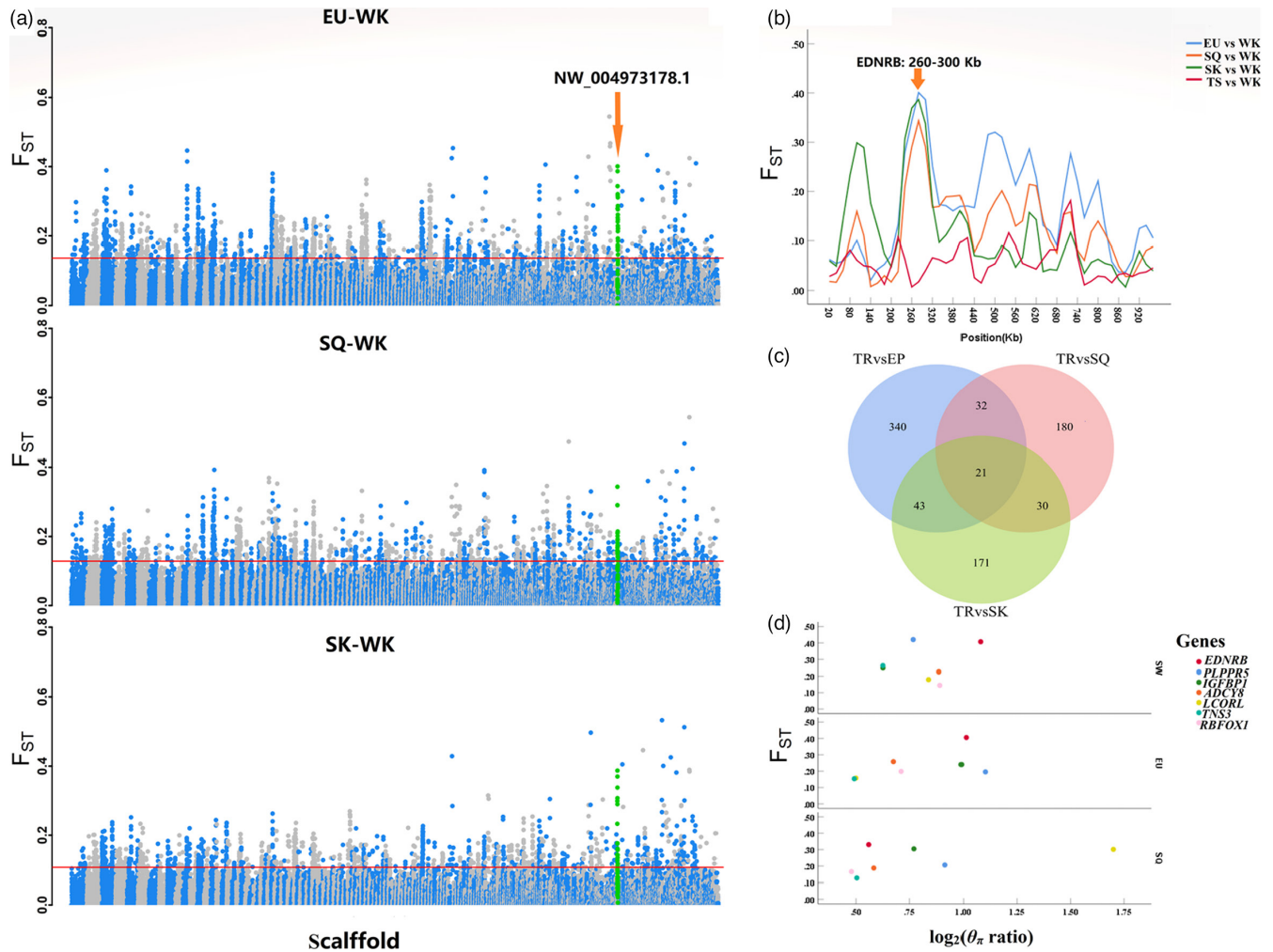
FIGURE 4 (a) F_{ST} plot of the comparison of the white pigeon with WK. The threshold line represents the top 1% of the F_{ST} value. (b) F_{ST} corresponding to the selective sweep of white plumage color on scaffold NW_004973178.1 encompassing *EDNRB*. (c) Venn diagram showing the shared gene number between three white commercial pigeon breeds, with local TR pigeons used as the control group (F_{ST} and θ_π analyses). (d) Seven key genes were selected as associated with white plum

TABLE 1 HPO annotation of candidate genes

Term ID	Term name	Intersections
HP:0000152	Abnormality of head or neck	*SYNE1, DMD, SOS1, CTDP1, TLR3, BRAF, GRIA4, SGCD, COG8, CDH1, GAS8, TUBB3*
HP:0002817	Abnormality of the upper limb	*SYNE1, DMD, SOS1, CTDP1, BRAF, SGCD, COG8, GAS8, TUBB3*
HP:0011805	Abnormal skeletal muscle morphology	*SYNE1, DMD, SOS1, CTDP1, BRAF, GRIA4, SGCD, COG8, TUBB3*
HP:0000271	Abnormality of the face	*SYNE1, DMD, SOS1, CTDP1, BRAF, SGCD, COG8, CDH1, GAS8, TUBB3*
HP:0011821	Abnormality of facial skeleton	*SOS1, CTDP1, BRAF, COG8, CDH1, GAS8, TUBB3*
HP:0000492	Abnormal eyelid morphology	*DMD, SOS1, CTDP1, BRAF, COG8, CDH1, TUBB3*
HP:0030319	Weakness of facial musculature	*SYNE1, DMD, SGCD, TUBB3*
HP:0003560	Muscular dystrophy	*SYNE1, DMD, SGCD*
HP:0002212	Curly hair	*SOS1, BRAF*
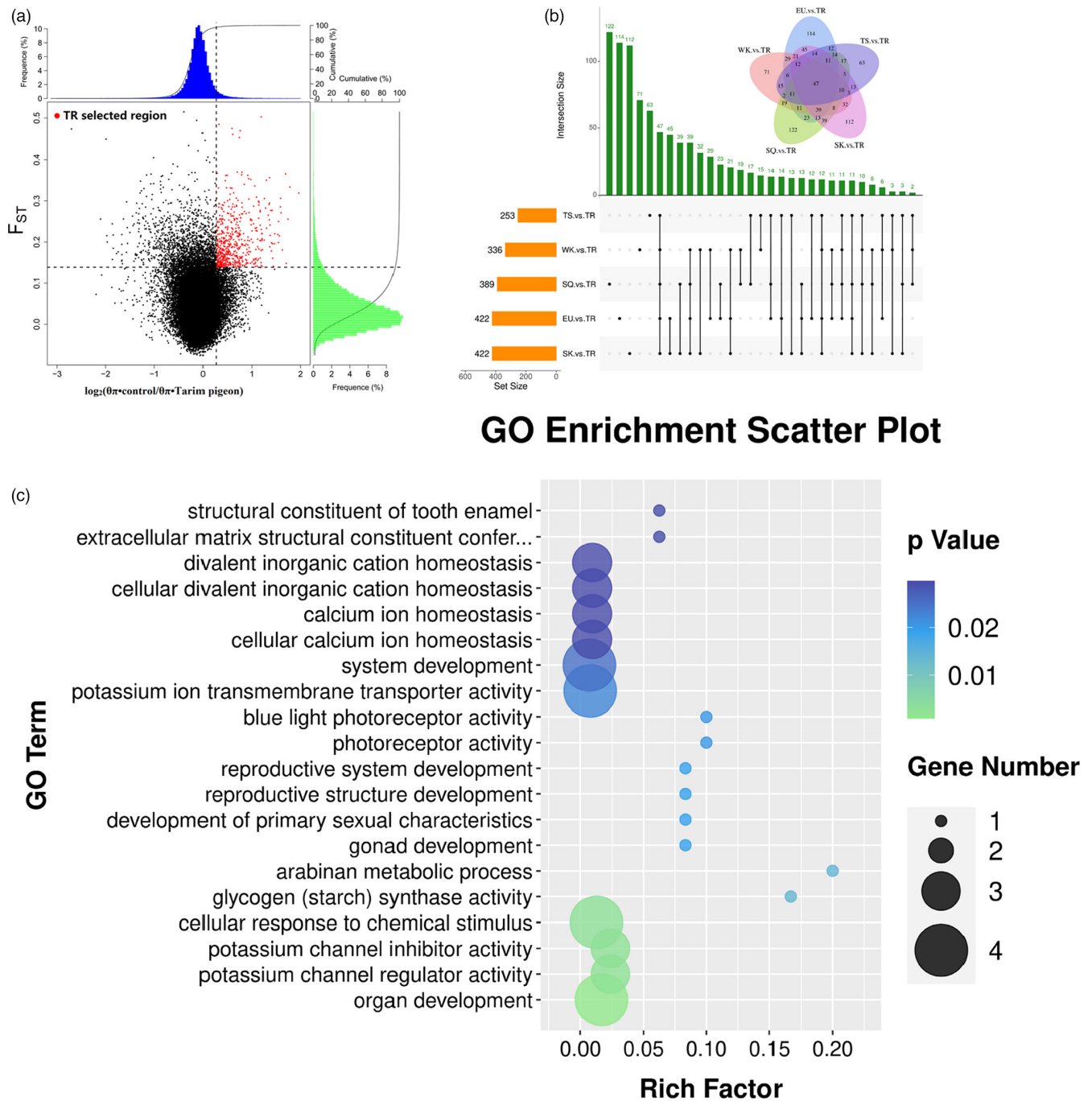
FIGURE 5 (a) The top 5% of distribution of $\log_2$ values (θ_π•control/θ_π•Tarim pigeon) and highest F_{ST} values calculated in 40-kb sliding windows with 20-kb increments between the Tarim pigeon and the control commercial population. (b) Upset and Venn diagrams show the overlapping genes between TR and the five commercial breeds. (c) Enriched GO terms for key genes detected by selective sweep according to the F_{ST} and θ_π ratio

ASIP, *WNT6*, and *WNT10A*. Multiple studies report the involvement of *ASIP* in determining coat color in domestic animals, including sheep (Zhang, Li, et al., 2017), horse (Grilz-Seger et al., 2019), donkey (Abitbol et al., 2015), cattle (Xu et al., 2015), and buffalo (Liang et al., 2020). Additionally, variation in the 5′ region of the gene in Japanese quails can cause feather color dilution (Robic et al., 2019), and the expression of the gene is associated with chicken sexual dimorphism (Oribe et al., 2012). Moreover, *WNT6* and *WNT10A* are

related to the color pattern of butterfly wings (Martin & Reed, 2014), and subsequent studies showed that *WNT6* is involved in sex-related feather color patterns (Iijima et al., 2019). Furthermore, *WNT10A* is associated with hypohidrotic ectodermal dysplasia, which is usually inherited in an X-linked form and features light pigmentation (Wright et al., 1993).

In the WK pigeon population, *ASIP* was only identified in high-flying pigeons, whereas *SLC45A1* and *CREB1* were identified in

comparisons with other groups. *SLC45A1* encodes a protein that plays a role in glucose uptake and is implicated in the regulation of glucose homoeostasis in the brain (Bartölke et al., 2014). There are few reports on the relationship between *SLC45A1* and pigment deposition, although *SLC45A2* is associated with skin and hair pigmentation (Fracasso et al., 2016), and its mutation is related to chicken Silver Feather (Gunnarsson et al., 2007). Additionally, *SLC45A2* mutation is associated with classical color phenotypes of pigeons and offers a mechanistic explanation of their dominance and epistatic relationships (Domyan et al., 2014). Furthermore, evidence indicates that inherited abnormalities in *CREB1* pigmentation-related genes can not only increase the risk of cutaneous melanoma but also influence patient clinicopathological features (Loureno et al., 2020).

We identified *MC1R* in HF during comparison with other breeds and encodes a protein that regulates pigment deposition (Mountjoy et al., 1992). Variation in *MC1R* in different species can lead to a dominant black-coat color phenotype or recessive red or yellow phenotype (Robbins et al., 1993). In pigeons, variation in *MC1R* resulting in a V85 M substitution is associated with phenomenalism (Guernsey et al., 2013).

4.1.2 | Genes related to production

The production traits of meat pigeons mainly include meat traits and reproductive traits. Commercial pigeon breeders pursue larger body size and higher meat production, mainly based on the sales of squab at 28 days old. The weight of commercial meat pigeons is generally 500–800 g, while that of Chinese traditional ornamental pigeons and local pigeons is only about 350 g. Compared with local breeds, we identified *LCORL*, *TNS3*, and *IGFBP1* as associated with growth and development in white meat pigeons. The *LCORL* region has been identified as a locus for human height (Wood et al., 2014) and weight (Horikoshi et al., 2013), and genome-wide analysis of multiple species revealed this region as related to body size, including in pig (Rubin et al., 2012), horse (Srikanth et al., 2019), cattle (Xu et al., 2015), and sheep (Yurchenko et al., 2019). The present study is the first identification of this gene as being related to production in pigeons. *TNS3* plays an important role in development and growth, and its inactivation in mice results in growth retardation and postnatal lethality (Chiang et al., 2005). *TNS3* gene was enriched in muscle organ development (GO: 0007517) and muscle structure development (GO: 0061061), and *TNS3* is associated with fossil bone length in Pekin ducks (Deng et al., 2019). *IGFBP1* is secreted by hepatocytes and other cell types (Baxter, 2014), and studies report that women with elevated *IGFBP1* levels are more likely to have a low relative muscle mass (Stilling et al., 2017).

Compared with other breeds, we identified reproduction-related genes in WK, including *RAMP3*, *KIAA0556*, *VAMP3*, and *GSG1L*. *RAMP3* encodes an adrenomedullin receptor (McLatchie et al., 1998) involved in uterine quiescence during pregnancy and regulated by steroid hormones (Thota et al., 2003). Additionally, *RAMP3* expression correlates with temporary sperm storage in and possible

sequential sperm release from the chicken uterovaginal junction following artificial insemination (Yang et al., 2020). Balanced chromosome rearrangements in unaffected individuals possess high reproductive risks, including infertility, abnormal offspring, and pregnancy loss, with *KIAA0556* detected in families harboring these rearrangements (Tan et al., 2020). *GSG1L* and *VAMP3* play important roles in the development of animal gonads (Boonanuntanasarn et al., 2020), and *VAMP3* is important to sperm fertilization in pig (Tsai et al., 2010) and associated with testis weight in chickens (Zhang, Yu, et al., 2017).

4.1.3 | Genes related to ornamental traits

Compared with other breeds, the genes identified in high-flying pigeons are mostly related to rare human diseases, especially muscular dystrophy and special facial features. This might be related to the direction chosen by breeders, such as a light body, short beak, big eyes, and feather color. *SYNE1* is associated with Emery–Dreifuss muscular dystrophy (Chen et al., 2017; Heller et al., 2020; Sandra et al., 2019), and mutation of *DMD*, as the largest in the human genome (total intron content: >2.2 Mb) (Keegan, 2020), causes Duchenne muscular dystrophy and Becker muscular dystrophy (Yang et al., 2019). *SOS1* and *BRAF* are associated with Noonan syndrome, an autosomal-dominant disorder characterized by short stature, congenital heart disease, curly hair, and facial dysmorphia (Allanson & Roberts, 2001; El Bouchikhi et al., 2016; Quaio et al., 2013). *CTDP1* is the only gene in which pathogenic variants are known to cause congenital cataracts, facial dysmorphism, and neuropathy characterized by abnormalities of the eye (Kalaydjieva & Chamova, 1993). *SGCD* is associated with recessive limb-girdle muscular weakness and Pompeii disease (Bevilacqua et al., 2020).

4.2 | Adaptive traits

Compared with commercial pigeon breeds and in addition to selection pressures for meat and fertility, local TR pigeons had to adapt to a warm arid climate in Kashgar (Liang et al., 2019) characterized by strong solar radiation, and large daily and annual temperature ranges (Abdul Rexiti Aji, 2002). Additionally, sulfate concentrations exceed the groundwater quality standard in 73.2% of the unconfined groundwater area and in 53.2% of the confined groundwater area in Kashgar Delta (Wei et al., 2019). Studies have focused on plant soil chemical tolerance (Bian et al., 2020), and a recent report demonstrated the adaptability of limestone langurs to a calcium ion chemical environment (Liu et al., 2020). *KLHL8* was enriched in a pathway related to sulfate transmembrane transporter activity (GO:0015116, $p = 0.03$). *GLRA2* is a member of the ligand-gated ion channel superfamily (Feng et al., 2001) that plays an important role in maintaining potassium and calcium homeostasis. It is speculated that these genes may be related to the water environmental adaptability of TR pigeon.

PPARGC1A (also known as *PGC-1α*) is related to metabolism and starch synthesis by encoding a nuclear transcriptional coactivator that plays a pivotal role in metabolic processes, including mitochondrial biogenesis, thermogenesis, respiration, insulin, secretion, and gluconeogenesis (Baar, 2014). Human variants of *PPARGC1A* are associated with endurance (Ahmetov et al., 2016) and might be involved in pigeon energy maintenance. Moreover, *PPARGC1A*, *METTL15*, and *PGAM5* play an important role in mitochondria (Magalhaes et al., 2018; Van Haute et al., 2019; Yu et al., 2020), with deletion of *PGAM5* resulting in accelerated retinal pigment epithelial senescence *in vitro* and *in vivo* (Greenway et al., 2020). Furthermore, *ADGRL3* expression is highly regulated during brain development and peaks during the prenatal and postnatal periods (Arcos-Burgos et al., 2010), with numerous studies reporting that *ADGRL3 (LPHN3)* is related to attention-deficit/hyperactivity disorder (Acosta et al., 2016; Huang et al., 2019; Hwang et al., 2015). *ADGRL3* gene is enriched in the blue light photoreceptor activity (GO:0009882, $p = 0.02$). Photoreceptors are essential for circadian rhythm in animals. It is speculated that this gene may be related to the rhythmic behavior of TR pigeons. *NTNG1* is associated with neurological diseases, including Rett syndrome (Archer et al., 2006), schizophrenia, and bipolar disorder (Eastwood & Harrison, 2008; Wilcox & Quadri, 2014). In the present study, we found that pathways enriched in the selected gene regions of TR pigeons were mainly concentrated in organ development, inorganic ion transport, circadian rhythm, the olfactory system, and metabolism.

5 | CONCLUSIONS

This study elucidated the genetic and evolutionary relationship among seven pigeon breeds. Inbreeding or genetic diversity assessment revealed the degree of artificial selection of ornamental breeds, local breeds, and commercial pigeon breeds. The genomic imprints left by artificial selection revealed the *EDNRB* gene that affects white feather traits and the *LCORL* gene that affects body weight or size, which can be used as candidate genes for molecular breeding of meat pigeons. Compared with the choices of pigeons in production and ornamental traits, the adaptability of human-mediated selection was more complex and diverse, including chemical and physical environments. This research insights into how the Tarim pigeon has evolved an effective adaptive mechanism to cope with the adverse conditions of local drought, brackish water, strong light, and large temperature differences. Screening genomic regions of pigeons related to economic traits and adaptability not only broadens the understanding of selection and evolutionary processes in pigeons but also helps make better use of genetic resources for breeding improvements.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Haobin Hou   https://orcid.org/0000-0002-3430-6361

REFERENCES

Ababaikeri, B., Abduriyim, S., Tohetahong, Y., Mamat, T., Ahmat, A., & Halik, M. (2020). Whole-genome sequencing of Tarim red deer (Cervus elaphus yarkandensis) reveals demographic history and adaptations to an arid-desert environment. *Frontiers in Zoology*, *17*, 31. https://doi.org/10.1186/s12983-020-00379-5

Abdul Rexiti Aji, W. S. (2002). *The History of Kashgar*. Xinjiang People's Publishing House. (in Chinese).

Abitbol, M., Legrand, R., & Tiret, L. (2015). A missense mutation in the agouti signaling protein gene (ASIP) is associated with the no light points coat phenotype in donkeys. *Genetics Selection Evolution*, *47*(1), 28. https://doi.org/10.1186/s12711-015-0112-x

Acosta, M. T., Swanson, J., Stehli, A., Molina, B. S., Martinez, A. F., Arcos-Burgos, M., & Muenke, M. (2016). ADGRL3 (LPHN3) variants are associated with a refined phenotype of ADHD in the MTA study. *Molecular Genetics & Genomic Medicine*, *4*(5), 540–547. https://doi.org/10.1002/mgg3.230

Ahmetov, I. I., Egorova, E. S., Gabdrakhmanova, L. J., & Fedotovskaya, O. N. (2016). Genes and athletic performance: an update. *Medicine and Sport Science*, *61*, 41–54. https://doi.org/10.1159/000445240

Allanson, J. E., & Roberts, A. E. (2001). Noonan Syndrome. In M. P. Adam, H. H. Ardinger, R. A. Pagon, S. E. Wallace, L. J. H. Bean, K. Stephens, & A. Amemiya (Eds.), *GeneReviews(®)* (pp. 1993–2021). University of Washington, Seattle.

Archer, H. L., Evans, J. C., Millar, D. S., Thompson, P. W., Kerr, A. M., Leonard, H., Christodoulou, J., Ravine, D., Lazarou, L., Grove, L., Verity, C., Whatley, S. D., Pilz, D. T., Sampson, J. R., & Clarke, A. J. (2006). NTNG1 mutations are a rare cause of Rett syndrome. *American Journal of Medical Genetics A*, *140*(7), 691–694. https://doi.org/10.1002/ajmg.a.31133

Arcos-Burgos, M., Jain, M., Acosta, M. T., Shively, S., Stanescu, H., Wallis, D., Domené, S., Vélez, J. I., Karkera, J. D., Balog, J., Berg, K., Kleta, R., Gahl, W. A., Roessler, E., Long, R., Lie, J., Pineda, D., Londoño, A. C., Palacio, J. D., … Muenke, M. (2010). A common variant of the latrophilin 3 gene, LPHN3, confers susceptibility to ADHD and predicts effectiveness of stimulant medication. *Molecular Psychiatry*, *15*(11), 1053–1066. https://doi.org/10.1038/mp.2010.6

Baar, K. (2014). Nutrition and the adaptation to endurance training. *Sports Medicine*, *44*(Suppl 1), S5–12. https://doi.org/10.1007/s40279-014-0146-1

Barrett, J. C., Fry, B. A., Maller, J. B., & Daly, M. J. (2005). HAPLOVIEW: analysis and visualization of LD and haplotype maps. *Bioinformatics*, *21*(2), 263–265. https://doi.org/10.1093/bioinformatics/bth457

Bartölke, R., Heinisch, J. J., Wieczorek, H., & Vitavska, O. (2014). Proton-associated sucrose transport of mammalian solute carrier family 45: an analysis in Saccharomyces cerevisiae. *Biochemical Journal*, *464*(2), 193–201. https://doi.org/10.1042/BJ20140572

Baxter, R. C. (2014). IGF binding proteins in cancer: mechanistic and clinical insights. *Nature Reviews Cancer, 14*(5), 329–341. https://doi.org/10.1038/nrc3720

Beall, C. M. (2006). Andean, Tibetan, and Ethiopian patterns of adaptation to high-altitude hypoxia. *Integrative and Comparative Biology*, *46*(1), 18–24. https://doi.org/10.1093/icb/icj004

Belekhova, M. G., Chudinova, T. V., Kenigfest, N. B., & Veselkin, N. P. (2009). Metabolic activity of the mesencephalic auditory center in the pigeon. *Doklady Biological Sciences*, *426*(1), 197–200. https://doi.org/10.1134/s0012496609030016

Bertolini, F., Servin, B., Talenti, A., Rochat, E., Kim, E. S., Oget, C., Palhière, I., Crisà, A., Catillo, G., Steri, R., Amills, M., Colli, L., Marras, G., Milanesi, M., Nicolazzi, E., Rosen, B. D., Van Tassell, C. P., Guldbrandtsen, B., Sonstegard, T. S., ... Crepaldi, P. (2018). Signatures of selection and environmental adaptation across the goat genome post-domestication. *Genetics Selection Evolution*, *50*(1), 57. https://doi.org/10.1186/s12711-018-0421-y

Bevilacqua, J. A., Guecaimburu Ehuletche, M. D. R., Perna, A., Dubrovsky, A., Franca, M. C. Jr, Vargas, S., Hegde, M., Claeys, K. G., Straub, V., Daba, N., Faria, R., Periquet, M., Sparks, S., Thibault, N., & Araujo, R. (2020). The Latin American experience with a next generation sequencing genetic panel for recessive limb-girdle muscular weakness and Pompe disease. *Orphanet Journal of Rare Diseases, 15*(1), 11. https://doi.org/10.1186/s13023-019-1291-2

Bian, J., Cui, L., Wang, X., Yang, G., Huo, F., Ling, H., Chen, L., She, K., Du, X., Levi, B., Levi, A. J., Yan, Z., Nie, X., & Weining, S. (2020). Genomic and phenotypic divergence in wild barley driven by microgeographic adaptation. *Advanced Science (Weinh), 7*(24), 2000709. https://doi.org/10.1002/advs.202000709

Blasco, R., Finlayson, C., Rosell, J., Marco, A. S., Finlayson, S., Finlayson, G., Negro, J. J., Pacheco, F. G., & Vidal, J. R. (2014). The earliest pigeon fanciers. *Scientific Reports*, *4*, 5971. https://doi.org/10.1038/srep05971

Boer, E. F., Van Hollebeke, H. F., Park, S., Infante, C., Menke, D. B., & Shapiro, M. D. (2019). Pigeon foot feathering reveals conserved limb identity networks. *Developmental Biology*, *454*(2), 128–144. https://doi.org/10.1016/j.ydbio.2019.06.015

Boonanuntanasarn, S., Jangprai, A., & Na-Nakorn, U. (2020). Transcriptomic analysis of female and male gonads in juvenile snakeskin gourami (Trichopodus pectoralis). *Scientific Reports*, *10*(1), 5240. https://doi.org/10.1038/s41598-020-61738-0

Bruders, R., Van Hollebeke, H., Osborne, E. J., Kronenberg, Z., Maclary, E., Yandell, M., & Shapiro, M. D. (2020). A copy number variant is associated with a spectrum of pigmentation patterns in the rock pigeon (Columba livia). *LOS Genetics, 16*(5), e1008274. https://doi.org/10.1371/journal.pgen.1008274

Caspermeyer, J. (2018). Using whole-genome analysis to home in on racing pigeon performance. *Molecular Biology and Evolution*, *35*(5), 1296. https://doi.org/10.1093/molbev/msy064

Chen, C., Liu, Z., Pan, Q., Chen, X., Wang, H., Guo, H., & Shi, W. (2016). Genomic analyses reveal demographic history and temperate adaptation of the newly discovered honey bee subspecies apis mellifera sinisxinyuan n. ssp. *Molecular Biology and Evolution*, *33*(5), 1337–1348. https://doi.org/10.1093/molbev/msw017

Chen, Z., Ren, Z., Mei, W., Ma, Q., Shi, Y., Zhang, Y., Li, S., Xiang, L. I., & Zhang, J. (2017). A novel SYNE1 gene mutation in a Chinese family of Emery-Dreifuss muscular dystrophy-like. *BMC Medical Genetics*, *18*(1), 63. https://doi.org/10.1186/s12881-017-0424-5

Chiang, M. K., Liao, Y. C., Kuwabara, Y., & Lo, S. H. (2005). Inactivation of tensin3 in mice results in growth retardation and postnatal lethality. *Developmental Biology, 279*(2), 368–377. https://doi.org/10.1016/j.ydbio.2004.12.027

Cnotka, J., Mohle, M., & Rehkamper, G. (2008). Navigational experience affects hippocampus size in homing pigeons. *Brain Behavior and Evolution*, *72*(3), 233–238. https://doi.org/10.1159/000165102

Darwin, C. (1868). *The Variation of Animals and Plants under Domestication*, Vol. *1*. John Murray.

Deng, M. T., Zhu, F., Yang, Y. Z., Yang, F. X., Hao, J. P., Chen, S. R., & Hou, Z. C. (2019). Genome-wide association study reveals novel loci associated with body size and carcass yields in Pekin ducks. *BMC Genomics, 20*(1), 1. https://doi.org/10.1186/s12864-018-5379-1

Domyan, E. T., Guernsey, M. W., Kronenberg, Z., Krishnan, S., Boissy, R. E., Vickrey, A. I., Rodgers, C., Cassidy, P., Leachman, S., Fondon, J., Yandell, M., & Shapiro, M. D. (2014). Epistatic and combinatorial effects of pigmentary gene mutations in the domestic pigeon. *Current Biology*, *24*(4), 459–464. https://doi.org/10.1016/j.cub.2014.01.020

Domyan, E. T., Kronenberg, Z., Infante, C. R., Vickrey, A. I., Stringham, S. A., Bruders, R., Guernsey, M. W., Park, S., Payne, J., Beckstead, R. B., Kardon, G., Menke, D. B., Yandell, M., & Beckstead, R. B. (2016b). Molecular shifts in limb identity underlie development of feathered feet in two domestic avian species. *eLife*, *5*, (2016–02-19), 5. https://doi.org/10.7554/eLife.12115

Domyan, E. T., & Shapiro, M. D. (2016a). Pigeonetics takes flight: Evolution, development, and genetics of intraspecific variation. *Developmental Biology*, *427*(2), 241–250. https://doi.org/10.1016/j.ydbio.2016.11.008

Eastwood, S. L., & Harrison, P. J. (2008). Decreased mRNA expression of netrin-G1 and netrin-G2 in the temporal lobe in schizophrenia and bipolar disorder. *Neuropsychopharmacology*, *33*(4), 933–945. https://doi.org/10.1038/sj.npp.1301457

El Bouchikhi, I., Belhassan, K., Moufid, F. Z., Iraqui Houssaini, M., Bouguenouch, L., Samri, I., Atmani, S., & Ouldim, K. (2016). Noonan syndrome-causing genes: Molecular update and an assessment of the mutation rate. *International Journal of Pediatrics and Adolescent Medicine*, *3*(4), 133–142. https://doi.org/10.1016/j.ijpam.2016.06.003

Feng, J., Craddock, N., Jones, I. R., Cook, E. H. Jr, Goldman, D., Heston, L. L., Peltonen, L., DeLisi, L. E., & Sommer, S. S. (2001). Systematic screening for mutations in the glycine receptor alpha2 subunit gene (GLRA2) in patients with schizophrenia and other psychiatric diseases. *Psychiatric Genetics*, *11*(1), 45–48. https://doi.org/10.1097/00041444-200103000-00009

Flori, L., Moazami-Goudarzi, K., Alary, V., Araba, A., Boujenane, I., Boushaba, N., Casabianca, F., Casu, S., Ciampolini, R., Coeur D'Acier, A., Coquelle, C., Delgado, J.-V., El-Beltagi, A., Hadjipavlou, G., Jousselin, E., Landi, V., Lauvie, A., Lecomte, P., Ligda, C., ... Gautier, M. (2019). A genomic map of climate adaptation in Mediterranean cattle breeds. *Molecular Ecology*, *28*(5), 1009–1029. https://doi.org/10.1111/mec.15004

Fogel, B. L., Wexler, E., Wahnich, A., Friedrich, T., Vijayendran, C., Gao, F., Parikshak, N., Konopka, G., & Geschwind, D. H. (2012). RBFOX1 regulates both splicing and transcriptional networks in human neuronal development. *Human Molecular Genetics 21*(19), 4171–4186. https://doi.org/10.1093/hmg/dds240

Fracasso, N. C. D. A., de Andrade, E. S., Wiezel, C. E. V., Andrade, C. C. F., Zanão, L. R., da Silva, M. S., Marano, L. A., Donadi, E. A., C. Castelli, E., Simões, A. L., & Mendes-Junior, C. T. (2016). Haplotypes from the SLC45A2 gene are associated with the presence of freckles and eye, hair and skin pigmentation in Brazil. *Legal Medicine*, *25*, 43–51. https://doi.org/10.1016/j.legalmed.2016.12.013

Fumagalli, M., Moltke, I., Grarup, N., Racimo, F., Bjerregaard, P., Jørgensen, M. E., Huerta-Sanchez, E., Schmidt, E. B., Pedersen, O.,

Hansen, T., Albrechtsen, A., & Nielsen, R. (2015). Greenlandic Inuit show genetic signatures of diet and climate adaptation. *Science*, *349*(6254), 1343–1347. https://doi.org/10.1126/science.aab2319

Gazda, M. A., Andrade, P., Afonso, S., Dilyte, J., Archer, J. P., Lopes, R. J., Faria, R., & Carneiro, M. (2018). Signatures of selection on standing genetic variation underlie athletic and navigational performance in racing pigeons. *Molecular Biology and Evolution*, *35*(5), 1176–1189. https://doi.org/10.1093/molbev/msy030

George, P., Hein, V. G., Shapiro, M. D., Gilbert, M. T. P., & Garrett, V. F. (2020). Darwin's fancy revised: an updated understanding of the genomic constitution of pigeon breeds. *Genome Biology and Evolution*, *12*(3), 136–150. https://doi.org/10.1093/gbe/evaa027

Ghoreishifar, S. M., Eriksson, S., Johansson, A. M., Khansefid, M., Moghaddaszadeh-Ahrabi, S., Parna, N., Davoudi, P., & Javanmard, A. (2020). Signatures of selection reveal candidate genes involved in economic traits and cold acclimation in five Swedish cattle breeds. *Genetics Selection Evolution*, *52*(1), 52. https://doi.org/10.1186/s12711-020-00571-5

Greenway, R., Barts, N., Henpita, C., Brown, A. P., Arias Rodriguez, L., Rodríguez Peña, C. M., Arndt, S., Lau, G. Y., Murphy, M. P., Wu, L., Lin, D., Shaw, J. H., Kelley, J. L., & Shaw, J. H. (2020). Convergent evolution of conserved mitochondrial pathways underlies repeated adaptation to extreme environments. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(28), 16424–16430. https://doi.org/10.1073/pnas.2004223117

Grilz-Seger, G., Neuditschko, M., Ricard, A., Velie, B., Lindgren, G., Mesarič, M., Cotman, M., Horna, M., Dobretsberger, M., Brem, G., & Druml, T. (2019). Genome-wide homozygosity patterns and evidence for selection in a set of European and Near Eastern horse breeds. *Genes (Basel)*, *10*(7), 491. https://doi.org/10.3390/genes10070491

Guernsey, M. W., Ritscher, L., Miller, M. A., Smith, D. A., Schöneberg, T., & Shapiro, M. D. (2013). A Val85Met mutation in melanocortin-1 receptor is associated with reductions in eumelanic pigmentation and cell surface expression in domestic rock pigeons (Columba livia). *PLoS One*, *8*(8), e74475. https://doi.org/10.1371/journal.pone.0074475

Gunnarsson, U., Hellstrom, A. R., Tixier-Boichard, M., Minvielle, F., BedHom, B., Ito, S., Jensen, P., Rattink, A., Vereijken, A., & Andersson, L. (2007). Mutations in SLC45A2 cause plumage color variation in chicken and Japanese quail. *Genetics*, *175*(2), 867–877. https://doi.org/10.1534/genetics.106.063107

Heller, S. A., Shih, R., Kalra, R., & Kang, P. B. (2020). Emery-Dreifuss muscular dystrophy. *Muscle & Nerve*, *61*(4), 436–448. https://doi.org/10.1002/mus.26782

Horikoshi, M., Yaghootkar, H., Mook-Kanamori, D. O., Sovio, U., Taal, H. R., Hennig, B. J., Bradfield, J. P., St Pourcain, B., Evans, D. M., Charoen, P., Kaakinen, M., Cousminer, D. L., Lehtimäki, T., Kreiner-Møller, E., Warrington, N. M., Bustamante, M., Feenstra, B., Berry, D. J., Thiering, E., … Freathy, R. M. (2013). New loci associated with birth weight identify genetic links between intrauterine growth and adult height and metabolism. *Nature Genetics*, *45*(1), 76–82. https://doi.org/10.1038/ng.2477

Huang, X., Zhang, Q., Gu, X., Hou, Y., Wang, M., Chen, X., & Wu, J. (2019). LPHN3 gene variations and susceptibility to ADHD in Chinese Han population: a two-stage case-control association study and gene-environment interactions. *European Child & Adolescent Psychiatry*, *28*(6), 861–873. https://doi.org/10.1007/s00787-018-1251-8

Hwang, I. W., Lim, M. H., Kwon, H. J., & Jin, H. J. (2015). Association of LPHN3 rs6551665 A/G polymorphism with attention deficit and hyperactivity disorder in Korean children. *Gene*, *566*(1), 68–73. https://doi.org/10.1016/j.gene.2015.04.033

Iijima, T., Yoda, S., & Fujiwara, H. (2019). The mimetic wing pattern of Papilio polytes butterflies is regulated by a doublesex-orchestrated gene network. *Communications Biology*, *2*, 257. https://doi.org/10.1038/s42003-019-0510-7

Issa, S., Bondurand, N., Faubert, E., Poisson, S., Lecerf, L., Nitschke, P., Deggouj, N., Loundon, N., Jonard, L., David, A., Sznajer, Y., Blanchet, P., & Pingault, V. (2017). EDNRB mutations cause Waardenburg syndrome type II in the heterozygous state. *Human Mutation*, *38*(5), 581–593. https://doi.org/10.1002/humu.23206

Julia, M., Gerd, R., & Joy, R. L. (2017). The orientation of homing pigeons (Columba livia f.d.) with and without navigational experience in a two-dimensional environment. *PLoS One*, *12*(11), e0188483. https://doi.org/10.1371/journal.pone.0188483

Kalaydjieva, L., & Chamova, T. (1993). Congenital Cataracts, Facial Dysmorphism, and Neuropathy. In M. P. Adam, H. H. Ardinger, R. A. Pagon, S. E. Wallace, L. J. H. Bean, K. Stephens, & A. Amemiya (Eds.), *GeneReviews(®)*. University of Washington, Seattle.

Keegan, N. P. (2020). Pseudoexons of the DMD gene. *Journal of Neuromuscular Diseases*, *7*(2), 77–95. https://doi.org/10.3233/jnd-190431

Kim, E., Elbeltagy, A. R., Aboulnaga, A. M., Rischkowsky, B., Sayre, B. L., Mwacharo, J. M., & Rothschild, M. F. (2016). Multiple genomic signatures of selection in goats and sheep indigenous to a hot arid environment. *Heredity*, *116*(3), 255–264. https://doi.org/10.1038/hdy.2015.94

Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics*, *25*(14), 1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., & Durbin, R., Genome Project Data Processing, S (2009). The Sequence Alignment/Map format and SAMtools. *Bioinformatics*, *25*(16), 2078–2079. https://doi.org/10.1093/bioinformatics/btp352

Li, M., Tian, S., Jin, L., Zhou, G., Li, Y., Zhang, Y., Wang, T., Yeung, C. K. L., Chen, L., Ma, J., Zhang, J., Jiang, A., Li, J. I., Zhou, C., Zhang, J., Liu, Y., Sun, X., Zhao, H., Niu, Z., … Li, R. (2013). Genomic analyses identify distinct patterns of selection in domesticated pigs and Tibetan wild boars. *Nature Genetics*, *45*(12), 1431–1438. https://doi.org/10.1038/ng.2811

Li, M., Tian, S., Yeung, C. K., Meng, X., Tang, Q., Niu, L., Wang, X., Jin, L., Ma, J., Long, K., Zhou, C., Cao, Y., Zhu, L. I., Bai, L., Tang, G., Gu, Y., Jiang, An'an, Li, X., & Li, R. (2014). Whole-genome sequencing of Berkshire (European native pig) provides insights into its origin and domestication. *Scientific Reports*, *4*, 4678. https://doi.org/10.1038/srep04678

Liang, D., Zhao, P., Si, J., Fang, L., Pairo-Castineira, E., Hu, X., Xu, Q., Hou, Y., Gong, Y., Liang, Z., Tian, B., Mao, H., Yindee, M., Faruque, M. O., Kongvongxay, S., Khamphoumee, S., Liu, G. E., Wu, D.-D., Barker, J. S. F., … Zhang, Y. (2020). Genomic analysis revealed a convergent evolution of LINE-1 in coat color: A case study in water buffaloes (Bubalus bubalis). *Molecular Biology and Evolution*, *38*, 1122–1136. https://doi.org/10.1093/molbev/msaa279

Liang, Y. Y., Gui Qiang, L., Daohua, H., Zewu, W., & Yitian, C. (2019). Protection, utilization and development of meat pigeon resources in Kashgar of Xinjiang. *Guangdong Feed*, *28*(06), 14–16. (in Chinese).

Liu, X., Zhang, Y., Li, Y., Pan, J., Wang, D., Chen, W., Zheng, Z., He, X., Zhao, Q., Pu, Y., Guan, W., Han, J., Orlando, L., Ma, Y., & Jiang, L. (2019). EPAS1 gain-of-function mutation contributes to high-altitude adaptation in Tibetan horses. *Molecular Biology and Evolution*, *36*(11), 2591–2603. https://doi.org/10.1093/molbev/msz158

Liu, Z., Zhang, L., Yan, Z., Ren, Z., Han, F., Tan, X., Xiang, Z., Dong, F., Yang, Z., Liu, G., Wang, Z., Zhang, J., Que, T., Tang, C., Li, Y., Wang, S., Wu, J., Li, L., Huang, C., … Li, M. (2020). Genomic mechanisms of physiological and morphological adaptations of limestone langurs to karst habitats. *Molecular Biology and Evolution*, *37*(4), 952–968. https://doi.org/10.1093/molbev/msz301

Loureno, G. J., Oliveira, C., Carvalho, B. S., Torricelli, C., & Lima, C. S. P. (2020). Inherited variations in human pigmentation-related genes modulate cutaneous melanoma risk and clinicopathological

features in Brazilian population. *Scientific Reports*, *10*(1), 12129. https://doi.org/10.1038/s41598-020-68945-9

Magalhaes, J., Gegg, M. E., Migdalska-Richards, A., & Schapira, A. H. (2018). Effects of ambroxol on the autophagy-lysosome pathway and mitochondria in primary cortical neurons. *Scientific Reports*, *8*(1), 1385. https://doi.org/10.1038/s41598-018-19479-8

Mainuer Slamu, G. Y. (2017). The characteristics and current situation of Tarim pigeon. *China Livestock and Poultry Breeding*, *13*(005), 139. (in Chinese).

Martin, A., & Reed, R. D. (2014). Wnt signaling underlies evolution and development of the butterfly wing pattern symmetry systems. *Developmental Biology*, *395*(2), 367–378. https://doi.org/10.1016/j.ydbio.2014.08.031

McLatchie, L. M., Fraser, N. J., Main, M. J., Wise, A., Brown, J., Thompson, N., Solari, R., Lee, M. G., & Foord, S. M. (1998). RAMPs regulate the transport and ligand specificity of the calcitonin-receptor-like receptor. *Nature*, *393*(6683), 333–339. https://doi.org/10.1038/30666

McQuillan, R., Leutenegger, A. L., Abdel-Rahman, R., Franklin, C. S., Pericic, M., Barac-Lauc, L., Smolej-Narancic, N., Janicijevic, B., Polasek, O., Tenesa, A., MacLeod, A. K., Farrington, S. M., Rudan, P., Hayward, C., Vitart, V., Rudan, I., Wild, S. H., Dunlop, M. G., Wright, A. F., … Wilson, J. F. (2008). Runs of homozygosity in European populations. *The American Journal of Human Genetics*, *83*(3), 359–372. https://doi.org/10.1016/j.ajhg.2008.08.007

Metallinos, D. L., Bowling, A. T., & Rine, J. (1998). A missense mutation in the endothelin-B receptor gene is associated with Lethal White Foal Syndrome: an equine version of Hirschsprung Disease. *Mammalian Genome*, *9*(6), 426–431. https://doi.org/10.1007/s003359900790

Miwa, M., Inoue-Murayama, M., Aoki, H., Kunisada, T., Hiragaki, T., Mizutani, M., & Ito, S. (2007). Endothelin receptor B2 (EDNRB2) is associated with the panda plumage colour mutation in Japanese quail. *Animal Genetics*, *38*(2), 103–108. https://doi.org/10.1111/j.1365-2052.2007.01568.x

Miwa, M., Inoue-Murayama, M., Kobayashi, N., Kayang, B. B., & Ito, S. I. (2006). Mapping of panda plumage color locus on the microsatellite linkage map of the Japanese quail. *BMC Genetics*, *7*, 1–5.

Morimoto, N., Mutai, H., Namba, K., Kaneko, H., Kosaki, R., & Matsunaga, T. (2018). Homozygous EDNRB mutation in a patient with Waardenburg syndrome type 1. *Auris, Nasus, Larynx*, *45*(2), 222–226. https://doi.org/10.1016/j.anl.2017.03.022

Moscatelli, G., Bovo, S., Schiavo, G., Mazzoni, G., Bertolini, F., Dall'Olio, S., & Fontanesi, L. (2020). Genome-wide association studies for iris pigmentation and heterochromia patterns in Large White pigs. *Animal Genetics*, *51*(3), 409–419. https://doi.org/10.1111/age.12930

Mountjoy, K. G., Robbins, L. S., Mortrud, M. T., & Cone, R. D. (1992). The cloning of a family of genes that encode the melanocortin receptors. *Science*, *257*(5074), 1248–1251. https://doi.org/10.1126/science.1325670

Oribe, E., Fukao, A., Yoshihara, C., Mendori, M., Rosal, K. G., Takahashi, S., & Takeuchi, S. (2012). Conserved distal promoter of the agouti signaling protein (ASIP) gene controls sexual dichromatism in chickens. *General and Comparative Endocrinology*, *177*(2), 231–237. https://doi.org/10.1016/j.ygcen.2012.04.016

Patterson, N., Price, A. L., & Reich, D. (2006). Population structure and eigenanalysis. *PLoS Genetics*, *2*(12), e190. https://doi.org/10.1371/journal.pgen.0020190

Pomianowski, J., Mikulski, D., Pudyszak, K., Cooper, R. G., Angowski, M., Joźwik, A., & Horbanczuk, J. O. (2009). Chemical composition, cholesterol content, and fatty acid profile of pigeon meat as influenced by meat-type breeds. *Poultry Science*, *88*(6), 1306–1309. https://doi.org/10.3382/ps.2008-00217

Price, T. D. (2002). Domesticated birds as a model for the genetics of speciation by sexual selection. *Genetica*, *116*(2–3), 311–327.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A., Bender, D., Maller, J., Sklar, P., de Bakker, P. I. W., Daly, M. J., & Sham, P. C. (2007). PLINK: a tool set for whole-genome association and population-based linkage analyses. *The American Journal of Human Genetics*, *81*(3), 559–575. https://doi.org/10.1086/519795

Qiu, Q., Wang, L., Wang, K., Yang, Y., Ma, T., Wang, Z., Zhang, X., Ni, Z., Hou, F., Long, R., Abbott, R., Lenstra, J., & Liu, J. (2015). Yak whole-genome resequencing reveals domestication signatures and prehistoric population expansions. *Nature Communications*, *6*, 10283. https://doi.org/10.1038/ncomms10283

Quaio, C. R., de Almeida, T. F., Brasil, A. S., Pereira, A. C., Jorge, A. A., Malaquias, A. C., Kim, C. A., Bertola, D. R. (2013). Tegumentary manifestations of Noonan and Noonan-related syndromes. *Clinics (Sao Paulo)*, *68*(8), 1079–1083. https://doi.org/10.6061/clinics/2013(08)03

Rehkämper, G., Frahm, H. D., & Cnotka, J. (2007). Mosaic evolution and adaptive brain component alteration under domestication seen on the background of evolutionary theory. *Brain, Behavior and Evolution*, *71*(2), 115–126. https://doi.org/10.1159/000111458

Robbins, L. S., Nadeau, J. H., Johnson, K. R., Kelly, M. A., Roselli-Rehfuss, L., Baack, E., Mountjoy, K. G., & Cone, R. D. (1993). Pigmentation phenotypes of variant extension locus alleles result from point mutations that alter MSH receptor function. *Cell*, *72*(6), 827–834. https://doi.org/10.1016/0092-8674(93)90572-8

Robic, A., Morisson, M., Leroux, S., Gourichon, D., Vignal, A., Thebault, N., Fillon, V., Minvielle, F., Bed'Hom, B., Zerjal, T., Pitel, F. (2019). Two new structural mutations in the 5' region of the ASIP gene cause diluted feather color phenotypes in Japanese quail. *Genetics Selection Evolution*, *51*(1), 12. https://doi.org/10.1186/s12711-019-0458-6

Rubin, C. J., Megens, H. J., Martinez Barrio, A., Maqbool, K., Sayyab, S., Schwochow, D., Wang, C., Carlborg, O., Jern, P., Jorgensen, C. B., Archibald, A. L., Fredholm, M., Groenen, M. A. M., & Andersson, L. (2012). Strong signatures of selection in the domestic pig genome. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(48), 19529–19536. https://doi.org/10.1073/pnas.1217149109

Sandra, M., Maria Pia, L., Stefano, C., Pietro, P., Crociani, P., Aldo, R., Giuseppe, D. S., Massimo, C. (2019). Emery-Dreifuss muscular dystrophy type 4: A new SYNE1 mutation associated with hypertrophic cardiomyopathy masked by a perinatal distress-related spastic diplegia. *Clinical Case Reports*, *7*(5), 1078–1082. https://doi.org/10.1002/ccr3.2140

Santschi, E. M., Purdy, A. K., Valberg, S. J., Vrotsos, P. D., Kaese, H., & Mickelson, J. R. (1998). Endothelin receptor B polymorphism associated with lethal white foal syndrome in horses. *Mammalian Genome*, *9*(4), 306–309. https://doi.org/10.1007/s003359900754

Sasaki, T., Mann, R. P., Warren, K. N., Herbert, T., & Biro, D. (2018). Personality and the collective: Exploratory homing pigeons occupy higher leadership ranks in flocks. *Philosophical Transactions of the Royal Society of London*, *373*(1746), 1–8. https://doi.org/10.1098/rstb.2017.0038

Sendell-Price, A. T., Ruegg, K. C., & Clegg, S. M. (2020). Rapid morphological divergence following a human-mediated introduction: the role of drift and directional selection. *Heredity (Edinb)*, *124*(4), 535–549. https://doi.org/10.1038/s41437-020-0298-8

Shao, Y., Tian, H. Y., Zhang, J. J., Kharrati-Koopaee, H., Guo, X., Zhuang, X. L., Li, M.-L., Nanaie, H. A., Dehghani Tafti, E., Shojaei, B., Reza Namavar, M., Sotoudeh, N., Oluwakemi Ayoola, A., Li, J.-L., Liang, B., Esmailizadeh, A., Wang, S., & Wu, D. D. (2020). Genomic and phenotypic analyses reveal mechanisms underlying homing ability in pigeon. *Molecular Biology and Evolution*, *37*(1), 134–148. https://doi.org/10.1093/molbev/msz208

Shapiro, M. D., Kronenberg, Z., Li, C., Domyan, E. T., Pan, H., Campbell, M., Tan, H., Huff, C. D., Hu, H., Vickrey, A. I., Nielsen, S. C. A., Stringham, S. A., Hu, H., Willerslev, E., Gilbert, M. T. P., Yandell, M., Zhang, G., & Wang, J. (2013). Genomic diversity and evolution of the head crest in the rock pigeon. *Science*, *339*(6123), 1063–1067. https://doi.org/10.1126/science.1230422

Srikanth, K., Kim, N. Y., Park, W., Kim, J. M., Kim, K. D., Lee, K. T., Son, J.-H., Chai, H.-H., Choi, J.-W., Jang, G.-W., Kim, H., Ryu, Y.-C., Nam, J.-W., Park, J.-E., Kim, J.-M., & Lim, D. (2019). Comprehensive genome and transcriptome analyses reveal genetic relationship, selection signature, and transcriptome landscape of small-sized Korean native Jeju horse. *Scientific Reports*, *9*(1), 16672. https://doi.org/10.1038/s41598-019-53102-8

Stilling, F., Wallenius, S., Michaëlsson, K., Dalgård, C., Brismar, K., & Wolk, A. (2017). High insulin-like growth factor-binding protein-1 (IGFBP-1) is associated with low relative muscle mass in older women. *Metabolism*, *73*, 36–42. https://doi.org/10.1016/j.metabol.2017.04.013

Stringham, S. A., Mulroy, E. E., Xing, J., Record, D., Guernsey, M. W., Aldenhoven, J. T., Osborne, E., & Shapiro, M. D. (2012). Divergence, convergence, and the ancestry of feral populations in the domestic rock pigeon. *Current Biology*, *22*(4), 302–308. https://doi.org/10.1016/j.cub.2011.12.045

Tan Rui, C. Y. (2011). Protection and utilization of local poultry genetic resources in Xinjiang. *Chinese Poultry*, *33*(9), 55–57. (in Chinese).

Tan, Y. Q., Tan, Y. Q., & Cheng, D. H. (2020). Whole-genome mate-pair sequencing of apparently balanced chromosome rearrangements reveals complex structural variations: two case studies. *Mol Cytogenet*, *13*, 15. https://doi.org/10.1186/s13039-020-00487-1

Tang, H., Peng, J., Wang, P., & Risch, N. J. (2005). Estimation of individual admixture: Analytical and study design considerations. *Genetic Epidemiology*, *28*(4), 289–301. https://doi.org/10.1002/gepi.20064

Thota, C., Gangula, P. R., Dong, Y. L., & Yallampalli, C. (2003). Changes in the expression of calcitonin receptor-like receptor, receptor activity-modifying protein (RAMP) 1, RAMP2, and RAMP3 in rat uterus during pregnancy, labor, and by steroid hormone treatments. *Biology of Reproduction*, *69*(4), 1432–1437. https://doi.org/10.1095/biolreprod.103.015628

Tigano, A., & Friesen, V. L. (2016). Genomics of local adaptation with gene flow. *Molecular Ecology*, *25*(10), 2144–2164. https://doi.org/10.1111/mec.13606

Tsai, P. S., Garcia-Gil, N., van Haeften, T., & Gadella, B. M. (2010). How pig sperm prepares to fertilize: stable acrosome docking to the plasma membrane. *PLoS One*, *5*(6), e11204. https://doi.org/10.1371/journal.pone.0011204

Van Haute, L., Hendrick, A. G., D'Souza, A. R., Powell, C. A., Rebelo-Guiomar, P., Harbour, M. E., Ding, S., Fearnley, I. M., Andrews, B., & Minczuk, M. (2019). METTL15 introduces N4-methylcytidine into human mitochondrial 12S rRNA and is required for mitoribosome biogenesis. *Nucleic Acids Research*, *47*(19), 10267–10281. https://doi.org/10.1093/nar/gkz735

Vickrey, A. I., Domyan, E. T., Horvath, M. P., & Shapiro, M. D. (2015). Convergent evolution of head crests in two domesticated columbids is associated with different missense mutations in EphB2. *Molecular Biology and Evolution*, *32*(10), 2657–2664. https://doi.org/10.1093/molbev/msv140

Vickrey, A. I., Rebecca, B., Zev, K., Emma, M., Bohlender, R. J., Maclary, E. T., Maynez, R., Osborne, E. J., Johnson, K. P., Huff, C. D., Yandell, M., & Shapiro, M. D. (2018). Introgression of regulatory alleles and a missense coding mutation drive plumage pattern diversity in the rock pigeon. *eLife*, *7*, e34803. https://doi.org/10.7554/eLife.34803

Wang, K., Li, M., & Hakonarson, H. (2010). ANNOVAR: functional annotation of genetic variants from high-throughput sequencing data. *Nucleic Acids Research*, *38*(16), e164. https://doi.org/10.1093/nar/gkq603

Wei, C., Wang, H., Liu, G., Zhao, F., Kijas, J. W., Ma, Y., Lu, J., Zhang, L. I., Cao, J., Wu, M., Wang, G., Liu, R., Liu, Z., Zhang, S., Liu, C., & Du, L. (2016). Genome-wide analysis reveals adaptation to high altitudes in Tibetan sheep. *Scientific Reports*, *6*, 26770. https://doi.org/10.1038/srep26770

Wei, X., Zhou, J. L., Nai, W. H., Zeng, Y. Y., Fan, W., & Li, B. (2019). Chemical characteristics and sources of groundwater sulfate in the Kashgar delta, Xinjiang. *Huan Jing Ke Xue*, *40*(8), 3550–3558. https://doi.org/10.13227/j.hjkx.201812130

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*(6), 1358–1370. https://doi.org/10.1111/j.1558-5646.1984.tb05657.x

Wilcox, J. A., & Quadri, S. (2014). Replication of NTNG1 association in schizophrenia. *Psychiatric Genetics*, *24*(6), 266–268. https://doi.org/10.1097/ypg.0000000000000061

Wilkinson, S., Lu, Z. H., Megens, H. J., Archibald, A. L., Haley, C., Jackson, I. J., Groenen, M. A. M., Crooijmans, R. P. M. A., Ogden, R., & Wiener, P. (2013). Signatures of diversifying selection in European pig breeds. *PLoS Genetics*, *9*(4), e1003453. https://doi.org/10.1371/journal.pgen.1003453

Wood, A. R., Esko, T., Yang, J., Vedantam, S., Pers, T. H., Gustafsson, S., Chu, A. Y., Estrada, K., Luan, J., Kutalik, Z., Amin, N., Buchkovich, M. L., Croteau-Chonka, D. C., Day, F. R., Duan, Y., Fall, T., Fehrmann, R., Ferreira, T., Jackson, A. U., … Frayling, T. M. (2014). Defining the role of common variation in the genomic and biological architecture of adult human height. *Nature Genetics*, *46*(11), 1173–1186. https://doi.org/10.1038/ng.3097

Wright, J. T., Grange, D. K., & Fete, M. (1993). Hypohidrotic Ectodermal Dysplasia. In M. P. Adam, H. H. Ardinger, R. A. Pagon, S. E. Wallace, L. J. H. Bean, K. Stephens, & A. Amemiya (Eds.), *GeneReviews(®)*. University of Washington, Seattle.

Xu, L., Bickhart, D. M., Cole, J. B., Schroeder, S. G., Song, J., Tassell, C. P., Sonstegard, T. S., & Liu, G. E. (2015). Genomic signatures reveal new evidences for selection of important traits in domestic cattle. *Molecular Biology and Evolution*, *32*(3), 711–725. https://doi.org/10.1093/molbev/msu333

Yang, L., Zheng, X., Mo, C., Li, S., & Mou, C. (2020). Transcriptome analysis and identification of genes associated with chicken sperm storage duration. *Poultry Science*, *99*(2), 1199–1208. https://doi.org/10.1016/j.psj.2019.10.021

Yang, Y. M., Yan, K., Liu, B., Chen, M., Wang, L. Y., Huang, Y. Z., Qian, Y.-Q., Sun, Y.-X., Li, H.-G., & Dong, M. Y. (2019). Comprehensive genetic diagnosis of patients with Duchenne/Becker muscular dystrophy (DMD/BMD) and pathogenicity analysis of splice site variants in the DMD gene. *Journal of Zhejiang University-SCIENCE B*, *20*(9), 753–765. https://doi.org/10.1631/jzus.B1800541

Ye, M., Xu, M., Chen, C., He, Y., Ding, M., Ding, X., Wei, W., Yang, S., Zhou, B. (2018). Expression analyses of candidate genes related to meat quality traits in squabs from two breeds of meat-type pigeon. *Journal of Animal Physiology and Animal Nutrition*, *102*(3), 727–735. https://doi.org/10.1111/jpn.12869

Yu, B., Ma, J., Li, J., Wang, D., Wang, Z., & Wang, S. (2020). Mitochondrial phosphatase PGAM5 modulates cellular senescence by regulating mitochondrial dynamics. *Nature Communications*, *11*(1), 2549. https://doi.org/10.1038/s41467-020-16312-7

Yu, L., Wang, G. D., Ruan, J., Chen, Y. B., Yang, C. P., Cao, X., Wu, H., Liu, Y.-H., Du, Z.-L., Wang, X.-P., Yang, J., Cheng, S.-C., Zhong, L. I., Wang, L. U., Wang, X., Hu, J.-Y., Fang, L. U., Bai, B., Wang, K.-L., … Zhang, Y. P. (2016). Genomic analysis of snub-nosed monkeys (Rhinopithecus) identifies genes and processes related to high-altitude adaptation. *Nature Genetics*, *48*(8), 947–952. https://doi.org/10.1038/ng.3615

Yurchenko, A. A., Deniskova, T. E., Yudin, N. S., Dotsev, A. V., Khamiruev, T. N., Selionova, M. I., Egorov, S. V., Reyer, H., Wimmers, K., Brem, G., Zinovieva, N. A., & Larkin, D. M. (2019). High-density genotyping reveals signatures of selection related to acclimation and economically important traits in 15 local sheep breeds from Russia. *BMC Genomics*, *20*(Suppl 3), 294. https://doi.org/10.1186/s12864-019-5537-0

Zhang, H., Yu, J. Q., Yang, L. L., Kramer, L. M., Zhang, X. Y., Na, W., Reecy, J. M., & Li, H. (2017). Identification of genome-wide SNP-SNP interactions associated with important traits in chicken. *BMC Genomics*, *18*(1), 892. https://doi.org/10.1186/s12864-017-4252-y

Zhang, W., Yang, M., Zhou, M., Wang, Y., Wu, X., Zhang, X., Ding, Y., Zhao, G., Yin, Z., & Wang, C. (2020). Identification of Signatures of Selection by Whole-Genome Resequencing of a Chinese Native Pig. *Front Genet*, *11*, 566255. https://doi.org/10.3389/fgene.2020.566255

Zhang, X., Li, W., Liu, C., Peng, X., Lin, J., He, S., Li, X., Han, B., Zhang, N., Wu, Y., Chen, L., Wang, L., MaYila, Huang, J., & Liu, M. (2017). Alteration of sheep coat color pattern by disruption of ASIP gene via CRISPR Cas9. *Scientific Reports*, *7*(1), 8149. https://doi.org/10.1038/s41598-017-08636-0

Zhang, Z., Jia, Y., Almeida, P., Mank, J. E., van Tuinen, M., Wang, Q., Jiang, Z., Chen, Y. U., Zhan, K., Hou, S., Zhou, Z., Li, H., Yang, F., He, Y., Ning, Z., Yang, N., & Qu, L. (2018). Whole-genome resequencing reveals signatures of selection and timing of duck domestication. *Gigascience*, *7*(4), 1–12. https://doi.org/10.1093/gigascience/giy027

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Hou, H., Wang, X., Ding, W., Xiao, C., Cai, X., Lv, W., Tu, Y., Zhao, W., Yao, J., & Yang, C. (2022). Whole-genome sequencing reveals the artificial selection and local environmental adaptability of pigeons (*Columba livia*). *Evolutionary Applications*, 15, 603–617. https://doi.org/10.1111/eva.13284