



新疆地方鸡遗传关系和基因组差异研究

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摘 要: 旨在揭示拜城油鸡、和田鸡和吐鲁番鸡等3种新疆地方鸡相互之间的遗传关系和基因组差异, 从而在基因组层面为新疆地方鸡遗传资源的保护与开发提供科学依据。本研究以65份鸡的全基因组重测序数据为对象, 借助Rstudio、Plink、Pedstats等软件对数据实施过滤处理; 通过状态同源(identical by state, IBS)多维标度分析不同鸡种的群体遗传结构, 利用Treemix及Dsuite开展基因渗入(gene introgression)分析, 采用群体间单倍体扩增纯合性检测(cross population extended haplotype homozygosity, XP-EHH)及跨群体的符合似然比检验(cross population composite likelihood ratio test, XP-CLR)挖掘选择信号。数据质控后, 10 228 705个常染色体的单核苷酸多态位点(single nucleotide polymorphism, SNP)用于基因渗入和选择信号的研究, 4 657 217个最小等位基因频率(minor allele frequency, MAF) ≥ 0.2 的常染色体SNPs则被用来进行遗传关系分析。群体遗传关系分析显示, 拜城油鸡和吐鲁番鸡的遗传距离最远, 遗传分化系数达到(genetic differentiation coefficient, F_{ST}) 0.077 7, 和田鸡与拜城油鸡及吐鲁番鸡的遗传距离较近, F_{ST} 分别为0.053 5和0.056 3。且和田鸡与吐鲁番鸡之间存在一次基因渗入, 渗入信号最强的区域位于4号染色体, 该区域包含*ABLIM2*等与耐热性能相关的基因。而在拜城油鸡与吐鲁番鸡的选择信号分析中, 共筛选出70个参与关键生物学进程的候选基因。其中,*CLCN6*、*ACTA2*、*CRIM1*、*IARS2*等基因可能与耐热性能相关; *BNIP2*、*DTNA*、*RAB3GAP2*等基因可能涉及肌肉生长调控; *AGMO*、*TSNARE1*等基因则可能与斗鸡攻击性行为的形成有关。研究清晰地揭示了新疆3种地方鸡种之间存在的遗传关系, 发现了和田鸡与吐鲁番鸡之间存在的基因组渗入区域及相关基因, 鉴定了拜城油鸡和吐鲁番鸡之间的基因组选择区域及其中包括的与耐热性、肌肉生长、斗鸡攻击性行为等特色性状相关的候选基因, 从而为新疆地方鸡种特色性状的保护和利用提供分子依据。

关键词: 全基因组重测序; 鸡; 遗传结构; 基因渗入; 选择信号

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Study on Genetic Relationships and Genomic Differences of Local Chicken Breeds in Xinjiang

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Abstract: This study aimed to reveal the genetic relationships and genomic differences among 3 Xinjiang local chicken breeds including Baicheng-You chickens, Hetian chickens, and Tulufan chickens, so as to provide references for the protection and utilization of genetic resources of local domestic chickens in Xinjiang at the genomic level. The research took 65 chickens whole-genome

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resequencing datasets as the research objects and utilized softwares such as Rstudio, Plink, and Pedstats to filter the data. The population genetic structure of different chicken breeds was analyzed through identical by state (IBS) multi-dimensional scaling. Gene infiltration analysis was carried out using Treemix and Dsuite. The selection signals were mined by using the cross population extended haplotype homozygosity (XP-EHH) and cross population composite likelihood ratio test (XP-CLR) methods. After filtering, a total of 10 228 705 autosomal single nucleotide polymorphisms (SNPs) were obtained for analyzing the introgression and selection signals, while 4 657 217 autosomal SNPs with minor allele frequency (MAF) ≥ 0.2 were used for genetic relationship analysis. The results of genetic relationship showed that the genetic distance between Baicheng-You and Tulufan chickens was farthest, and their genetic differentiation coefficient (F_{ST}) was 0.077 7, while the genetic distance between Hetian and Baicheng-You, Tulufan chickens were close and the F_{ST} was 0.053 5 and 0.056 3, respectively. Furthermore, there was an introgression event between Hetian and Tulufan chickens. The highest score of introgression region located in the chromosome 4, which contained some genes associated with heat tolerance, such as *ABLM2*. While selection signals analysis between Baicheng-You and Tulufan chickens identified 70 candidate genes involved in important biological processes. Among them, genes such as *CLCN6*, *ACTA2*, *CRIM1*, and *IARS2* might be related to the heat resistance performance; Genes such as *BNIP2*, *DTNA*, and *RAB3GAP2* might be involved in the regulation of muscle growth; Genes such as *AGMO*, *TSNARE1* might be related to the formation of aggressive behavior in cockfighting. The research clearly revealed the genetic relationships among 3 local chicken breeds in Xinjiang, discovered the genomic infiltration regions and related genes between the Hetian and Tulufan chickens, and identified the genomic selection regions between the Baicheng-You and Tulufan chickens and the candidate genes related to characteristic traits such as heat tolerance, muscle growth, and aggressive behavior of fighting chickens. Thus providing molecular basis for the protection and utilization of the characteristic traits of chicken breeds in Xinjiang.

Keywords: whole genome resequencing; chickens; genetic structure; gene introgression; selection signal

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新疆地区拥有丰富的地方鸡种资源,包括拜城油鸡、和田鸡、吐鲁番鸡等多个具有独特种质特性的国家级地方鸡品种^[1-2]。其中拜城油鸡原产于新疆阿克苏地区拜城县,骨细肉多,肉味鲜美,育肥后的拜城油鸡皮下均匀分布一层脂肪,因此得名油鸡^[2]。吐鲁番鸡原产于新疆吐鲁番盆地,是中国斗鸡的重要品种之一,它以体大、健壮、善斗著称,具有耐高温干旱,抗病力强等特性^[2]。和田鸡产于民丰、洛浦两县,具有耐粗饲、耐高温干旱、抗病力强等特点^[2]。然而由于长期散养在民间,保种意识和措施欠缺,导致基因混杂问题突出,纯种鸡群数量呈现持续下降趋势^[3],解析其品种之间的遗传关系和特征性状相关的分子基础对于新疆地方鸡品种的保护及利用具有重要的科学意义和应用价值。

目前,对于新疆地方鸡品种的研究多集中在其

生长和肉蛋性状等方面,如汪家骏等^[4]探讨了拜城油鸡不同时期脂肪代谢相关基因的表达规律。古丽娜·巴克和赵晨名^[5]分析了 *A-FABP* 和 *H-FABP* 基因在和田鸡与吐鲁番鸡中的表达模式及其与肌肉脂肪 (intramuscular fat, IMF) 沉积的相关性。而 Wang 等^[6]从全基因组层面揭示了含拜城油鸡、和田鸡等 10 个中国土鸡品种与体重相关的选择区域与候选基因。Zhang 等^[7]则从脂质组学角度阐释了和田鸡蛋黄质地的优异表现。尽管上述研究在生长和肉蛋性状方面取得了进展,但对于新疆地方鸡在抗逆性等特色性状方面的遗传机制仍缺乏系统解析。

近年来,全基因组重测序技术为系统挖掘种质资源特征性状的遗传基础提供了有效手段。该技术在是在已知参考基因组的前提下,针对某物种的不同个体或群体开展基因组层面的测序工作,可在

基因组层面系统解析不同品种鸡的遗传差异,为鸡特色性状的育种研究提供潜在的分子标记资源^[8-10]。因此,本研究利用65只鸡的基因组重测序数据,系统剖析了新疆3种地方鸡的群体遗传结构,揭示了品种间的基因交流模式及选择信号特征,以期从基因组水平为新疆地方鸡特色种质资源的保护与利用提供科学依据。

1 材料与方法

1.1 数据集来源信息

本研究共整合65份鸡的全基因组重测序数据,其中31只拜城油鸡数据来源于SRA数据库(PRJNAT792508)^[11],19只和田鸡、8只吐鲁番鸡和7只绿原鸡数据均取自Chicken SD数据库(<http://bigd.big.ac.cn/chickensd/>)^[12]。拜城油鸡样本采自新疆拜城油鸡保种场、和田鸡与吐鲁番鸡分别源自新疆和田与吐鲁番地区、绿原鸡则来自印度尼西亚巴厘岛及中爪哇地区。在测序方面,拜城油鸡DNA取自血样并经苯酚-氯仿法提取,质检、建库后于Illumina NovaSeq 6000平台完成测序^[11];和田鸡、吐鲁番鸡和绿原鸡的DNA取自血液或肌肉并经苯酚-氯仿法提取,质检、建库后在Illumina HiSeq/NextSeq平台进行测序^[12]。

1.2 SNP标记的开发、注释及过滤

对下载的原始测序数据进行质控,具体标准如下:1)过滤含有接头序列的reads;2)剔除N碱基占比超过10%的reads;3)去除低质量reads(其中质量值 $Q \leq 3$ 的碱基数量占该read总碱基数量的50%以上)。随后借助Burrows-Wheeler Aligner v0.7.15软件^[13]的mem-t命令,把得到的Clean reads与鸡参考基因组(Gallus gallus_GRCg6a版本)进行序列比对,并使用PICARD 1.57软件的MarkDuplicates命令(github.com/broadinstitute/picard),对重复序列进行标记并剔除。使用GATK 4.0.0.0软件进行SNP calling^[14],具体参数如下:“QD<2.0”,“FS>200.0”,“SOR>10.0”,“MQRankSum<-12.5”,“ReadPosRankSum<-8.0”。使用PLINK v1.90对SNPs进行过滤,在缺失率GENO<0.15的前提下,保留最小等位基因频率(minor allele frequency, MAF)>0.1的SNPs^[15],再利用PEDSTATS 0.6.12程序对常染色体位点实施哈迪-温伯格平衡(Hardy-Weinberg equilibrium, HWE)筛选,设定筛选阈值为HWE<0.01^[16]。

1.3 群体遗传结构分析

运用RStudio软件中的“adeigenet”包测算群体内平均基因多样性(heterozygosity, Hs)^[17],分别运用PLINK v1.90软件的--het和--cluster--matrix命令计算观测杂合度(observed heterozygosity, Ho)和状态同源(identical by state, IBS)的多维标度^[15]。采用VCFTOOLS 0.1.15软件中的--weir-fst-pop参数测算两个群体间的遗传分化系数(genetic differentiation coefficient, F_{ST})^[18]。

1.4 基因渗入分析

研究选取与新疆鸡种遗传距离较远且无明显亲缘关系的绿原鸡作为外群,使用Dsuite的Dtrios命令计算拜城油鸡、和田鸡和吐鲁番鸡两两组合间的f4统计量和D统计量^[19],在f4统计分析中,正值意味不同群体间有基因流动现象。同时借助Dsuite软件的Dtrios命令,对每个滑动窗口的距离分数d_f进行测算^[20],设定窗口大小5 000 bp,步长500 bp,通过RStudio中的“scale”函数对距离分数d_f进行标准化处理,将标准化后d_f值处于前1%的区域确定为候选渗入区域^[21]。此外,本研究运用Treemix软件开展基因流分析,并借助RStudio的“plot_tree”函数,将分析结果可视化呈现为最大似然树图谱^[22]。

1.5 选择信号分析

本研究采用两种方法分析新疆不同鸡种间的选择区域及候选基因,一种方法是基于连锁不平衡的群体间单倍体扩增纯合性检测(cross population extended haplotype homozygosity, XP-EHH),具体步骤如下:1)使用Beagle 4.1软件的java-Xmx[GB] g-jar beagle.jar命令对VCF文件进行单倍体分型,随后在SELSCAN 1.3.0上使用selscan xp-ehh程序计算每个SNP的XP-EHH值^[23-24],由于XP-EHH的正负值仅由计算时参考群体与观察群体的选择方向决定,且该值无需标准化处理,因此后续研究采用绝对|XP-EHH|值开展分析^[25-26];2)将|XP-EHH|值处于前0.1%的SNP判定为差异极显著的位点^[27-28];3)把|XP-EHH|≥1的SNPs界定为差异显著的位点;4)以差异极显著的SNP为核心向两侧延伸,直至出现连续2个以上差异不显著的SNPs时停止延伸。此外,当某个区域内包含5个以上差异显著的SNPs,并且相邻的SNPs间隔不含有2个或2个以上差异不显著的SNPs时,该区域也会被认定为候选区域。另一种方法是基于等位基因频率变化的跨群体的符合似然比检验(cross population

composite likelihood ratio test, XP-CLR)^[29], 本研究设置非重叠式滑动窗口长度为 25 kb, 每个窗口内最多包含 500 个 SNPs, 连锁不平衡值 (linkage disequilibrium, LD) 设定为 0.95^[30], 将 XP-CLR_norm 值位于前 1% 的区域确定为候选区域。最后, 将所得到的候选区域与 Ensembl 参考基因组注释文件进行比对, 以此来确定候选基因, 并在 STRING 数据库 (<https://cn.string-db.org/>) 进行候选基因蛋白互作网络构建。

2 结果

2.1 测序数据特征

通过对重测序数据质量进行统计, 拜城油鸡、

和田鸡、吐鲁番鸡与绿原鸡质控后 Clean reads 平均长度分别为 30 857 287、50 129 299、44 540 522、43 561 060 bp, 平均覆盖深度分别为 $7.67\times$ 、 $6.06\times$ 、 $5.41\times$ 、 $5.13\times$, 平均映射比率分别为 98.40%、98.65%、98.90%、97.96%。

2.2 SNP 质量控制

经过基因组比对和 SNP 注释后, 在 65 个样本上共获得 31 217 947 个 SNPs, 经过质控后, 共计 10 228 705 个常染色体 SNPs 用于基因渗入和选择信号分析 (图 1)。同时, 本研究中使用 $MAF \geq 0.2$ 的 4 657 217 个常染色体 SNPs 进行群体遗传关系分析。

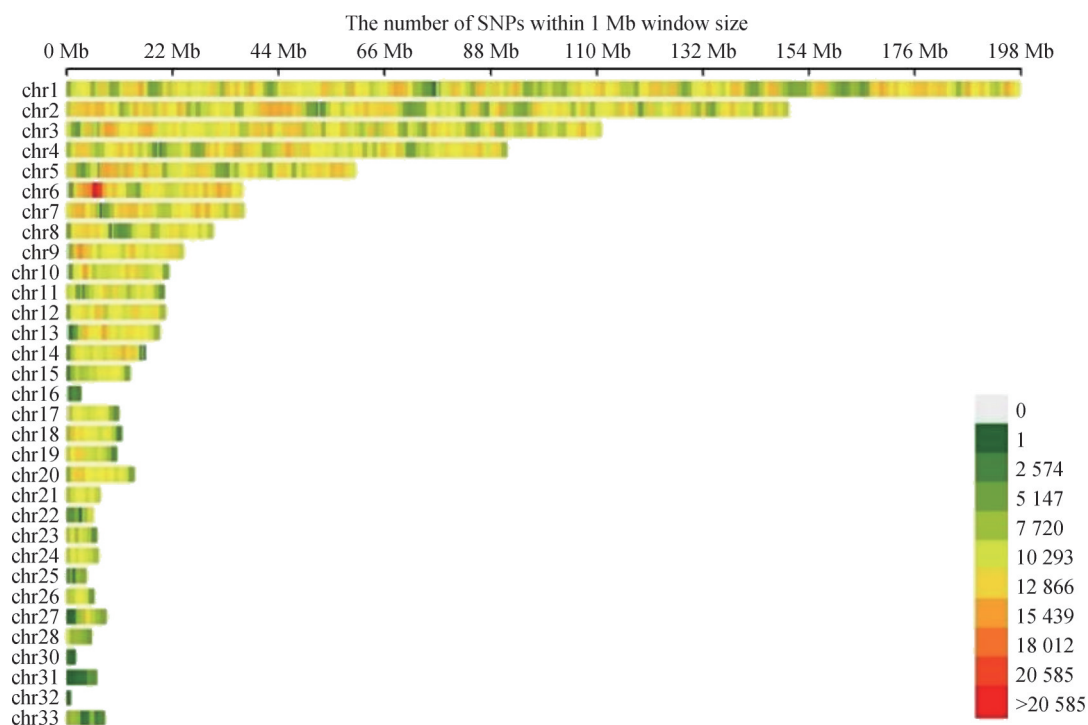


图 1 质控后 SNPs 的染色体分布示意图

Fig. 1 Schematic diagram of SNPs on chromosomes after quality control

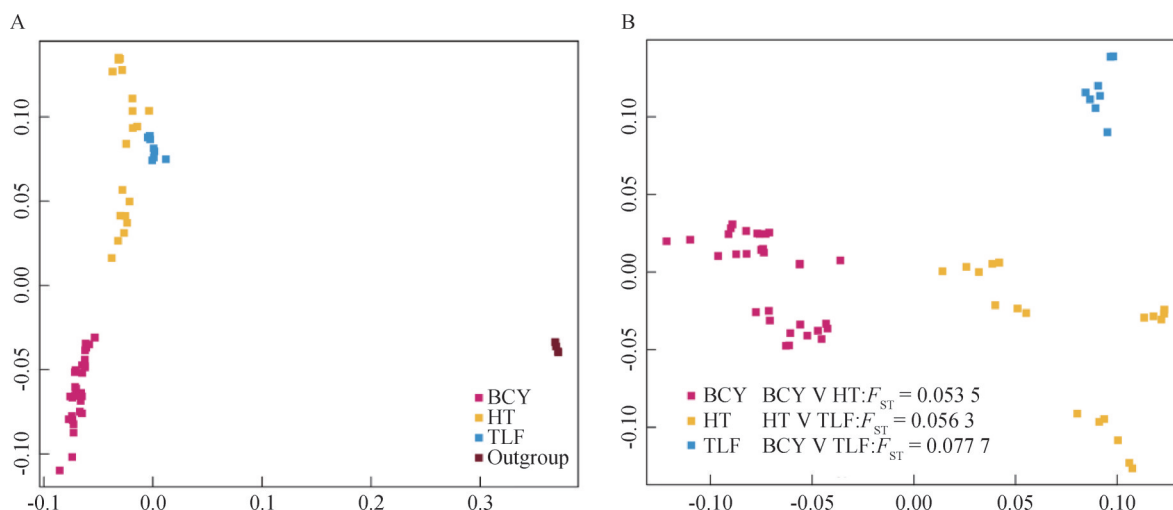
2.3 群体遗传关系分析

IBS 多维标度分析结果显示, 拜城油鸡和吐鲁番鸡的成对 F_{ST} 值为 0.077 7, 在 3 组比较中遗传分化程度最大, 和田鸡与拜城油鸡及吐鲁番鸡的 F_{ST} 值分别为 0.053 5 和 0.056 3, 显示出较近的遗传距离 (图 2)。同时, 在 IBS 多维标度中绿原鸡单独聚为一簇 (图 2A), 与新疆 3 种本地鸡种间显示出较远的遗传距离。此外, 拜城油鸡、和田黑鸡和吐鲁番鸡的观测杂合度分别为 0.364 5、0.285 5、0.296 0,

群体内基因多样性分别为 0.567 7、0.565 7、0.490 9。

2.4 基因渗入分析

Dsuite 结果显示, 当以拜城油鸡为 P1, 和田鸡为 P2, 吐鲁番鸡为 P3 时, D 统计值为 0.003 7, f_4 -ratio 为 0.046 2, 这表明三者之间可能存在基因渗入。进一步借助 TreeMix 分析发现, 拜城油鸡、和田鸡和吐鲁番鸡之间存在一次迁移事件, 为和田鸡向吐鲁番鸡的基因渗入 (图 3)。随后对每个滑动窗口的距离分数 d_f 进行了计算^[20], 共得到 13 647 个选



A. 拜城油鸡、和田鸡、吐鲁番鸡和绿原鸡的 IBS 多维标度图; B. 拜城油鸡、和田鸡、吐鲁番鸡的 IBS 多维标度图及成对 F_{ST} 值。BCY 代表拜城油鸡, HT 代表和田鸡, TLF 代表吐鲁番鸡, Outgroup 为绿原鸡

A. The IBS multidimensional scale maps of Baicheng-You chickens, Hetian chickens, Tulufan chickens, and Green jungle fowls; B. The IBS multidimensional scale maps and pair-wise F_{ST} of Baicheng-You chickens, Hetian chickens and Tulufan chickens. BCY, HT, TLF, and Outgroup represent Baicheng-You chickens, Hetian chickens, Tulufan chickens, and Green jungle fowl, respectively

图2 新疆3种地方鸡群体遗传结构分析

Fig. 2 Genetic structure analysis of 3 local chicken populations in Xinjiang

择区域。从其中选取 Z-score d_f 排名前 1% 的 136 个区域作为候选区域进行基因挖掘^[21], 分析显示排名居前的渗入区域主要分布在 2、4 和 11 号染色体上, 其中位于 4 号染色体的 80 624 337-81 362 351 区域得分最高(表 1 和图 4), 该区域涵盖 *ABLIM2*、*SH3TC1*、*HTRA3*、*ACOX3*、*TRMT44* 和 *GPR78* 等基因。排名前 20 渗入区域内的基因蛋白互作网络显示交互得分最高的基因对为 *ABLIM2* 和 *SH3TC1*(图 5)。

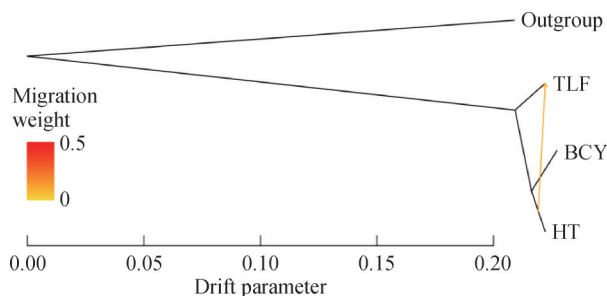


图3 新疆3种地方鸡群体间的基因渗入示意图

Fig. 3 Schematic diagram of gene introgression among 3 chicken populations in Xinjiang

2.5 拜城油鸡和吐鲁番鸡的选择信号分析

通过使用 XP-EHH 的方法筛选出的 2 481 个差

异区域, 涉及 433 个基因, XP-CLR 方法则获得了包含 233 个基因的 384 个差异区域。进一步选取两种方法的交集, 最终确定 70 个候选基因, 发现其中包括 *CLCN6*、*ACTA2* 等和耐热性能相关的基因, *BNIP2*、*DTNA*、*RAB3GAP2* 等和肌肉生长相关的基因, 以及 *AGMO*、*TSNARE1* 等和攻击性行为相关的基因(表 2)。此外, 这些基因中还包括具有极高 |XP-EHH| 值的 *PARD3*、*CRIM1*, 以及位于极高 XP-CLR 区域内的 *IARS2*、*ARHGAP22* 和 *SLIT3* 等基因(图 6)。70 个候选基因蛋白互作网络显示交互得分其最高的基因对为 *IARS2* 和 *EPRS*(图 7)。

3 讨论

新疆地域广袤, 吐鲁番鸡、和田鸡和拜城油鸡分布于不同区域, 各地自然条件差异显著, 加之牧民养殖过程中受不同程度人工选择的影响, 这些地方鸡种在表型及生产性能上呈现出不同程度的差异。本研究结果显示, 拜城油鸡、和田鸡和吐鲁番鸡在 IBS 多维标度分析中明显分为 3 类, 其中拜城油鸡与吐鲁番鸡的遗传距离较远, 而和田鸡与拜城油鸡及吐鲁番鸡的遗传距离较近(图 2), 基因渗入分析结果进一步证实, 吐鲁番鸡与和田鸡之间存在基因流动现象(图 3)。虽缺乏和田鸡与吐鲁番鸡杂

表 1 和田鸡与吐鲁番鸡排名前 20 的渗入区域及基因

Table 1 The top 20 introgression areas and their related genes between Hetian and Tulufan chickens

区域排名 Region ranking	区域位置 Region position		染色体 Chromosome	基因位置 Gene position		基因 Gene
1	80624337	81362351	4	80649049	80786524	<i>ABLIM2</i>
1	80624337	81362351	4	80793977	80825261	<i>SH3TC1</i>
1	80624337	81362351	4	80855311	80877258	<i>HTRA3</i>
1	80624337	81362351	4	80933353	80968494	<i>ACOX3</i>
1	80624337	81362351	4	80968536	80981295	<i>TRMT44</i>
1	80624337	81362351	4	81142872	81147963	<i>GPR78</i>
1	80624337	81362351	4	81163250	81197855	<i>CPZ</i>
2	80690000	81424671	4	81401297	81403526	<i>SOHO-1</i>
2	80690000	81424671	4	81409978	81412649	<i>HMX1</i>
3	80492569	81115546	4	79986601	80511445	<i>SORCS2</i>
3	80492569	81115546	4	80530710	80589183	<i>AFAP1</i>
6	115118700	115583816	2	115110507	115125929	<i>VXN</i>
6	115118700	115583816	2	115139370	115162145	<i>MYBL1</i>
6	115118700	115583816	2	115177217	115191152	<i>VCPIP1</i>
6	115118700	115583816	2	115207256	115264028	<i>SGK3</i>
6	115118700	115583816	2	115277568	115277646	<i>SNORD87</i>
6	115118700	115583816	2	115280942	115286441	<i>TCF24</i>
6	115118700	115583816	2	115289879	115308471	<i>PPP1R42</i>
6	115118700	115583816	2	115315596	115326952	<i>COPS5</i>
6	115118700	115583816	2	115379044	115463018	<i>ARFGEF1</i>
6	115118700	115583816	2	115482232	115569184	<i>CPA6</i>
8	4797296	5576303	11	4645274	4873781	<i>FTO</i>
8	4797296	5576303	11	4878175	4936909	<i>RPGRIP1L</i>
8	4797296	5576303	11	4976046	4988616	<i>AKTIP</i>
8	4797296	5576303	11	4991886	5011381	<i>RBL2</i>
8	4797296	5576303	11	5015742	5089734	<i>CHD9</i>
8	4797296	5576303	11	5176684	5176790	<i>U6</i>
8	4797296	5576303	11	5223979	5345307	<i>TOX3</i>
10	65570685	66428389	1	65833774	66173568	<i>SOX5</i>
11	115230557	115708914	2	115620395	115787873	<i>PREX2</i>
13	80802442	81599620	4	81576968	81578308	<i>ADRA2C</i>
14	65645081	66496818	1	66453732	66480164	<i>ETNK1</i>
17	115318072	115835589	2	115821712	115984273	<i>C8orf34</i>
19	23676537	24481736	1	23662850	23926311	<i>KCND2</i>
19	23676537	24481736	1	24435899	24484038	<i>ANKRD26</i>
20	115041718	115539645	2	115081599	115082672	<i>RRS1</i>

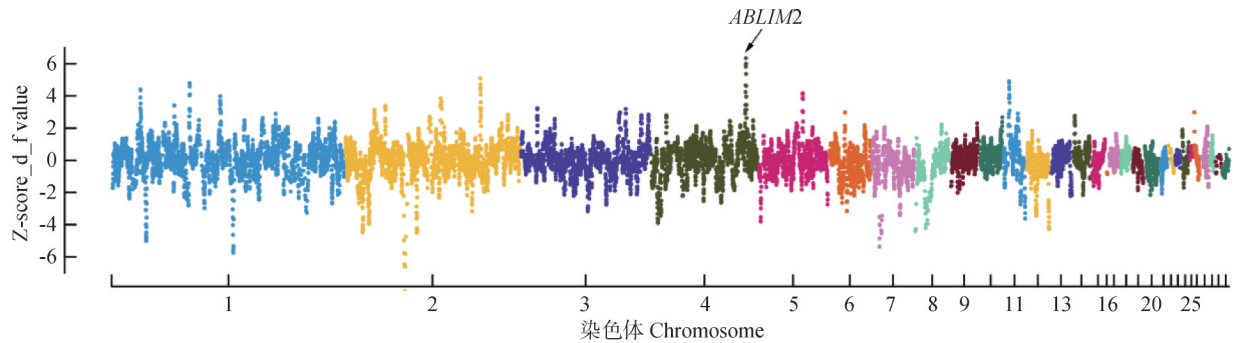
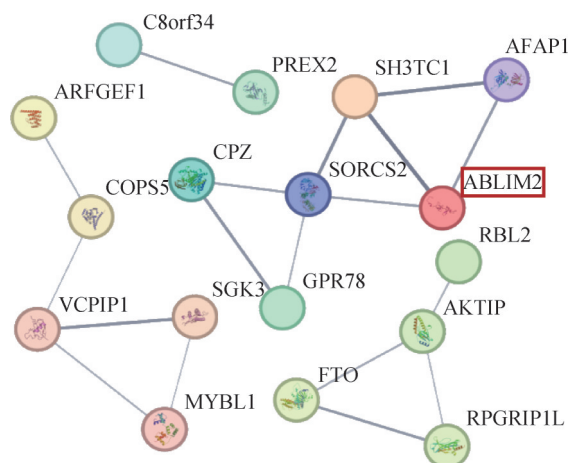


图 4 和田鸡与吐鲁番鸡基因渗入区域的 Z-score d_f 分布图

Fig. 4 The Z-score d_f distribution map of introgression region between Hetian and Tulufan chickens



本图仅保留有互作关系的蛋白,线条粗度表示相互作用的置信预测度

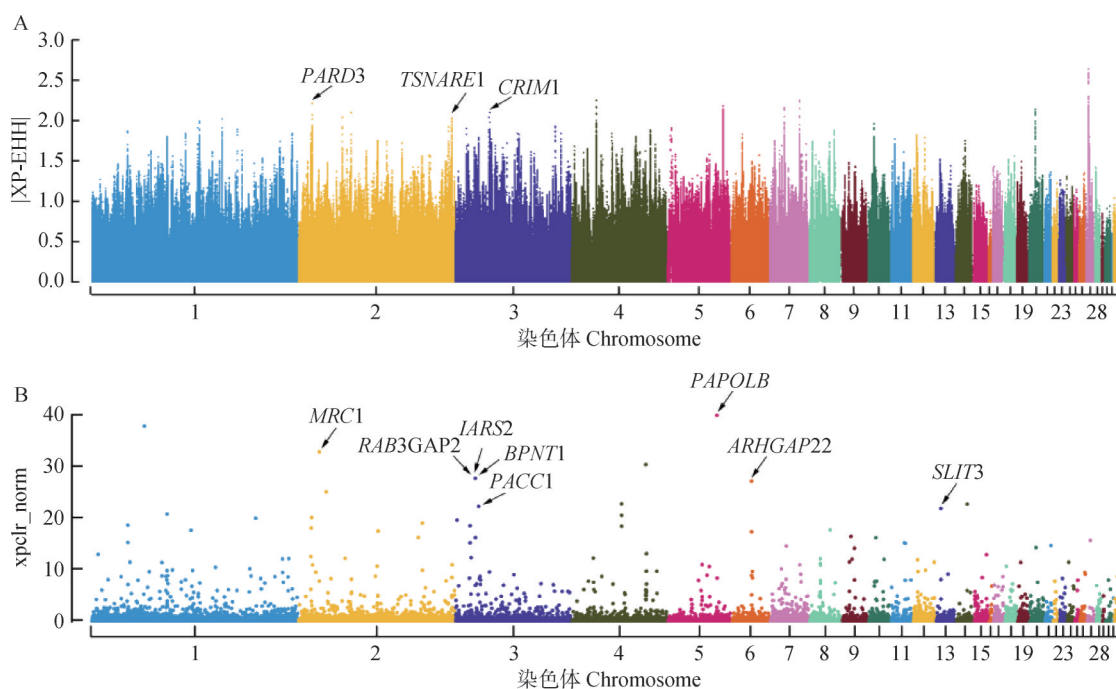
This figure only retains proteins with interaction relationships, line thickness indicates the strength of data support

图5 和田鸡与吐鲁番鸡排名前20的渗入区域内候选基因

Fig. 5 Protein-protein interaction network diagrams of candidate genes in the top 20 introgression regions of Hetian and Tulufan chickens

交的直接历史记载,但古丝绸之路中段途经和田与吐鲁番地区^[48],频繁的贸易往来为两地区鸡种的血缘交流创造了便利条件。一般来说,吐鲁番盆地与和田地区年平均气温均较高,尤其吐鲁番地区夏季气温高达49.7℃^[49],而拜城油鸡产地气候温和,年均气温17℃^[2],由此,为适应炎热的气候,当地的鸡种可能具有更好的耐热性。

本研究在和田鸡与吐鲁番鸡间排名第一的基因渗入区域中发现 *ABLIM2* 这一与心血管系统相关的候选基因,结合禽类通过调节体表血流量(如鸡冠、裸足等部位)和呼吸道蒸发作用维持体温平衡的生理学基础^[50-52],提示该基因可能通过调控血管舒张或血液循环参与禽类热应激响应机制。值得注意的是,早期胚胎发育阶段的热应激可能通过调控 *ABLIM2* 基因的甲基化水平影响心肌细胞增殖^[53],这一现象在高温孵化降低雏鸡心脏重量的研究中得到佐证^[54, 55]。由此推测,自然选择可能通过保留 *ABLIM2* 基因的特定变异,以调控胚胎期心脏发育的方式提升成年鸡种在高温环境下的生存适



A、B. 拜城油鸡与吐鲁番鸡间的|XP-EHH|值(A)及XP-CLR得分(xpclr_norm)(B)的曼哈顿图。箭头标记的基因包含极高的|XP-EHH|位点,或该基因位于极高的XP-CLR得分区域内。|XP-EHH|和XP-CLR极高点阈值分别设为2和20

A, B. Manhattan graph of |XP-EHH| values (A) and XP-CLR scores (xpclr_norm) (B) between Baicheng-You and Tulufan chickens. The genes marked by the arrows contained SNPs with extremely high |XP-EHH| values or located the regions with extremely high XP-CLR scores. The thresholds of the extremely high points of |XP-EHH| and extremely high regions of XP-CLR are set to 2 and 20, respectively

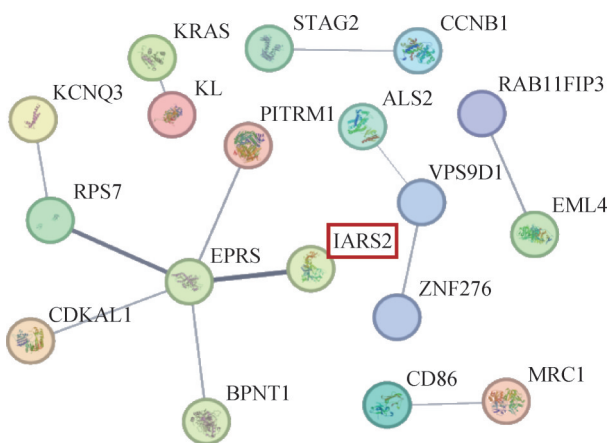
图6 拜城油鸡与吐鲁番鸡的选择信号分析

Fig. 6 Selection signals analysis between Baicheng-You and Tulufan chickens

表 2 拜城油鸡与吐鲁番鸡差异区域间部分与重要生物学过程相关的基因

Table 2 Some genes related to important biological processes in the differential regions between Baicheng-You and Tulufan chickens

染色体 Chromosome	基因位置 Gene position		基因 Gene	功能 Function
1	34535707	34549257	<i>HELB</i>	牛的环境适应性(Environmental adaptability of cattle) ^[31]
1	67188237	67209122	<i>KRAS</i>	牛骨骼肌生成(Bovine skeletal myogenesis) ^[32]
2	11439678	11481488	<i>PFKP</i>	参与鸡的体细胞重编程过程(Participate in the process of somatic reprogramming of chickens) ^[33]
2	27838091	28021352	<i>AGMO</i>	斗鸡攻击性行为(Aggressive behavior of gamecock chickens) ^[34]
2	107360212	107534708	<i>DTNA</i>	鸡肌肉发育(Muscle development in chickens) ^[35]
2	118477237	118542230	<i>CRISPLD1</i>	人类心力衰竭(Human heart failure) ^[36]
2	146916969	147397126	<i>TSNARE1</i>	斗鸡情绪调节和神经系统发育相关(Emotion regulation and nervous system development of gamecock chickens) ^[37]
3	18846742	18887139	<i>RAB3GAP2</i>	调节人肌纤蛋白分泌(Regulate myocilin secretion of human) ^[38]
3	18886888	18911956	<i>IARS2</i>	调节人血管生成(Regulates human angiogenesis) ^[39]
3	32394497	32555854	<i>CRIM1</i>	人冠状血管内皮细胞发育(Coronary vascular endothelial cell development of human) ^[40]
6	19118047	19156066	<i>ARHGAP22</i>	鼠上调节肌动蛋白细胞骨架(Regulates actin cytoskeleton of mice) ^[41]
6	20062668	20118932	<i>ACTA2</i>	鸡羽毛更新循环(Cycle of chicken feather renewal) ^[42]
7	11545922	11578947	<i>ALS2</i>	人肌萎缩侧索硬化(Amyotrophic lateral sclerosis of human) ^[43]
10	5823812	5839785	<i>BNIP2</i>	调节人成肌细胞分化(Regulate the differentiation of human myoblast) ^[44]
10	7185220	7263560	<i>MYO1E</i>	抑制小鼠破骨细胞分化(Suppresses osteoclast differentiation of mice) ^[45]
13	4953827	5426056	<i>SLIT3</i>	促进鸡细胞肌源性分化(Promote myogenic differentiation of chicken cells) ^[46]
21	5586241	5605153	<i>CLCN6</i>	小鼠血管平滑肌收缩力(Vascular smooth muscle contractility of mice) ^[47]



本图仅保留有交互关系的蛋白,线条粗细表示相互作用的置信预测度

This figure only retains proteins with interaction relationships, line thickness indicates the strength of data support

图 7 拜城油鸡和吐鲁番鸡间 70 个候选基因的蛋白互作网络图

Fig. 7 Protein-protein interaction network diagrams of 70 candidate genes between Baicheng-You and Tulufan chickens

应性。此外,蛋白互作网络分析显示,*ABLM2*和*SH3TC1*之间存在最高的互作评分,然而目前尚未见*SH3TC1*在鸡或相关功能中的研究报道。而在吐鲁番鸡与拜城油鸡的对比中,同样发现了可能与鸡耐热性能相关的基因,如与鸡羽毛更新循环相关的*ACTA2*以及与循环和心血管系统发育相关的*CLCN6*、*Crim1*和*IARS2*等。其中,*ACTA2*将真皮乳头干细胞划分以促进鸡从用于保温的出生羽毛到用于简单飞行的幼年羽毛的更新^[42],这可能改善其耐热性能。*CLCN6*则可能通过影响高尔基体钙储备来调节血压、维持血管平滑肌功能等途径在极端高温中保障禽类外周血管舒张的生理响应^[47,56]。而*Crim1*和*IARS2*虽在鸡中尚未建立与耐热性的直接关联,但基于其在小鼠心脏形态发生(*Crim1*)和人血管生成调控(*IARS2*)中的功能基础^[39,57],推测*Crim1*和*IARS2*可能通过影响心血管系统发育,间接增强高温环境下血液循环系统的代偿能力。此外,蛋白互作网络显示*IARS2*和*EPRS*之间存在

最高的互作评分,目前尚未看到 *EPRS* 在鸡上的研究,但鼠上的研究显示其与心脏纤维化之间存在联系^[58]。这些发现提示,吐鲁番鸡的耐干热适应性可能源于心血管功能相关基因的多层次协同演化—既包含直接影响血管动态调节的即时响应基因(如 *CLCN6*),也涉及决定心血管系统发育潜力的基础调控基因(*Crim1*、*IARS2*)。尽管目前针对以上基因在鸡上的功能研究尚不完善,但本研究通过物种间功能类比和机制探讨,为解析鸡耐热性状的分子调控网络提供了新的基因素材。

另一方面,本研究也在拜城油鸡与吐鲁番鸡的选择信号中鉴定出了一批与肌肉生长相关的基因,如 *RAB3GAP2*、*Bnip-2* 和 *DNTA* 等。已有的研究发现,相同日龄拜城公母鸡的腿肌率均比吐鲁番鸡要高^[59-60],这些基因可能通过协同调控肌细胞分化与发育的分子网络,塑造其独特的肌肉生长模式。具体而言,*RAB3GAP2* 作为肌纤蛋白 MYOC 分泌的调控枢纽,或通过激活 TGF- β 信号通路增强 C2C12 肌肉细胞分化效率,从而提升骨骼肌的累积速率^[38,61]; *Bnip-2* 则可能通过与促进肌生成的细胞表面受体 Cdo 相互作用,刺激 GTP 酶 Cdc42 活性,进而促进 p38 α / β 活性和肌原性分化,为肌纤维的发育提供分子基础^[62]。目前 *RAB3GAP2* 和 *Bnip-2* 在小鼠细胞上的研究已经表明它们与肌肉发育过程息息相关,但在鸡上功能仍然知之甚少。值得注意的是,*DNTA* 基因外显子区检测到与鸡肌肉发育显著相关的突变位点,提示该基因可能通过调控肌细胞直接影响肌肉组织生长^[35]。这些发现共同揭示了拜城油鸡肌肉发育优势的潜在遗传机制,包括肌原性分化通路的正向调控元件(*RAB3GAP2*、*Bnip-2*)与肌细胞增殖的关键调控靶点(*DNTA*)等,为解析地方鸡种肌肉生长性状的分子调控框架提供了新线索。

此外,本研究在拜城油鸡与吐鲁番鸡之间还鉴定出了 *AGMO* 和 *TSNARE1* 等可能与斗鸡攻击行为相关的候选基因。中国斗鸡的攻击性行为 and 生存竞争与社会层级建立等活动相关^[63],虽然可能有利于其生存,但同时可能导致鸡身体损伤、死亡率增加以及造成外观缺陷,从而产生严重的经济损失^[64]。已有的关于中国斗鸡选择信号的研究发现 *AGMO* 基因位于最强的择性信号区域内^[34],同时,人上的研究表明 *AGMO* 变异与神经发育障碍有关^[65],这暗示 *AGMO* 基因可能通过调控神经系统

的方式参与斗鸡攻击性行为的中枢调控网络。此外,在 Ren 等^[37]关于全球斗鸡起源模式与选择标签的研究中,*TSNARE1* 作为唯一一个被 6 个斗鸡种群选择的基因而引起关注,它可能通过作用于斗鸡情绪调节和神经系统发育而影响其攻击性。需要指出的是,由于吐鲁番鸡的样本数有限,以上结果后续还需要更多的研究来支持。

4 结 论

本研究基于全基因组重测序数据揭示了新疆 3 种地方鸡种之间的遗传关系,发现拜城油鸡与吐鲁番鸡遗传距离较远,和田鸡与拜城油鸡及吐鲁番鸡的遗传距离较近,且和田鸡与吐鲁番鸡存在一定程度的基因渗入,在二者之间存在 136 个候选渗入区域,其中渗入得分最高的区域内包含了 *ABLM2* 等与耐热性能相关的基因,为揭示新疆地方鸡适应高温干旱环境的遗传机制提供了关键线索。此外,在拜城油鸡和吐鲁番鸡的选择信号中共鉴定出 70 个参与重要生物学过程的候选基因,其中包括 *CLCN6*、*ACTA2*、*Crim1*、*IARS2* 等与耐热性能相关的基因,*Bnip-2*、*DTNA*、*RAB3GAP2* 等与肌肉生长相关的基因以及 *AGMO* 和 *TSNARE1* 等与斗鸡攻击性行为相关的基因,为揭示新疆地方鸡品种耐热性、肌肉发育以及攻击性行为等特色性状的遗传机制提供依据。然而,上述候选基因如何影响特色性状目前尚缺乏试验性证据,因此后续需进一步对这些基因功能进行深入研究,以验证候选基因的生物作用。研究结果所鉴定的特色性状相关基因为今后开展针对性分子选育、性状改良及品种纯化提供了关键靶点,对推动地方鸡种资源保护与可持续利用具有明确的实践意义。

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