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Original Article

RNA-seq Reveals the Effects of Light on Reproductive Traits in Domesticated Geese

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ABSTRACT

Studying the molecular mechanism of light regulation in goose reproduction can provide an important reference for domestic goose breeding. In this study, 2720 geese (first 18 weeks 2720, last 13 weeks 255) were divided into 12-h and 13-h light groups. The entire egg laying process was recorded and blood samples were taken at three times. The transcriptome was analysed on day 150. The results showed that melatonin and oestradiol increased gradually. On day 150, 17 genes were differentially expressed in the hypothalamus, pituitary and ovary. At this time, gonadotrophin-releasing hormone (*GnRH*) in the blood directly or indirectly inhibited the expression of *GnRH* in the pituitary and ovaries. The high oestradiol concentration in the blood suppressed the expression of *neuropeptide Y* in the hypothalamus, pituitary, and ovary tissues, and promoted the differentiation of ciliated epithelial cells in the oviduct. This study may provide a reference for light regulation of reproduction in poultry.

INTRODUCTION

Poultry industrialisation is an important source of meat for humans (Tan *et al*., 2023). Domestic geese hold a higher economic value than broilers and have a significant consumer market in China (Liu *et al*., 2023a). However, the low reproductive efficiency of geese severely limits their industrialisation. A goose typically lays no more than 100 eggs per year, with many breeds laying fewer than 50 eggs (Wang *et al*., 2009; Chang *et al*., 2016b). It is widely believed that the number of eggs laid by birds is strictly controlled by the hypothalamic–pituitary–gonadal (HPG) axis during the breeding process. Natural light induces a series of responsive changes in birds through the retina, pineal gland, and deep-brain photoreceptor cells. The melatonin secreted by the pineal gland plays a crucial role in this process (Wang *et al*., 2012; Bao *et al*., 2023).

Birds' response to this process is determined by the duration of light exposure. Gonadotrophin-releasing hormone (*GnRH*) mRNA levels increase in Beijing ducks exposed to 18 hours of light and 6 hours of darkness (18L:6D), and decrease in those exposed to 6 hours of light and 18 hours of darkness (6L:18D) (Haas *et al*., 2017). RNA-sequencing (RNA-seq) analysis of Zhedong white geese exposed to long (15L:9D) and short (9L:15D) artificial light conditions revealed 93 differentially expressed genes (Xu *et al*., 2022).

Light is critical for regulating the seasonal oestrus cycle in birds. In a light manipulation experiment, neurons with gonadotropin-inhibitory hormone (GnIH) were larger in birds at the breeding season than other times (Bentley *et al*., 2003). Many studies have focused on this area in an attempt to increase birds' egg production (Gou *et al*., 2022; Gratta *et al.*, 2023; Kliphuis *et al.*, 2024). We previously reported that light affects reproductive traits and gene expression in geese (Liu *et al.*, 2020). Although numerous studies have examined light regulation in broilers (Pan *et al.*, 2023; Wu *et al.*, 2023), no studies have focused on the molecular mechanism of light regulation in goose reproduction. Moreover, geese lay a small number of eggs each year, usually only around a dozen (Liu *et al.*, 2023b),

leading to relatively limited research in this area. This situation has seriously constrained the molecular breeding of geese.

Transcriptome analysis serves as an important research method to compare different breeds of domestic geese (Liu *et al.*, 2023b). In the present study, we used a combination of methods to reveal how light affects goose reproductive traits. The results of the study provide an important reference for domestic goose breeding, as well as for how light regulates poultry reproduction.

MATERIALS AND METHODS

2.1 Ethics statement

The study design was approved by the Committee for Animal Welfare of the Institute of Animal Husbandry, Heilongjiang Academy of Agricultural Sciences (No. NKY-20140506).

2.2 Animals

The experimental geese were reared on Fulaerji farm (47.35N, 123.92E), where the average annual temperature ranged from −1℃ to 10℃. The average daytime temperature reached a maximum of 37℃ in June, with the longest daylight duration being 15 hours. In January, the minimum nighttime temperature was −14℃, and the shortest daytime light duration was 10 hours. A total of 2,720 Sanhua geese (first 18 weeks 2720, last 13 weeks 255) were used in the present study. All geese were kept at natural temperatures and allowed to move freely in the exercise yard during the day. At night, they entered the room to either supplement light or avoid light. All geese received the same feed, and water was freely available. The male:female ratio was between 1:4 and 1:5 (Liu *et al.*, 2023a).

2.3 Egg-laying measurements

On 1 February 2022, after at least 6 months of feeding together, the geese were randomly divided into two experimental groups: a 12-hour light group comprising 1,110 geese and a 13-hour light group comprising 1,610 geese. A LED (light-emitting diode) light source with a color temperature of 5000K and a ground illumination of 20 lx was used. This date was considered day 1 of the experiment, and the entire experiment lasted 35 weeks. On 1 July 2022, a total of 2,018 geese were sold for commercial reasons, leaving 255 geese in each group. Egg production was recorded from 2 March to 3 October, for a total of 31 weeks. The data for the first 18 weeks was sourced from 2770 geese, and for the last 13 weeks it was sourced from 255 geese. Eggs laid outside this period were not counted. The number of eggs laid was recorded in a way that minimised stress for the geese. The laying rate and average number of eggs laid were calculated as follows:

$$\text{laying rate} = \frac{\text{number of eggs}}{\text{number of geese}} \text{ x } 100\%$$

$$\text{avarege number of eggs laid} = \frac{\text{total number of eggs}}{\text{total number of geese}}$$

The laying rate was divided into time stages according to week and month, and compared using one-way analysis of variance.

2.4 Measurement of blood biochemical indices

Between 9:00 and 11:00 am on days 38, 108, and 150, 10 healthy female geese were randomly selected from each group for blood collection. The blood samples were quickly put in liquid nitrogen, stored at −70℃ refrigerator, and transported using dry ice to Youxuan Biotechnology Co., Ltd. (Shanghai, China; http://www.sinobestbio.com). An enzyme-linked immunosorbent assay kit was used to measure the concentrations of *GnRH*, prolactin, triiodothyronine (T3), thyroxine (T4), follicle-stimulating hormone (FSH), luteinising hormone (LH), melatonin, progesterone, and oestradiol. The sensitivity of Goose oestradiol (E2) ELISA kit is 1.0 μ g/ml (YX-E052G, Shanghai, China; http://www.sinobestbio.com). The oviducts and uterus were collected on day 150. Tissue blocks were cut into approximately 3- to 4-mm fragments, which were then immersed in 4% paraformaldehyde for fixation. A 1:7 ratio of tissue block volume to 4% paraformaldehyde was used. After dehydration, the tissue was embedded in paraffin wax, sectioned, and stained with hematoxylin-eosin (HE) stain.

2.5 Tissue collection and RNA-seq

Five female geese were randomly selected from each group, and euthanised on day 150 in strict accordance with animal welfare protocols. The body weight, oviduct length, oviduct weight, and uterus weight were measured. The entire length of a single-sided oviduct and uterus weight percentages were calculated. The oviducts and uterus were divided. The hypothalamus, pituitary, and ovaries (removing the follicle) were taken from four geese, and RNA-seq was performed. Briefly, mRNA was purified from total RNA using poly-T oligo-attached magnetic beads for eukaryotes. The StepOnePlus™ Real-Time PCR System (Thermo Fisher Scientific, Waltham, MA, USA) was used, ensuring the library had a valid concentration of >10 nM. Sequencing was performed using the Illumina HiSeq™ X TEN (Illumina, San Diego, CA, USA). Differentially expressed genes in the hypothalamus, pituitary, and ovary between the 12-hour and 13-hour light groups were identified. Differentially expressed genes in at least two of the three tissues were subjected to Gene Ontology (GO) and Kyoto Encylopedia of Genes and Genomes (KEGG) enrichment analyses. The 'topGO' package (version 2.26.0) in R software (version 4.2.3) was used for GO analysis. KEGG analysis was conducted using the web-based online analysis tool KOBAS (2024).

RESULTS

3.1 Analysis of goose egg laying

The overall analysis of the egg-laying records revealed no significant difference in the laying rate between the 12-hour and 13-hour light groups. Figure 1A shows that in both the weekly and monthly analyses, there were significant differences at different stages. For example, from the second to the sixth week, there was a significant difference between the two groups, particularly at the 150 days mark, when the laying egg rate reached its peak. The differences were particularly significant at the beginning of the experiment. The figure shows that until 206 days, the average laying egg figure per goose did not exceed 60. At this time, the laying egg rate of the group was less than 5%, which means that the average annual number of laying eggs per goose is less than 60 under both lighting conditions.

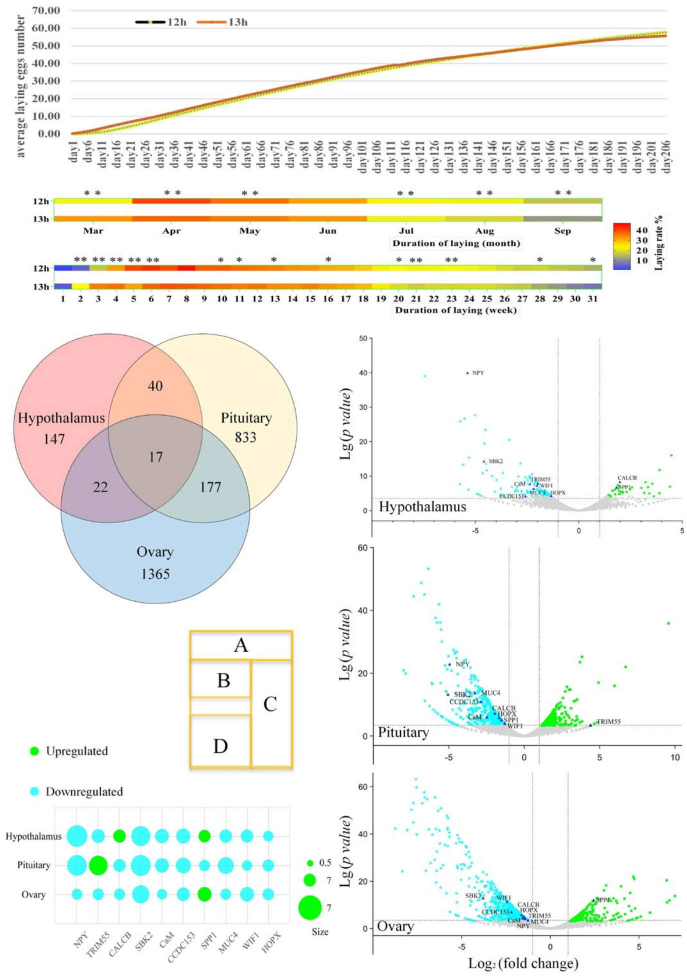

Figure 1 – Effects of light on egg production and tissue gene expression in geese. (A) The upper half shows the accumulated average number of eggs laid per goose, and the lower half shows the laying rate heatmap for the 31-week experiment and the average number of eggs laid in the 206 days (*p<0.05 and **p<0.01). Before 30 June, the 12-hour light group contained >810 females and >218 males, and the 13-hour light group contained 1,120 females and 380 males. Between 1 July and 3 October, the 12-hour light group contained 159 females and 46 males, and the 13-hour light group contained 168 females and 45 males. (B) Venn diagram comparing the differentially expressed genes in the hypothalamus, pituitary, and ovary between the 13-hour and 12-hour light groups. (C) Volcano plot of the differentially expressed genes in the hypothalamus, pituitary, and ovary. (D) Bubble plot of the differentially expressed genes in the three tissues. The dot size represents the log2 fold change. Seven genes were downregulated in all three tissues. The yellow grids in the figure indicate each labelling.

3.2 RNA-seq and KEGG enrichment analysis

Figure 1B shows a Venn diagram of differentially expressed genes in the hypothalamus, pituitary, and ovary. We identified 17 differentially expressed genes common to all three tissues. Of these, 10 genes have assigned symbols. These 10 genes are labelled in the volcano plot (Figure 1C). Notably, the direction of differential expression between the 13-hour and 12-hour light groups was not consistent across all three tissues. The bubble plot in Figure 1D shows the differences in positive and negative expression of these 10 genes in the three tissues. *TRIM55* were downregulated in the hypothalamus and ovary, but upregulated in the pituitary; *CALCB* were downregulated in the pituitary and ovary, but upregulated in the hypothalamus; and *SPP1* were upregulated in the hypothalamus and ovary, but downregulated in the pituitary. The other 7 genes were downregulated in the same direction. A total of 239 genes showed differential expression in two of the three tissues. The GO enrichment analysis did not yield significant results, so it not presented here. The KEGG enrichment analysis results for the differentially expressed gene *GnRH1* are shown in Figure 2.

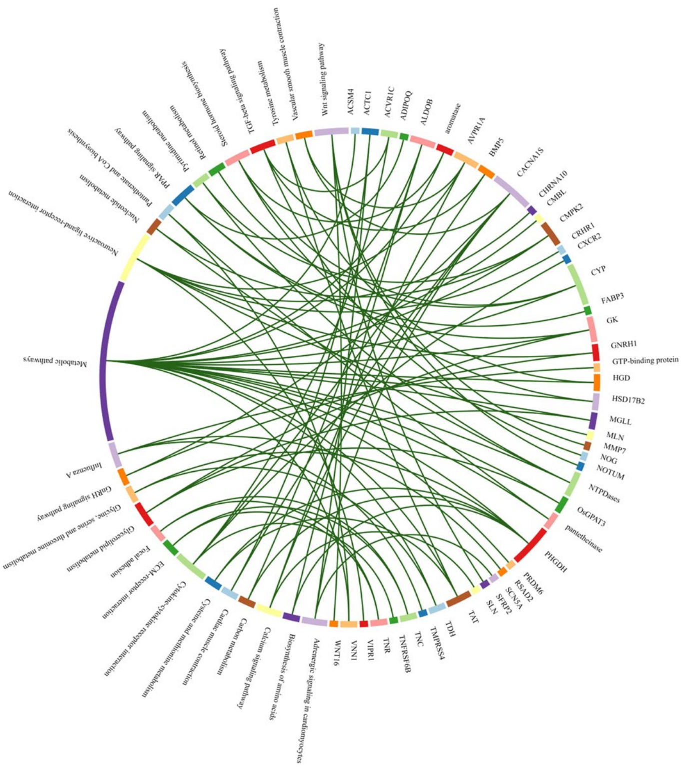

Figure 2 – Chordal graph for the KEGG enrichment analysis of differentially expressed genes comparing the 13-h and 12-h light groups. Signalling pathways are on the left, genes are on the right, and the arcs are the connections between genes and the enriched signalling pathways. The coloured arcs represent genes or signalling pathways, and the sizes of the arcs represent the number of connections.

3.3 Changes in blood hormone levels

Figure 3 shows the changes in the blood levels of *GnRH*, prolactin, T3, T4, FSH, LH, melatonin, progesterone, and oestradiol at different stages of the experiment. At the three evaluated time points (days 38, 108, and 150), prolactin, T4, and LH showed significant differences between the groups, and *GnRH* showed a downward and then upward trend from day 38 to day 150. Melatonin and oestradiol showed a gradual upward trend, and LH showed an upward trend followed by a downward one.

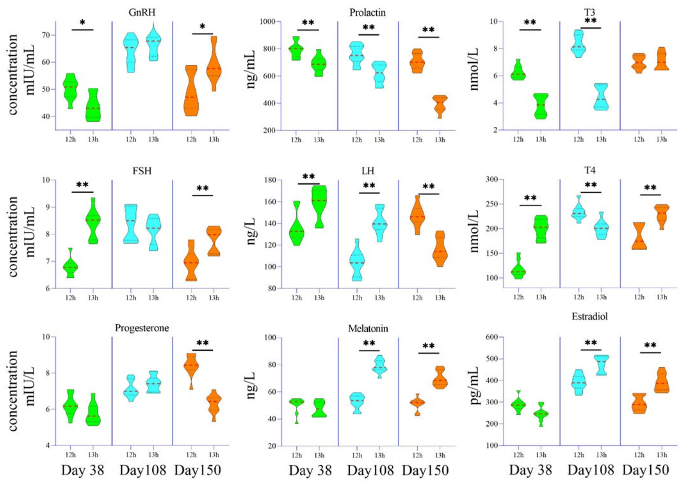

Figure 3 – Violin plots of hormone levels in the blood. Nine biochemical indices were evaluated in the 12-hour and 13-hour light groups at different stages of the experiment. Specifically, T4 and LH showed reversals on day 108 and day 150, respectively. $*p<0.05$ and $**p<0.01$ (n = 10). Gonadotrophin-releasing hormone (*GnRH*, mIU/mL), prolactin (ng/mL), triiodothyronine (T3, nmol/L), thyroxine (T4, nmol/L), follicle-stimulating hormone (FSH, mIU/mL), luteinising hormone (LH, ng/L), melatonin (ng/L), progesterone (mIU/L), and oestradiol (pg/mL) were evaluated.

3.4 Histological changes in uterus and ovaries

Figure 4 shows that light had no effect on the oviduct length or oviduct weight percentage. There was also no significant difference in the uterus weight percentage. Tissue sections showed no significant difference in mucosal thickness between the groups. However, the 13-h light group showed a higher number of cilia in the ciliated epithelium of the oviduct mucosa than the 12-hour light group.

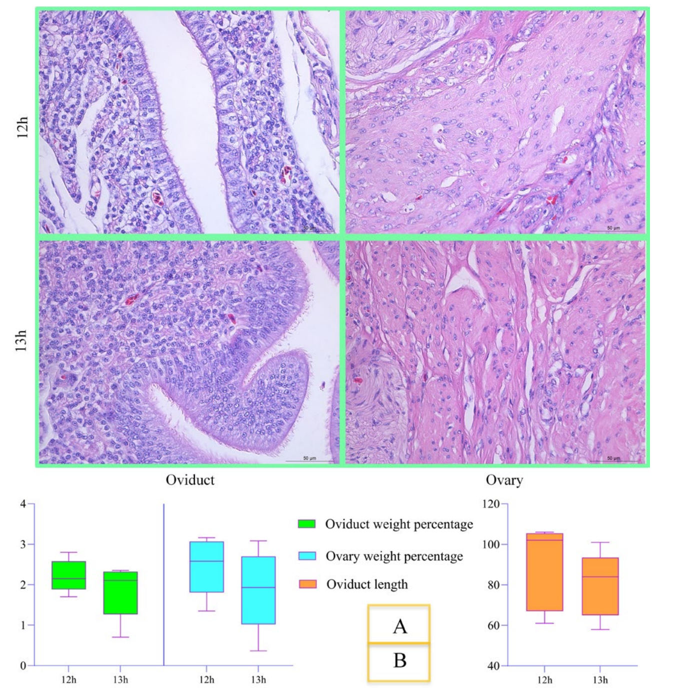

Figure 4 – Effect of light on gonadal tissue structure. (A) Micrographs of haematoxylin- and eosin-stained oviductal mucosal epithelium and uterus ampulla. A multilayered arrangement of the oviductal epidermal cells and cilia can be seen. (B) Box plot of the oviduct and ovary weight percentages and the oviduct length. The absence of a label indicates that there is no significant difference.

DISCUSSION

Research and applications in domestic goose breeding lag far behind those of chickens. Moreover, geese have significantly lower reproductive efficiency than chickens (Liu *et al*., 2023b). Goose reproduction is highly seasonal, and some breeds exhibit a strong tendency toward broodiness (Liu *et al*., 2023a). Elucidating the molecular mechanisms by which light affects egg-laying traits in geese has important theoretical and practical implications for the goose industry.

4.1 Light affects egg-laying traits in geese

Geese have typical seasonal breeding characteristics, with only a few months of egg production happening each year (Liu *et al*., 2023b). Different breeds of geese have completely different egg laying seasons (Wang *et al*., 2009; Yao *et al*., 2019). This process is jointly regulated by changes in environmental temperature (Frigerio *et al*., 2021) and natural environmental lighting (Liu *et al*., 2020). Numerous studies describe successful manipulations of sexual maturity and laying performance in broiler chickens through light-control practices (Gou *et al*., 2022; Gratta *et al*., 2023; Kliphuis *et al*., 2024). Recent studies have revealed that the pineal gland in geese directly perceives the annual cycle of daylight length, which in turn regulates gonad development and seasonal breeding patterns (Bao *et al*., 2023). Light-induced changes in goose egg-laying traits differ over time (Chang *et al*., 2016a). Throughout the entire 7-month period of our study, the egg-laying rate was not significantly different between the 12-hour and 13-hour light groups. However, a significant difference between the two groups was observed when we only considered the first 3 months of egg laying. Especially in the later part of the experiment, after selling a batch of geese in July, the average egg production rate was higher in the 12-hour than the 13-hour group (Figure 1A). This was caused by the long-term 13-hour light exposure, which helped the experimental group to adapt to the extended light period. A study on this topic demonstrated that prolonged light stimulation can lead to photorefractoriness (Hanlon *et al*., 2023). In other goose studies, extended light exposure affected egg production from days 23 to 178 (Wang *et al*., 2002a; Wang *et al*., 2002b; Wang *et al*., 2005; Wang *et al*., 2009; Chang *et al*., 2016a; Hanlon *et al*., 2023). Notably, there are also reports that shortening the length of light does not affect the number of eggs or the laying hours of geese (Chang *et al*., 2016a). In one study, white Roman geese laid eggs for 178 days while researchers compared 12.0 and 13.5 hours of light exposure, and the difference in the number of eggs laid was significant (Wang *et al*., 2009). By comparing these reports with our results, we can conclude that light affects the reproductive traits of domesticated geese.

4.2 Light-induced changes in blood hormone levels in geese

We found that on day 150 of extended light exposure, the *GnRH*, T4, FSH, melatonin, and oestradiol concentrations significantly increased, whereas the prolactin, LH, and progesterone concentrations significantly decreased (Figure 3). The melatonin and oestradiol concentrations gradually increased throughout the laying process. Similar to our results, another study has also shown that light caused a gradual increase in the oestradiol level of geese (Chang *et al*., 2016a). Figure 5 shows our mapping of how light affects reproduction in domestic geese. Light indirectly affects avian pineal glands, making them release melatonin (Scheiber *et al*., 2017; Hanuszewska-Dominiak *et al*., 2021; Ziolkowska & Lewczuk, 2021), which promotes the secretion of *GnRH* (Zhang *et al*., 2017; Wang *et al*., 2022), which in turn enters the bloodstream and has effects throughout the body. We found a gradual increase in the blood melatonin level in the geese of our study. This change may have been due to photorefractoriness (Hanlon *et al*., 2023), a special physiological state during which birds do not respond to light stimulation (Kosonsiriluk *et al*., 2016). Thus, the body cannot suddenly accumulate very high concentrations of melatonin. Excess melatonin may interfere with normal physiological functions (Holliman and Chyka, 1997; Johnson *et al*., 2019). In rats, melatonin downregulates the HPG axis and inhibits testosterone secretion (Yilmaz *et al*., 2000).

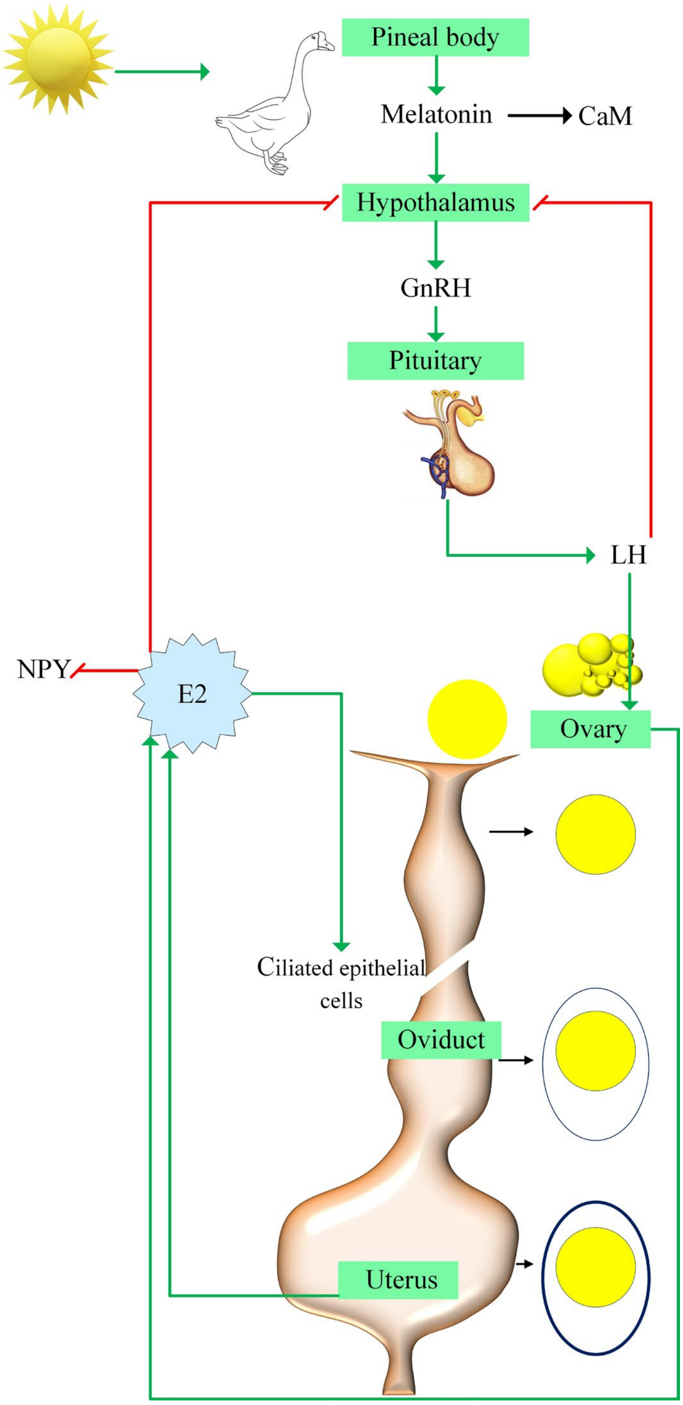

Figure 5 – Proposed model of the effects of light on the reproduction of domestic geese. The green arrows indicate facilitation, and the red flat-end lines indicate inhibition.

4.3 Light-induced structural changes in goose tissues and organs

Birds' flight characteristics, particularly their circadian rhythms and photoperiodic sensitivity, play a crucial role in regulating their sexual development. The HPG axis in birds is particularly responsive to changes in day length, which is a key environmental cue for many avian species. During the breeding season, also known as the photoperiodic breeding window, the HPG axis is activated, stimulating a surge in gonadotropic hormones such as LH and FSH. This surge triggers the rapid growth and maturation of the gonads, often resulting in a significant increase in size, sometimes by a factor of more than 100, preparing the birds for reproduction (Sengupta and Kumar Maitra, 2006). This hormonal response is a well-coordinated biological mechanism that ensures birds breed at the optimal time for survival and offspring success, and it often aligns with the availability of food resources.

We found that prolonged light exposure increased the number of cilia in the oviductal mucosal epithelium (Figure 4A). The oviductal mucosal epithelium contains both ciliated and non-ciliated cells (Desantis *et al.*, 2022). Oestradiol promotes the differentiation of ciliated epithelial cells in the fallopian tubes (Okada *et al.*, 2004). We found a significantly higher blood oestradiol level on day 150 in the 13-hour light group than in the 12-hour light group. There was no significant difference in melatonin between the groups on day 38, but there was a significant difference on days 108 and 150. These results indicate that naturally produced melatonin requires a process of accumulation. This process was not drastic and did not alter the oviduct length or the oviduct weight percentage.

4.4 Light affects gene expression in geese

A study of Zhedong white geese showed that exposure to light induces changes in ovarian follicles and leads to differential expression of multiple genes that are implicated in fatty acid metabolism and protein conversion (Xu *et al.*, 2022). We identified 10 genes that were simultaneously differentially expressed in three tissues (thalamus, pituitary, and ovary) (Figure 1D). Oestradiol inhibits *neuropeptide Y* (NPY) expression in murine neuronal cells (Stincic *et al.*, 2018). We also found that extended light exposure increased the blood oestradiol level (Figure 3), resulting in downregulation of *neuropeptide Y* expression in all three tissues (Figure 1D). *Neuropeptide Y* is a key gene that regulates the feeding behaviours of domesticated ducks. Short term (4 h) prohibition of food intake can lead to a decrease in *neuropeptide Y* expression (Liu *et al.*, 2008). Low level expression of *neuropeptide Y* can lead to a decrease in duck feed intake (Zeng *et al.*, 2016). Melatonin can bind to calmodulin, a key regulatory factor in the calmodulin pathway in mice (Argueta *et al.*, 2022). The results of our study suggest that prolonged light exposure during the egg-laying phase increases and decreases *SPP1* in each of the three tissues (Figure 1D). A light experiment in broiler chicken embryos showed no difference in *SPP1* (van der Pol *et al*., 2019). Hence, *SPP1* may be involved in a negative feedback inhibition pathway. Liu (Liu *et al*., 2022) reported that *GnRH* expression was increased in geese treated with extended light for 52 days. We found that after extended light exposure for 150 days, *GnRH1* expression was downregulated in the pituitary and ovary (Figure 2). However, the blood *GnRH* level was increased. These data suggest that blood *GnRH* directly or indirectly inhibits pituitary and ovarian *GnRH* expression.

4.5 Limitation

Some studies argue that light (Wang *et al*., 2009; Liu *et al*., 2020), temperature (Frigerio *et al*., 2021), and nutritional level (Chang *et al*., 2016a; Chen *et al*., 2023) are the three key factors determining the egg production of geese. This study was conducted with the same nutritional level and temperature between groups, changing only the lighting. The melatonin level of domesticated geese varies periodically within 24 hours (Alsiddig *et al*., 2017; Yu *et al*., 2024). The theoretically optimal melatonin sampling time is at night; however, geese have almost no vision at night, and having personnel enter the enclosure at this time can cause stress in the flock, affecting the overall experimental results. Therefore, we chose to collect test samples at the sports field.

CONCLUSION

Light affects domestic geese reproduction in a very complex manner. The slow increase and maintenance of melatonin and oestradiol at a high level may play a key role in this process, and oestradiol contributes to gonadal regulation of reproduction. We noted that at days 108 and 150, the blood melatonin and oestradiol levels were significantly higher in the 13-hour light group than in the 12-hour light group. In goose reproduction, the *GnRH* pathway is regulated by light. Multiple genes are involved in this process, and there are likely well-established negative feedback regulatory mechanisms that coordinate the HPG axis. In the future, light experiments should be executed in stages with well-established cage experiments while ensuring animal welfare. In particular, the mechanism of photorefractoriness in domestic geese should be clarified.

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AUTHOR CONTRIBUTIONS

XZ, SY and JS received the raw data. XZ, SY, JS, YZ, FP, ZM, HH and ML performed the analysis. XZ and ZG conceptualized the study.

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DATA AVAILABILITY STATEMENT

Please contact the author to request the data.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest to report.

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