Identification of the differentially expressed genes in the leg muscles of Zhedong white geese (Anser cygnoides) reared under different photoperiods

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ABSTRACT Light is a factor affecting muscle development and meat quality in poultry production. However, few studies have investigated the role of light in muscle development and meat quality in geese. In this experiment, 10 healthy 220-day-old Zhedong white geese were reared for 60 d under a long photoperiod (15L:9D, LL) and short photoperiod (9L:15D, SL). The gastrocnemius muscles were collected after slaughter to evaluate muscle fiber characteristics and meat color, and RNA-seq analysis. The results showed that compared to the LL group, the SL group had large muscle fiber diameter and cross-sectional area, few muscle fibers per unit area, high meat color a* value, and low L* value at 24 h postmortem. On comparing the 2 groups, 70 differentially expressed genes (DEGs) were identified. Compared to the SL group, the LL group had 25 upregulated and 45 downregulated genes. Gene Ontology (GO) enrichment analysis showed that these DEGs were mainly involved in cell, cell part, binding, cellular processes, and single-organism processes. Several significantly enriched pathways were identified in the Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway analysis, such as the calcium and PI3k-Akt signaling pathways. The expression of five randomly selected DEGs was verified using quantitative real-time PCR, and the results were consistent with the RNA-seq data. This study provides a theoretical basis for studying the molecular mechanisms by which light affects muscle development and meat color in geese.

Key words: muscle development, meat color, Zhedong White Geese, photoperiod, RNA-seq

INTRODUCTION

In the global meat market, goose meat is an excellent source of high-quality protein which contains all kinds of amino acids needed by humans (Haraf et al., 2021). The ideal high protein, low fat, and low cholesterol levels makes goose meat a popular nutritional health food among consumers (Buzafa et al., 2014; Journal, 2021; Orkusz, 2021). China is the largest producer and consumer of goose meat globally. However, owing to the lack of a scientific breeding method, the breeding cycle of geese is longer than that of other poultry, which seriously restricts the development of the goose industry (Gao et al., 2021a). Therefore, exploring scientific methods to improve muscle development and meat quality of Chinese local geese is a useful way to overcome the current predicament.
light during duck feeding or only short light in the early stages to maintain a higher redness value of duck meat (Starčević et al., 2021). Dim light reduces the brightness of broiler meat color (Fidan et al., 2017), whereas long light makes the chicken meat color lighter and increases muscle lipid oxidation and protein denaturation (Tuell et al., 2020b). Prolongation of the photoperiod may negatively affect muscle oxidative stability and color by altering muscle metabolites (Tuell et al., 2020a). However, whether light affects geese meat color and the underlying molecular mechanisms by which light regulates poultry meat color remain to be further investigated.

Since RNA-seq technology was proposed in 2008, it has been widely used in biological research, medical diagnosis and treatment (Ghosh et al., 2018; Kloet et al., 2020). RNA-seq technology has been used to compare the skeletal muscle transcriptomes of Muscovy ducks at different developmental stages and many potential candidate genes have been identified (Hu et al., 2020). In a study of chicken meat color, 1,317 candidate genes related to glycolysis, fatty acid metabolism, and protein metabolism, were screened using RNA-seq technology (Sun et al., 2022). In addition, 397 differentially methylated genes highly correlated with cellular metabolic processes were identified after m6A transcriptome sequencing of the pectoralis muscle in Ding’an geese (Xu et al., 2021). Thus, whole genome sequencing technology plays an important role in exploring the molecular mechanism of poultry traits.

In this study, the Chinese local breed Zhedong White Geese was used as the experimental object. High-throughput sequencing technology and bioinformatics were used to identify differentially expressed genes and signaling pathways present in the gastrocnemius muscles of geese reared under different photoperiod conditions. The results of this study provide a theoretical basis for improving the meat production performance of geese.

**MATERIALS AND METHODS**

**Experimental Animals and Tissues**

The Zhedong white geese (Anser cygnoides) used in this study were raised at the East Zhejiang White Geese Original Breeding Farm, Xiangshan County, Zhejiang Province, China. Twenty healthy 220-day-old Zhedong white goose females with similar weights were randomly divided into 2 groups. One group was kept under a long photoperiod (15L:9D, LL) and the other was kept under a short photoperiod under (9L:15D, SL) using artificial light controlled at 30 lx. After 60 d of feeding, 6 geese were dissected from each group and leg muscle samples were collected. All samples were immediately frozen in liquid nitrogen and stored at −80°C until use.

All animal experimental procedures used in this study were approved by the Ethics Committee for Animal Experiments of Zhejiang A&F University and were performed in accordance with the Guidelines for Animal Experimentation of the University (Hangzhou, China).

**Total RNA Extraction, Library Construction, and Sequencing**

Total RNA was extracted from the gastrocnemius muscle of the legs using the TRizol method (Puch-Hau et al., 2019). To ensure that the samples qualified, quality testing was performed by the sample testing center of Majorbio Bio-pharm Technology Co., Ltd. (Shanghai, China). The quality reports are presented in Table S1. All RNA samples met the requirements for Optical density (OD) values (260/280 > 2.0) for further analysis. The RNA-seq transcriptome library was prepared using the TruSeq RNA sample preparation Kit from Illumina (San Diego, CA) using 1 μg of total RNA. Briefly, messenger RNA was isolated according to the polyA selection method using oligo (dT) beads and then fragmented using fragmentation buffer. Second, double-stranded cDNA was synthesized using a SuperScript double-stranded cDNA synthesis kit (Invitrogen, CA) with random hexamer primers (Illumina). The synthesized cDNA was then subjected to end-repair, phosphorylation, and ‘A’ base addition according to Illumina’s library construction protocol. Libraries were selected for cDNA target fragments of 300 bp on 2% low range ultra-agarose, followed by PCR amplification using Phusion DNA polymerase (NEB) for 15 PCR cycles. After quantification using TBS80, the paired-end RNA-seq sequencing library was sequenced using the Illumina HiSeq xten/NovaSeq 6000 sequencer (2 × 150 bp read length). Goose leg muscles of the SL group were numbered sl 1, sl 2, and sl 3, and those of the LL group were numbered ll 1, ll 2, and ll 3, for subsequent analysis.

**Sequencing Quality Assessment and Differentially Expressed Gene**

**Screening** The SeqPrep and Sickle software were used to remove low quality reads from the raw data. Q20, Q30, GC content, and sequence repeat levels were calculated using fastp. All downstream analyses were based on high-quality clean reads. The goose genome sequences were downloaded from the NCBI database (https://www.ncbi.nlm.nih.gov/genome/31397?genome_assembly_id=229313). The resulting clean reads were compared with the reference genome of the goose using Hisat2.

To identify differentially expressed genes (DEGs) in the 2 groups, the expression level of each transcript was calculated according to the transcripts per million reads (TPM) method. RSEM (http://deweylab.biostat.wisc.edu/rsem/) (Dewey and Li, 2011) was used to quantify gene abundances. Differential expression analysis was performed using the DESeq2 (Love et al., 2014), DESeq (Wang et al., 2010), and EdgeR (Robinson et al., 2010) method. Differentially expressed genes with |log2FC|>1 and Q value ≤ 0.05
DEGs in the KEGG pathways.

versity, China) to test the statistical enrichment of kegg/), we used the KOBAS software (2.1, Peking Uni-

Component (CC) were used for classification annotation. Based on the Kyoto Encyclopedia of Genes and Genomes (KEGG) database (http://www.genome.jp/kegg/), we used the KOBAS software (2.1, Peking University, China) to test the statistical enrichment of DEGs in the KEGG pathways.

Quantitative Real-Time PCR

Using the NCBI gene library, primers of 5 randomly selected DEGs and the house-keeping gene GAPDH were designed using Primer Premier 5 software (Table 1). Primers were synthesized by Hangzhou Youkang Biotechnology Co., Ltd. Total RNA was used to synthesize cDNA using the 5 × All-In-One MasterMix Kit (ABM, Zhengjiang, China). As the template, cDNA was used for quantitative PCR using the EvaGreen 2 × qPCR MasterMix Kit (ABM). Three replicates were performed for each sample. The relative expression of each gene was calculated using 2−ΔΔCT statistical analysis. All data are shown as mean ± SEM, and unpaired Student’s t tests were used to calculate P-values.

Analysis of Muscle Structure

Goose leg muscle samples were fixed with 4% paraformaldehyde and embedded in paraffin blocks. After the paraffin block was sectioned (5 μm), it was stained with hematoxylin and eosin solution, and the slides were placed in 70% ethanol for 20 s, 90% ethanol for 20 s, 100% ethanol for 1 min, and xylene for 3 min, and then air-dried and sealed (Wang et al., 2017). Sections were photographed using a fluorescence microscope (Olympus, Tokyo, Japan). Three samples were obtained from each group of geese, and 5 micrographs were randomly selected for each sample. A total of 90 muscle fibers per group were counted using the ImageJ software, and the average of 5 measurements was taken as the fiber cross-sectional area (μm²), diameter (μm), and density (fibers/mm²) (Zhang et al., 2014).

Detection of Meat Color

The goose meat color parameters were recorded on the L*a*b* color scale (Ganz and Pauli, 1995), using a Minolta Chromameter (Minolta Camera Co., Osaka, Japan). Goose meat color was measured 24 h after slaughter. The results are expressed as L* (lightness), a* (redness), and b* ( yellowness) and were calculated from the average of 5 different locations on each muscle (Orkusz et al., 2017).

RESULTS

Differences in Muscle Fiber Characteristics of Goose Leg Muscles Under Different Photoperiods

To explore the effect of photoperiod on muscle fiber characteristics in goose, gastrocnemius muscles were sectioned and stained. The results showed that the density of muscle fibers in the SL group was lower than that in the LL group, but the cross-sectional area and diameter of the muscle fibers were larger (Figures 1A–1D). Therefore, it was inferred that SL may promote goose muscle hypertrophy.

Effect of Different Photoperiods on Meat Color of Geese

To investigate whether light affects goose meat color, meat color measurements were performed of leg muscles of geese reared under different photoperiods (Figure 2). The results showed that SL significantly reduced the L* value (brightness) (P-value = 0.025) while increasing the a* value (redness) (P-value = 0.0315) of goose meat color compared to that under LL (Table 2).

Sequencing Quality Evaluation

During the sequencing process, the raw data were quality controlled and a quality assessment was provided to ensure the accuracy of the subsequent analysis. The results listed in Table 3 show that the values of Q20 (base quality > 20 and error rate < 0.01) are all above 98% and those of Q30 (base quality > 30 and error rate < 0.001) are all above 94%. The GC content ranged from 53 to 57%. The results indicated that the data had a low probability of error which met the sequencing requirements.

More than 68% of the reads were aligned to the reference genome and 65 to 75% of the clean reads

| Table 1. Primers used in the real-time PCR. |
|---|---|---|
| Gene name | Sequence (5′-3′) | Product size |
| GAPDH | F: TTCCTCCACCTTTTGATGCGG R: ACCATCAAGTCCACCACACG | 114bp |
| PHKB | F: CAAACATGGCAGTCCAGACC R: TTGGTGCTGACACAGCACC | 543bp |
| SOX6 | F: TGCGCTCGTGAGGAGGAGG | 188bp |
| GCK | F: GCCAGAAGTGGAGATGGA R: GTGACACGGGAAAGAGAA | 172bp |
| HSPB1 | F: GTATTTCGCTCGTCTGCC | 222bp |
| PHGDH | F: TGAAGGAAGCCAAAATGGG R: GGTCTCGGGGGGTGATGAT | 164bp |
had unique comparison positions on the reference genome (Table 4). This illustrates that the clean reads obtained were available for post-sequencing analysis.

Correlation analysis was performed to assess the quality of repeatability within the group. The results showed that there were differences between the groups and the biological replicates within the groups were good (Figure 3).

### Table 2. L* (brightness), a* (redness) and b* (yellowness) values of goose leg muscles at 24 h postmortem under different photoperiods (n = 10).

| Light/h | Brightness L*  | Redness a*        | Yellowness b* |
|---------|----------------|------------------|---------------|
| 15h     | 26.65 ± 1.21\(^a\) | 55.91 ± 0.81\(^b\) | 15.26 ± 0.59  |
| 9h      | 23.49 ± 1.60\(^a\) | 58.30 ± 1.40\(^b\) | 15.23 ± 1.19  |
| P-value | 0.0250          | 0.0315           | 0.4830        |

- In the same column, values with different lowercase superscripts indicate significant differences (P < 0.05).
Screening of DEGs

The total number of genes screened by RNA-Seq was 9,858. To display gene expression distribution, a volcano plot was constructed using -log10 (adjusted) as the vertical coordinate and log2 (FC) as the horizontal coordinate (Figure 4A). A total of 70 DEGs were identified. There were 45 upregulated genes and 25 downregulated genes in the SL group compared to the LL group (Figure 4A). The expression levels of 5 randomly selected DEGs, including 3 downregulated genes (GCK, HSPB1, and PHGDH) and 2 upregulated genes (PHKB and SOX6), were verified using quantitative real-time PCR. The results showed that their expression trends

| Sample | Clean reads | Clean bases | Q20(%) | Q30(%) | GC content(%) |
|--------|-------------|-------------|--------|--------|---------------|
| sl_1   | 54,313,760  | 80,26,863,149| 98.27  | 95.01  | 54.53         |
| sl_2   | 44,389,142  | 6,555,398,259| 98.35  | 95.26  | 56.73         |
| sl_3   | 48,539,644  | 7,211,469,150| 98.75  | 95.98  | 54.97         |
| ll_1   | 46,095,306  | 6,861,678,422| 98.76  | 95.99  | 54.88         |
| ll_2   | 51,839,210  | 7,677,991,815| 98.25  | 94.95  | 54.92         |
| ll_3   | 49,484,182  | 7,363,615,166| 98.74  | 95.92  | 53.94         |

sl and ll represent short and long photoperiod groups, respectively. 1/2/3 represent three biological replicates for each group. Clean reads: total number of sequencing data entries after quality control. Clean bases: total sequencing data volume after quality control (i.e., number of clean reads multiplied by the length of reads). Q20 and Q30: the percentage of bases with sequencing quality above 99% and 99.9% of the total bases, respectively. GC content: Quality control (QC) data corresponded to the sum of G and C bases as a percentage of the total bases.

Table 3. Quality assessment of sequencing data.

| Sample | Total reads | Total mapped | Multiple mapped | Uniquely mapped |
|--------|-------------|--------------|-----------------|-----------------|
| sl_1   | 54,313,760  | 40,223,184(74.06%) | 1,160,976(2.14%) | 39,062,208(71.92%) |
| sl_2   | 44,389,142  | 30,206,700(68.05%) | 1,050,449(2.37%) | 29,156,251(65.68%) |
| sl_3   | 48,539,644  | 35,760,428(73.67%) | 1,084,433(2.23%) | 34,675,995(71.44%) |
| ll_1   | 46,095,306  | 34,149,665(74.08%) | 1,158,824(2.51%) | 32,990,841(71.57%) |
| ll_2   | 51,839,210  | 37,800,821(72.92%) | 14,66,913(2.83%) | 36,333,908(70.99%) |
| ll_3   | 49,484,182  | 37,392,580(75.36%) | 11,01,398(2.23%) | 36,191,182(73.14%) |

sl and ll represent short and long photoperiod groups, respectively. 1/2/3 represent three biological replicates for each group. Total reads: total number of sequencing data entries after quality control (i.e., clean reads). Total mapped: number of clean reads localized to the genome. Multiple mapped: number of clean reads with multiple comparison positions in the reference sequence. Uniquely mapped: number of clean reads with a unique comparison position on the reference sequence.

Figure 3. Heat map of intersample correlation.
were highly consistent with the sequencing results, which proved the reliability of the microarray analysis (Figures 4B and 4C).

To ensure the accuracy of the analysis, the screened differentially expressed genes were subjected to hierarchical clustering analysis. The horizontal coordinates represent sample clustering. One column represents one sample, and clustering analysis was based on the similarity of gene expression patterns between samples. The closer the distance, the more similar were the samples (Figure 4D). These results suggest that these DEGs clearly divided the leg muscle samples into short and long photoperiod groups, indicating the reliability of our analysis.

**GO Annotation and Enrichment Analysis**

To further reveal the molecular characterization of these DEGs, they were analyzed using GO annotations. The results showed that 70 DEGs were annotated with 20 GO terms, including 11 biological processes, 7 cellular components, and 2 molecular function annotations. The major GO terms were significantly enriched in biological processes, which included positive regulation of biological processes, localization, development process, multicellular organismal process, signaling, response to stimulus, metabolism, regulation of biological processes, biological regulation, cellular processes, and single-organism processes. In addition, macromolecular complexes, membrane, extracellular region, extracellular region part, organelles, and cell part and cells were enriched among cellular components. The main functional term of molecular function were catalytic activity and binding, which were enriched in 11 and 24 genes, respectively (Figure 5).

**KEGG Pathway Enrichment Analysis**

To understand the signaling pathways in which the genes were distributed, a KEGG pathway analysis was performed. A total of 48 DEGs were mapped to 127 KEGG pathways, of which 20 were significantly enriched ($P < 0.05$). There were several significantly enriched signaling pathways, including amoebiasis, the calcium signaling pathway, and the PI3k-Akt signaling pathway (Figure 6).

**DISCUSSION**

Light plays an important role in goose productions and metabolism. Reasonable and effective use of light can greatly affect the production performance of geese (Wang et al., 2009; Liu et al., 2020). The present study showed that the Zhedong white geese in the SL group had a larger muscle fiber diameter and cross-sectional area, but had a smaller number of muscle fibers per unit area than those in the LL group. Melatonin levels in the blood of geese increase under dark conditions (Zawilska et al., 2003). Melatonin can promote proliferation of skeletal muscle satellite cells (Lamosová et al., 1998). Long-term exogenous addition of melatonin effectively prevents muscle atrophy (Lee et al., 2012). Therefore, melatonin may be a key hormone in light-induced muscle hypertrophy in geese. Our study also found that the meat color of geese under SL had a higher a*
parameter and lower L* parameter than those under LL conditions, thus having a high commercial value. Glucocorticoid downregulation in birds is caused by prolonged light exposure (House et al., 2021). In muscle cells, increased glucocorticoid levels reduce cellular respiration and shift the cellular metabolic phenotype to glycolysis (Torres-Velarde et al., 2021). Studies have shown that glycolysis is an important metabolic pathway that affects meat color, and meat with low glycolytic dehydrogenase activity has poor color stability (Xin et al., 2018; Gao et al., 2021b). Through RNA-seq analysis of leg muscles of geese reared under different photoperiods, 70 DEGs were identified, among which 5 DEGs were randomly selected for further verification of expression levels using qRT-PCR. Although the expression levels of the genes selected by the 2 methods were different, their expression trends were highly consistent, which proved the reliability of the sequencing analysis results.

The basic processes of muscle development in geese include cellular and biological processes and biological regulation. GO annotation analysis showed that 20 DEGs were enriched in the GO term: regulation of biological processes (Table S2). Among these DEGs, FMOD, HSPB1, and STC1 were upregulated in the goose leg muscles under SL conditions. FMOD promotes chicken myogenic cell differentiation and alleviates muscle atrophy (Yin et al., 2020). Inhibition of HSPB1 during myogenesis represses myotube formation (Kim et al.,...
gen (Watts et al., 2010), which improves meat color sta-
transferring electrons from NADH or succinate to oxy-
conditions that promote the reduction of MetMb by
Mitochondrial oxygen depletion establishes anaerobic
muscles (Mohan et al., 2010). GCK was signi-
santly inhibiting MUC16C-induced glycolysis in tumors
s (Wang et al., 2007). Knockdown of ALDOC signi-
ificantly downregulated under SL conditions. Mutations
in KCNJ2 cause malformations in muscle development
(Andelfinger et al., 2002). Therefore, we speculated that
these genes may play a key role in the regulation of goose
myoblast differentiation and muscle hypertrophy.

The energy metabolism of muscle after slaughter
affects meat color (Men et al., 2017). GO annotation
analysis revealed that 16 DEGs were enriched in meta-
bolic process-related GO terms (Table S2). Inhibition of
glycolysis in the skeletal muscle has been reported to
increase glycogen synthesis (Clark et al., 1987; Ren et al.,
1993). Research has shown that animals with high glyco-
gen levels tend to have worse meat color at 24 h postmor-
tem (Choe et al., 2008). ACSL6, AGL, and GPD2 were
upregulated in the LL group. Inhibition of ACSL6
reduces glucose uptake in the skeletal muscle (Jung and
Bu, 2020), which in turn reduces muscle glycogen synthe-
thesis (Ryder et al., 1999). Cancer cells with knockout of
AGL expression were more metabolically active and
dependent on glycolysis than cells that express AGL nor-
mally (Lew et al., 2015). GPD2 can inhibit glycolysis in
tumor cells (Wu et al., 2020; Zhao et al., 2021). In our
study, the KEGG pathway enrichment analysis results
indicated that the 2 most significantly enriched pathways
were related to the energy metabolism in muscles (Table
S3). ALDOC is active during the second stage of glycoly-
sis (Wang et al., 2007). Knockdown of ALDOC signifi-
cantly inhibits MUC16C-induced glycolysis in tumors
(Fan et al., 2020). Thus, we inferred that these DEGs
were activated during the process of light exposure,
affecting goose meat color.

After animal death, mitochondria continue to metab-
olize oxygen in the skeletal muscle (Tang et al., 2005).
Mitochondrial oxygen depletion establishes anaerobic
conditions that promote the reduction of MetMb by
transferring electrons from NADH or succinate to oxy-
gen (Watts et al., 2010), which improves meat color sta-
ibility. HSPB1 was upregulated in the SL group and was
significantly enriched in GO term metabolic processes
(Table S2). HSPB1 was found to restore the mitochon-
drial respiratory impairment caused by cellular stress
(Mule et al., 2021). Pyruvate, a product of glycolysis,
supports mitochondrial respiration in postmortem
muscles (Mohan et al., 2010). GCK was significantly
enriched in the glycolysis gluconeogenesis pathway
(Table S3) and highly expressed under SL conditions. During normal hepatocellular carcinogenesis, GCK
expression can link the central carbon metabolism and
stimulate mitochondrial respiration (Perrin-Cocon et al.,
2021). Thus, these DEGs may be involved in the process of light affecting goose meat color through
mitochondrial respiration.

KEGG enrichment analysis showed that the DEGs
were significantly enriched in the calcium signaling path-
way (Table S3). The intracellular calcium signaling
pathway is an important factor that influences meat
color (Lonergan et al., 2003; Ropka-Molik et al., 2017).
Among the genes upregulated in the LL group, PHKB
was significantly enriched in the calcium signaling path-
way (Table S3). PHKB is a key regulatory enzyme in
glycogen metabolism (Wühlrich-Schmoll and Kili-
mann, 1996), and mutations in PHKB can lead to the
accumulation of muscle glycogen (Burwinkel et al.,
1997). Muscles with high glycogen levels usually show a
poor meat color at 24 h postmortem (Choe et al., 2008).
In addition, the present study found that DEGs were
significantly enriched in the PI3K-Akt signaling path-
way (Table S3). FIGF was upregulated in the LL group.
A C>G mutation in the bird FIGF gene results in a dra-
matic increase in the number of muscle fibers
(Chen et al., 2013). The number of muscle fibers per
unit area was higher in the LL group, which may be
correlated with the function shown in FIGF.

Future research will be directed at determining the
optimal photoperiods to utilize these DEGs and signal-
pathways to regulate goose muscle development and
quality to enable further rapid development of the goose
industry.

CONCLUSIONS

The present study demonstrated that short light signif-
ically promoted goose muscle development, resulting in
a larger cross-sectional area and diameter of muscle fibers.
In addition, short light remarkably improved the redness of
goose meat. RNA-seq analysis provided a catalog of
mRNAs for the study of the mechanisms by which light
affects muscle development and meat color in geese, and
creened 3 signaling pathways (glycolysis gluconeogene-
sis, calcium signaling pathway, and PI3K-Akt signaling
pathway) that may be involved in this regulation. The
experimental data provided a theoretical basis for study-
ing the molecular mechanisms by which light affects
muscle development and meat color in geese.

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DISCLOSURES

The authors declare that there is no conflict of interest
regarding the publication of this paper.
SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.psj.2022.102193.

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