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Reproductive characteristics and methods to improve reproductive performance in goose production: A systematic review

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ABSTRACT

In the past two decades, the high demand of and significance of poultry meat have promoted the development of the goose industry. Despite the continuous expansion of the goose breeding scale and the generation of large economic benefits by the goose industry, low reproductive efficiency remains a barrier to limit vigorous development of the goose industry. Poor reproductive efficiency can be attributed to breeding seasonality, strong broody behavior, and poor semen quality. Based on the reproductive endocrine regulation mechanism of geese, an overview of past studies that have developed various methods to achieve a significant improvement in goose reproductive performance including physical facilities for artificial illumination control and dietary nutrition manipulation to improve breeder reproductivity, and artificial incubation equipment and technology for better hatchability. The most recent advances utilize immunoneutralization to regulate critical hormones involved in goose reproduction. This review provides new information for industry and academic studies of goose breeding.

Introduction

Goose (*Anas cygnoides*) is an economically-important waterfowl bred commercially in numerous regions worldwide (Shi et al., 2008). A recent archaeological study has shown that in Tianluoshan, Southern China, geese were already in the early stage of domestication around 7,000 years ago (Eda et al., 2022), making them the oldest domesticated poultry species. The long-standing domestication process has given rise to thirty Chinese goose breeds and one cultivated breed in China (Ministry of Agriculture and Rural Afairs of China, 2020). The main products derived from geese include meat, eggs, fat liver, goose fat, down, and feathers (Kozák, 2021). Goose meat can satisfy the human body's need for multiple nutrients, being particularly rich in amino acids and minerals (Okruszek et al., 2013; Goluch and Haraf, 2018). As of 2024, according to FAOSTAT (Food and agriculture data), China is the world's leading goose - producing country accounting for 89.0 % of the global goose stock and 95 % of goose meat production (FAOSTAT, 2024). Other major goose - producing countries globally are Myanmar, the Russian Federation, Ukraine, Madagascar, Egypt, and Türkiye.

However, being the oldest domesticated poultry doesn't necessarily mean being the most abundant today. In fact, domestic geese account for less than 1.3 % of the world's poultry population. In China, the growth in goose meat and eggs production predominantly arises from the expansion of the goose-breeding scale, rather than an improvement in production efficiency. Poor reproductive efficiency, manifested particularly as low egg-laying performance, remains a critical bottleneck factor hindering the vigorous development of the goose industry. This situation can be mainly attributed to breeding seasonality and pronounced broody behavior (Zeman et al., 1990; Zhu et al., 2019a). Most goose breeds lay only 30-70 eggs during the breeding season (Shi et al., 2008; Yao et al., 2019), resulting in a decline in the economic value of the goose industry.

Therefore, in addition to the economic benefits of producing more meat through breeding larger-bodied geese, improving reproductive performance to produce more eggs and offspring is of utmost importance. Reproductive performance is demonstrated by the laying rate, fertility, and hatchability (Sellier et al., 1995). This performance is contingent not only upon the selection of goose genotype with high productivity but also on multiple factors. These include environment elements (such as light, temperature, and humanity), breeding management practices, nutrition, incubation technology, as well as disease prevention and control measures (Romanov, 1999; Ying et al., 2017;

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Salamon, 2020; Akhtar et al., 2021a; Chen et al., 2022a).

To promote rapid and high-quality development of the goose industry, it is both necessary and meaningful to summarize the various factors influencing the reproductive efficiency of geese and explore relevant solutions. This review comprehensively expounds on the reproductive activity patterns of geese and sums up several well - established methods for promoting goose reproduction.

Endocrine mechanism of goose reproduction

The reproductive activity of poultry is thought to be regulated by hormones associated with the hypothalamus-pituitary-gonadal (HPG) axis. Gonadotropin-releasing-hormone (GnRH), a key component in the HPG axis, is secreted in a pulsed manner by the hypothalamus. It plays a crucial role in regulating the secretion of various reproductive hormones. GnRH can control the synthesis and release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the pituitary gland. These hormones, in turn, stimulate the secretion of estradiol (E_2), progesterone (P_4) and testosterone (T) from the gonads (Sharp et al., 1998; Dubois et al., 2002). GnRH also works with vasoactive intestinal peptide (VIP) to promote the pituitary gland to secrete prolactin (PRL) (Mauro et al., 1989). These hormones work together and are involved in follicular and testicular development, ovulation, and broodiness in poultry. Nevertheless, they can also engage in feedback regulation GnRH secretion (Bédécarrats, 2015). Another hypothalamic neuropeptide, the hypothalamic gonadotropin inhibitory hormone (GnIH), can enhance PRL function by binding to receptors in the hypothalamus and pituitary gland or by directly interacting with GnRH neurons, thereby exerting an inhibitory effect on GnRH synthesis/release (Tsutsui et al., 2000; Ubuka et al., 2012). In addition, the synthesis and release of GnIH are predominantly affected by melatonin (MT) secretion during seasons, indicating that MT is also involved in regulating the reproductive activity of geese (He et al., 2014; Bao et al., 2023). Serotonin (5-HT), as reported, regulates avian reproduction through directly inhibiting GnRH synthesis and LH secretion and also controls VIP synthesis and release (Sakurai et al., 1986; Rozenboim et al., 2022). The types and functions of hormones related to goose reproduction are presented in Table 1. (Table 2)

Table 1
Types and functions of reproductive hormones in geese.

Hormones	Production site	Function	References
GnRH	Hypothalamus	Directly or indirectly stimulate the synthesis and secretion of pituitary gonadal hormones FSH, LH, and PRL.	Dubois et al., 2002
GnIH	Hypothalamus and gonads	Directly inhibits the synthesis and secretion of FSH and LH, and act on GnRH neurons to inhibiting the synthesis and release of GnRH.	Tsutsui et al., 2000
FSH	Anterior pituitary gland and basophils	Stimulates follicles growth and estrogen secretion.	Woods and Johnson., 2005
LH	Anterior pituitary gland and basophils	Under the synergistic effect of FSH, promotes ovulation and controls estrogen and androgen production by mature ovarian follicles, and regulates androgen production by Leydig cells.	Sharp et al., 1998
PRL	Anterior pituitary gland and basophils	A key endocrine factor initiates and maintains broody behavior in poultry and inhibits expression of steroidogenic enzymes.	Edens, 2011; El Halawani and Rozenboim, 1993
VIP	Hypothalamus	Promotes PRL release by binding to vasoactive intestinal peptide receptors (VIPR) on the cell membrane	Mauro et al., 1992
E_2	Ovary	Promotes follicular growth and ovulation, an important regulatory factor to start and maintain egg production in poultry.	Caicedo Rivas et al., 2016
P_4	Ovary	Collaborates with LH in promoting the development of prehierarchical follicles to hierarchical follicles.	Yang et al., 2019a
MT	Pineal gland	Transforms external light stimuli into endocrine signals to regulate broody behavior.	Bao et al., 2023
5-HT	Hypothalamus	Directly inhibits GnRH synthesis and LH secretion and control VIP's synthesis and release.	Rozenboim et al., 2022
T	Testes and ovary	Affects spermatogenesis and testicular development, as well as stimulates P_4 production.	Gumułka et al., 2023

Reproductive characteristics of goose

The reproductive activity of geese adheres to an annual cycle rhythm of the "laying period-nesting period (broodiness)-recovery period". The length of the laying period differs among breeds and regions. The reproductive characteristics of geese include seasonality, broody behavior, poor semen quality, and mate-selection behavior. Research on the reproductive traits of geese has primarily concentrated on the first two of these aspects. The following briefly summarizes some of the internal factors contributing to the poor reproductive performance of geese.

Seasonality

Geese clearly exhibit a distinct seasonal reproduction pattern (Zeman et al., 1990). Seasonal reproduction is an adaptive evolutionary strategy adopted by animals inhabiting regions with obvious seasonal variations (Buck, 2016). The alternations between the phases of reproductive active and sexual quiescence serve to optimize the survival prospects of both offspring and parent (Sharp, 1996; Nishiwaki-Ohkawa and Yoshimura, 2016). This seasonal reproduction phenomenon is synchronized by periodically changing environmental factors. Among these, the day length (photoperiod) is particularly the predominant regulator of seasonal breeding behaviors (Gwinner, 2003; Sharp, 2005; Ono et al., 2009; Liddle et al., 2022). Birds likely possess more sophisticated photoperiod regulatory mechanisms compared to other vertebrates. The seasonal reproductive phases in birds are regulated by the neuroendocrine system, predominantly occurring at the HPG axis level. During the activation of the HPG axis within a year, GnRH stimulates the release of FSH and LH. Theses hormones, in turn, stimulate gametogenesis (spermatogenesis in male and oogenesis in females) and the manifestation of reproductive behaviors (Dawson et al., 2001; Huang et al., 2008; Zhao et al., 2017). The HPG axis is automatically switched off when the breeding season ends, LH secretion is inhibited, and the gonads begin to atrophy and cease reproductive activity; this is the so-called “photorefractoriness” phenomenon (Nicholls et al., 1988). Similarly, the photoperiod exerts a strongly regulatory influence on the secretion of PRL and VIP. These two substances also participate in regulating the seasonal reproductive activities of birds (Sharp and Blache, 2003; Huang et al., 2008). The periodic rhythmic changes in sunshine throughout the year determine the establishment of seasonal reproductive characteristics and the length of reproductive periods in poultry.

Table 2
Main reproductive characteristics of common breeds of geese.

Breeder	Age at first egg (d)	Breeding season	Annual egg production	Hatchability of fertile eggs(%)	References
Shitou	235	From September to April of the following year	25~35	85~90	Huang et al., 2008;
Magang	140~150	From July to March of the following year	30~40	87~92	China National Commission of Animal Genetic Resources, 2011;
Zhedong	180	From October to April of the following year	30~45	80~90	
Zi	185~205	From the end of February to July	70~100	85~90	
Wanxi	182	From January to April	30~36	91	Chen et al., 2013;
Yili	300	From March to May	10	81.9	
Yangzhou	160-180	From September to May and June of the following year	70~75	85~89	Yu et al., 2016a;
Huoyan (Wulong)	190~220	From January to July	80~110	86~93	Yang et al., 2019a
Sichuan white	220~240	From October to April of the following year	60~80	90~94	Zhu et al., 2017b;
Hungarian	240	From February to June, and August to November	30~50	80	Liu et al., 2021a;
White Roman	220	From March to April	25~50	88	
Landes	180	From October to May of the following year	35~40	65	Luo et al., 2024

All goose breeds used in China are seasonal breeders, and they can be classified into two types depending on their seasonality characteristics (Shi et al., 2008). Long-day breeders, including the Yangzhou, Huoyan (Wulong geese), Zi, Landaise, Jilin White and Hungarian White geese, engage in breeding during spring and early summer. In contrast, short-day breeders, such as the Shitou geese, Magang, and Zhedong White geese breed from late summer to the following spring. The long rest period in seasonal reproduction has greatly restricted the production of goslings and diminished breeding efficiency. In addition, as seasonal breeding species, the reproductive status of ganders also exhibit seasonal changes, such as fluctuations in mating activity, semen quality, and reproductive endocrine hormones (Shi et al., 2007; Gumułka and Rozenboim, 2013; Leska et al., 2015). Marked differences exist in testicular morphology and steroid hormone secretion functions between the peak breeding stages and non-breeding seasons (Gumułka et al., 2021). The decreased reproductive potential of geese caused by seasonal breeding has hindered the development of the goose industry. Therefore, overcoming the seasonal restrictions of goose breeding, perhaps mainly through light regulation, represents a crucial strategy for the advancement of the modern goose industry.

Broody behavior

Broodiness, a common maternal behavior of most domestic fowls, is characterized by the cessation of egg laying, persistent nesting, and protection of eggs in the nest (Romanov et al., 2002). This behavior is essential for ensuring natural reproduction and is a product of natural selection, as it involves producing new offspring through the natural incubating process. However, the advent of widely- adopted artificial incubation technology has confirmed its negative impact on egg production. Particularly, for some indigenous chicken and goose breeds, the broody behavior persists despite commercial egg incubation has been comprehensively applied (Yao et al., 2019; Sarkar, 2022).

As seasonally reproducing waterfowl, domestic geese are highly broody among poultry species. More than 90 % of goose species exhibit broodiness. Breeds such as the Zhedong White, Magang, and Xupu geese exhibit strict seasonality, an obvious broodiness tendency, and poor egg laying performance, producing only 30-40 eggs (Qin et al., 2013; Yu et al., 2016a, 2021). Therefore, their egg-laying performance is severely compromised, leading to a decline in the economic value of the goose industry. Conversely, some goose breeds, like Huoyan, Zi, and Taihu geese, show relatively weak broodiness and can lay 70-100 eggs annually (China National Commission of Animal Genetic Resouces, 2011; Liu et al., 2021a). The strong broodiness of geese markedly impedes the development of goose industry.

The HPG axis is a coordinated neuroendocrine system that modulates broody behavior in poultry. Among endocrine hormones, PRL is the dominant and most direct factor, triggering poultry to engage in nesting behavior (Edens, 2011; Yao et al., 2019). The regulatory mechanism of PRL on goose reproductive activity varies depending on its secretion level or blood concentration (El Halawani and Rozenboim, 1993; Li et al., 2011; Deng et al., 2023). After egg laying, the mRNA levels of GnRH in the hypothalamus decrease, while the mRNA level of VIP in the pituitary gland increase. Simultaneously, LH secretion declines, and the concentration of PRL in the blood gradually rises. The elevated PRL levels, following decreased P_4 and E_2, induce ovarian atrophy and a decline in ovarian function, ultimately resulting in brooding behavior (Yu et al., 2016b; Wang et al., 2021a). In addition, PRL exerts a dual-action effect on regulating the proliferation and apoptosis of goose granulosa cells (GCs) depends on its level. The stage of follicular development has also been identified using *in vitro* cultured GCs isolated from goose pre-hierarchical follicles (Deng et al., 2023). Hence, identifying appropriate s methods or technology to inhibit PRL synthesis and secretion, or immunization against its activity will be beneficial for suppressing broodiness, shortening the broodiness period, or eliminating broodiness, thereby improving the reproductive efficiency of goose.

Poor semen quality

Geese have lower reproductive efficiency (RE) than other poultry species like chickens and ducks. Besides the seasonality of reproductive behavior which is the primary limiting factor, low fertility also “significantly contributes” to this situation (Liu et al., 2008; Salamon, 2020). The fertilization rate of breeding eggs is determined by the combined action of both sexes. as such, it is greatly influenced by the egg quality and semen quality of males.

However, the testicular development of ganders remains relatively restricted even in adulthood, resulting in lower sperm quality. The percentages of live spermatozoa of 1- and 2-year-old ganders are similar. However, the proportion of live spermatozoa with normally morphology, a key determinant of the fertilization rate, is extremely higher in older ganders (Lukaszewiczl et al., 2000). Another study showed that 2-year-old ganders have a smaller semen volume but a higher percentage of morphologically normal viable spermatozoa than 1-year-old ganders (Boz et al., 2021). In addition, in Yangzhou ganders, the testis maturation period (227 days) is longer than the body maturation period (160-170 days). The presence of immature sperm in the early egg laying stages results in a lower fertilization rate within goose herds (Akhtar et al., 2020). Therefore, the low fertility rate in young geese can likely be attributed to the ganders.

The molecular mechanisms underlying the switch between quiescence and recrudescence in testicular morphometry, semen quality, and functions have not been fully elucidated. T and E_2 play crucial roles in tetis development, function and male reproduction (Liu et al., 2008; Leska et al., 2015). Moreover, PRL shows an inverse relationship with LH, T, and semen quality in ganders (Gumułka and Rozenboim, 2015). A more recent study indicated that the interaction between the process of cell proliferation and apoptosis may, in part, account for the annual changes in testicular weight and histological structure in domestic seasonal-breeding geese (Gumułka et al., 2022).

Artificial lighting to improve reproductive efficiency

All aspects of production, including nutrition, environmental factors (such as light and temperature), feeding methods, and diseases occurrences, can directly or indirectly influence laying rate, fertility, hatchability, and the number of health goslings produced (Djermanovic et al., 2023).

Photoperiod programs

In most avian species, light perception occurs at two major sites: the retinal photoreceptors and the extra-retinal deep brain photoreceptors (DBPs) which are associated with reproductive function (Menaker and Underwood, 1976; Nakane et al., 2010; Rozenboim et al., 2022). Once a lighting stimulus is received, neural signals from DBP are transmitted to the pars tuberalis (PT) and then affects the release of thyroid-stimulating hormone (TSH) from the pituitary gland (Kuenzel et al., 2015). Subsequently, the TSH induces the activation of the Type 2 deiodinase (Dio2)/Type 3 deiodinase (Dio3) system and converts the inactive thyroxine (T4) into its active form-triiodothyronine (T3). in turn, T3 regulates the production and release of GnRH/GnIH in the hypothalamus, thereby controlling the reproductive activities (Mishra et al., 2017; Zhu et al., 2019a).

Owing to the crucial regulatory role of light in seasonal reproduction, in modern goose production, artificial illumination is provided, and photoperiod programs have been developed to overcome the limitation of seasonal breeding and enhance productivity (Shi et al., 2008; Wang et al., 2002a, 2002b, 2005, 2009; Chang et al., 2016a; Zhu et al., 2017a). A meta-analysis conducted on White Roman geese revealed that supplementary artificial light increases the average egg production, the length of egg laying, and the fertility rate (Liu et al., 2020a). In the case of Zi geese from the northeast China, the average egg production and fertilization rate of the group exposed to 14-h light were higher than those of the group with12-h sunlight exposure (Zhao et al., 2020a). Our latest research showed that appropriately prolonged light exposure significantly reduces the mRNA expression of *spexin* in the hypothalamus and pituitary gland of female Yangzhou geese, thereby regulating reproductive activities (Liu et al., 2022).

Nevertheless, for typical short-day breeding geese, such as Zhedong White geese, when exposed to a photoperiod of 9L:15D, produce more eggs than exposure to a long photoperiod (15L:9D), making geese terminate nesting and resuming laying eggs (Chen et al., 2021). This reason might be that a long photoperiod induces ovarian atrophy and follicular atresia, thus inhibiting the development of follicles (Xu et al., 2022). Regarding Magang geese (also short-day breeding birds), a long photoperiod condition (18L:6D) led to a decreased laying rate of female geese and the atrophy and degenerate of testicular function, inhibiting the reproductive performance of the geese. Furthermore, the *THRb, TRH*, and *DIO*2 expression in the hypothalamus were downregulated, affecting the expression levels of reproductive axis related genes and the concentration of reproductive hormones (Pan et al., 2022). A recent study reported that the methylation of the serotonin metabolic pathway in the hypothalamus is also related to the cessation of reproductive activities in Magang geese during long light exposure (Liu et al., 2023).

In addition, artificial lighting programs have been employed to switch egg-laying period and achieve out-of-season breeding under water-fall ventilation house in geese production. Starting from winter and spring, a photo period-program consisting of an 18-h long photoperiod for two and a half months, followed by an 11-h short photoperiod, successfully enabled out-of-season summer breeding in the natural non-breeding seasons in Magang geese, resulting in economic benefits that were five to six times greater than conventional production (Sun et al., 2007). For long-day breeding Yangzhou geese, our previous study demonstrated that out-of-season breeding during the summer months can be achieved using a basic photo-program. This program involves an 8-h short photoperiod for 8 weeks and a 12-h illumination time and an additional 18-h ultra-long light exposure for 1 month prior to this basic program has a better promoting effect on egg-laying performance (Zhu et al., 2017a). The photoperiod, by regulating the expression and secretion of many reproductive hormone genes in the hypothalamic-pituitary region and under the coordination of PRL-VIP system, has made out-of-season breeding a success. The effects of photoperiod programs on the reproductive performances of breeding geese from 2002 to 2024 are presented in Tables 3.

Although the photoperiod is the primary cue used by birds to regulate seasonal reproduction, prolonged exposure to light does not always enhance their reproductive performance. Instead, they cease to respond to long days of light, a phenomenon known as photorefractoriness has begun (Dawson and Sharp, 2007). The main characteristics of photorefractoriness include not only the hyper-regulation of *GnIH* gene expression in the hypothalamus but also the upregulation of *VIP* and *TRH* expression in the pituitary gland of goose (Zhu et al., 2017b).

Light spectrum

In addition to photoperiod, intensity/brightness and spectrum (color) are also used to define and manifest light quality. these factors significantly affect poultry productivity (Prayitno et al., 1997; Parvin et al., 2014; Rault et al., 2017). Varying light spectra act different on photoreceptors, thereby influencing gonadal development and function (Lewis and Morris, 2000). Red light of long wavelength can penetrate the skull and tissues and stimulate extra-retinal photoreceptors (ERPRs), thus activating the gonadal axis (Mobarkey et al., 2010). It is also beneficial for egg laying and the age at first laying. Short wavelength light, such as blue and green light, is either ineffective or inhibitory to egg laying but enhances growth. The stimulatory effects of certain wavelengths do not require a functional retina (Baxter et al., 2014; Li et al., 2020; Rozenboim et al., 2022). When breeding Roman geese under red light-emitting diode (LED)-light, a longer laying period and a greater total number of egg were observed compared to blue or white LED-light, indicating that red light is more suitable for breeding management (Chang et al., 2016b). In another study, we reported that using white and red LED lighting with an 11L:13D photoperiod in Yangzhou geese resulted in better egg-laying performance than blue or green light treatments owing to differences in the expression of *PRL, VIP*, and *GnIH* genes under these lighting regimens (Zhu et al., 2019b). Red light also increased the egg production of Zi geese, accompanied by increased serum GnRH concentrations and decreased PRL, MT, and T4 levels (Li et al., 2022a). Metabonomics confirmed that pathways such as GnRH signaling pathway and the PRL signaling pathway are crucial in regulating the reproduction of Zi goose under red light (Li et al., 2022b). However, when white, red, and blue light were applied to 3-year-old Roman ganders, only white light improved semen quality and the proportion of morphologically normal spermatozoa, indicating that in terms of the semen quality of ganders, artificial supplementation with white light is more effective than red or blue lights (Chang et al., 2016c). These findings suggest that the photoreception of different light wavelengths may vary among different goose species and between different

Table 3
Summary of the effects of photoperiod programs on reproductive performances of breeding geese during 2002-2024.

Breeder	Ages	Light: Dark	Intensity (lux)	Significant effects	References
White Roman	19-40 weeks	14L:10D or 18L:6D followed by 10L:14D	40–50	The photoperiod of 14 h improved weight and fertility of eggs, and suppressed age at first egg laying (AFE)	Wang et al., 2002a
White Roman	38- weeks	20L:4D or 4L:20D or natural lighting	40-50	Short light day of 4 h prolonged the duration of egg production, while extreme long 20 h light stopped egg production in laying geese within a month	Wang et al., 2002b
White Roman	1.5 years	20L:4D or natural lighting	20, 120, 220	A tendency for the geese in 20 h group to produce more eggs annually than those in the control group	Wang et al., 2005
Magang	——	18L:6D followed by 11L:13D	——	Successfully achieved out-of-season lay in the natural non-breeding seasons in the spring and summer months.	Sun et al., 2007
White Roman	——	Between 12.0L:12.0D and 13.5L:10.5D	50	An earlier laying peak of the geese in the breeding season and higher egg production	Wang et al., 2009
White Roman	2.7 years	6.5L:17.5D or 19L:5D	30-40	Short light treatment had a higher laying intensity, fertility and hatchability, while long light treatment had a longer laying period.	Chang et al., 2016a
Yangzhou	77 D-46 weeks	Included or not 18L: 6D		Induced out-of-season breeding in summer and inclusion 18-h long photoperiod further improved the egg-laying rate	Zhu et al., 2017a
Zi	2 years	12 L:12D or 14L:10D	——	The average egg production, fertilization rate and the serum LH and FSH concentrations of the 14 L group were significantly higher than those of the 12 L group	Zhao et al., 2020a
Zhedong White	7 months	9 L:15D or 15L:9D	30	9 h short light treatment shortened the broody duration, increased egg production, and promoted their growth and development	Chen et al., 2021
Magang	1 year	18L:6D	——	The egg-laying rate decreased gradually and stopped on d30, and the gonadal indices decreased gradually.	Pan et al., 2022

genders.

Light intensity

The light intensity/brightness is measured in watts/m^2 or lux (lx). Regardingthe influence of lighting intensity on breeding geese, Pyrzak et al. (1984) reported that two lines of geese exposed to a light intensity of 20 lux for 16 h had better egg production than those under of 50 lux. Another study showed that, under the conditions of semi-open house, using a shading net in summer to reduce the light intensity could get better laying performance and eggshell quality of Northeast white geese during the later laying period (Zhao et al., 2020b). White Roman geese raised under a lighting intensity of 170 lux exhibited higher hatchability and egg weight than those in the 40 and 430 lux light groups (Chang et al., 2016d). These inconsistent results might be owing to the different spectral sensitivity of various goose breeds (Prescott et al., 2003) and the type of illuminants used. such factors lead to differences in the perception of light intensity and, consequently, diverse influences on reproduction. Considering the role of light intensity and spectrum in poultry reproduction, designing customized illumination with specific spectral ranges and providing different intensities can enhance reproductive activities through artificial illumination.

NUTRITION SUPPLEMENTATION TO IMPROVE REPRODUCTIVE EFFICIENCY

Nutrition is the foundation for the life activities of animals. The nutritional composition of feed affects the functionality of specific digestive enzymes (such as trypsin and chymotrypsin) in animals. It is also a crucial factor in maintaining stable reproductive performance. The levels of energy, protein, along with the content and proportion of vitamins and trace element in the feed are closely related to reproductive performance by regulating the expression of endocrine and reproductive axis-related genes in breeding geese.

Energy and crude protein (CP)

Energy and protein are the most indispensable substances in the diet of goose. Appropriate levels of metabolic energy (ME) and CP in the diet are critical to the reproduction of geese. The National Research Council (NRC) recommends that the diets for geese during the laying period should content 15 % CP and 12.13 MJ/kg of ME (NRC, 1994). The laying White Roman geese fed a diet containing 15 % CP had a higher hatchability than those fed an 18 %-CP diet (89.7 vs. 63.1 %); however, dietary CP had no obvious effects on eggs production, laying period, and fertility (Chang et al., 2016a). Under the condition of a constant ME level of 11 MJ/kg, Shitou geese in the high CP level groups (16 %, 17.5 %, and 19 %) had significantly higher egg production, hatchability, serum E_2 concentration and expression levels of pituitary *FSHβ* and ovarian *FSHR* than those in the low CP groups (13 %, 14.5 %,); however, the serum uric acid concentration in the 19 % level group was significantly higher than that in the other four groups, which indicates that increasing the dietary CP level within a certain range can improve reproductive performance by regulating endocrine and related gene expression, while an overly high CP level will cause protein waste (Zhang et al., 2015).

Feeding broiler breeders with high- or low-ME diets has been shown to decrease egg production (van Emous et al., 2015). In the case of breeding Yangzhou geese, a low dietary energy level of 9.65 MJ/kg was insufficient, resulting in low egg production; conversely, diets with an energy level of 11.75 MJ/kg decreased the hatchability of fertilized eggs and increased liver weight; an energy level ranging from 10.13 to 10.28 MJ/kg is recommended for use in the diets of breeding Yangzhou geese during the late laying period (Chen et al., 2023a).

There exists an inherent interaction between the CP and ME. The appropriate ratio of these two components is crucial for ensuring a balanced supply of primary nutrients in breeding geese. In actual production, increasing the dietary protein and energy levels can improve the production performance of breeding geese. However, this approach often leads to a high diet cost, and the benefits obtained are not always optimal. Therefore, determining the optimal nutritional level of the diet requires consideration of both the physiological needs of the geese and economic benefits. In addition, the recent shortage of raw protein materials has posed challenges to the feed industry. The protein requirement in animals primarily involves the demand of amino acids. The application of low-protein diet technology and synthetic amino acids can reduce the proportion of soybean meal in feed (Zhou et al., 2021; Liang et al., 2023). Low-protein diets also help to reducing environmental pollution caused by nitrogen and ammonia emissions (Liang et al., 2023). Currently, studies on the effects of low-protein diets on the reproductive performance of geese are scarce, making this a key research direction for future investigations.

Essential trace elements

Some essential trace elements, such as manganese (Mn), zinc (Zn), selenium (Se), and iron (Fe), serve as components and activators of various enzymes and exert a significant impact on reproduction in poultry (Latshaw et al., 1977; Inkee et al., 2009; Olgun, 2017; Liao et al., 2018).

Due to its relatively low content in the diet content and low absorption in the gut, Mn supplementation in poultry diets is necessary to meet the nutritional requirements (Liao et al., 2019). Dietary Mn supplementation at 10 mg/kg increased egg mass and improved sperm motility and hatchability in hens (Attia et al., 2010). Supplementing the basal diet (17.5 mg/kg of Mn) with 85-95 mg/kg of Mn can meet the needs of laying ducks (Zhang et al., 2020a). During the laying period, dietary appropriate Mn supplemental level (24.27-32.91 mg/kg) can improve the laying rate, fertilization rate, hatchability, eggshell thickness, eggshell strength, and the serum FSH content in breeding geese (Wang et al., 2019a). Another study showed that although dietary supplementation with 30 mg/kg Mn in breeding Wulong geese did not significantly affect egg quality, it significantly increased the laying rate and E_2 secretion and enhanced the total antioxidant capacity, especially the combination with 5.0×10^9 CFU/kg *Bacillus subtilis* (BS) yield the optimal effect (Wang et al., 2020a).

Se is a vital component of glutathione peroxidase and exhibits antioxidant properties. It also has a crucial influence on the reproductive function of animals, such as laying performance, spermatozoa fertilization capacity, and embryonic development (Ursini et al., 1999; Yuan et al., 2011; Liu et al., 2020b; Zhang et al., 2020b). When the commercial feed of White Koluda ganders was fed with Se (0.3 mg/kg) and vitamin E (100 mg/kg), semen quality and ejaculate volumes improved, and the percentage of immature sperm decreased (Jerysz and Lukaszewicz, 2013), thereby increasing the reproductive efficiency of geese. However, the application of Se in goose diets has mainly been focused on young geese. For instance, dietary selenomethionine (SeMet) improved the antioxidant capacity of breast muscle in male geese through the glutathione system (Wan et al., 2020). The impact of dietary Se on the egg production performance of breeding geese remains unreported. In laying hens, an increase in dietary Se content significantly increased egg production and resulted in the production of Se-enriched eggs (Liu et al., 2020b).

Zn is a pivotal microelements essential for normal reproduction function, such as semen quality, egg production, and hatchability (Huang et al., 2019). Zn deficiency led to poor semen quality, lower hatchability rate, lower egg production, abnormal embryonic development, and poor-performing offspring in poultry (Blamberg et al., 1960; Zhu et al., 2017). Dietary 35 mg/kg Zn dosage is suggested for laying hens by NRC (NRC., 1994). However, the Zn requirements of goose breeders were not recommended in the NRC. Shi et al. discovered that dietary Zn supplementation for breeding geese was beneficial for the qualified egg rate, fertilization rate, and hatchability rate, and they suggested dietary Zn dosage of 65 −70 mg/kg of feed for goose breeder (Shi et al., 2019). A further study showed that dietary *Bacillus subtilis* (BS) supplementation reduced the Zn requirement for Wulong goose breeders, and there were significant interactions between Zn and BS (Fan et al., 2022). Reportedly, organic Zn is better than inorganic Zn in improving egg production and eggshell thickness (da Silva et al., 2024).

Fe is also an essential trace mineral, and the dietary Fe concentration influences the Fe content in the yolk, and the hatchability of hens (Morck and Austic, 1981; Inkee et al., 2009; Taschetto et al., 2017). Both iron deficiency and overconsumption have detrimental effects on animals (Godyń et al., 2016; Li et al., 2024). Limited research has been conducted on Fe requirements of breeder geese. A study using Wulong breeder geese showed that supplementing Fe in the diet had promotional effects on egg weight, fertility, serum total antioxidant capacity, and hematopoietic function; in addition, there were interactions between dietary Fe and BS addition, with 60 mg/kg Fe and 5.0×10^9 CFU/kg BS demonstrating the best results (Zhang et al., 2020c). The effects of essential trace elements on the reproduction response of breeding geese are summarized in Table 4.

Vitamins

Although the proportion of vitamins in feed is relatively low, they are involved in the entire growth and developmental processes of poultry and are essential for the avian body. An optimum concentration of vitamins in poultry diets allow birds to perform their genetic potential.

As an important fat-soluble vitamin, the biological activities of vitamin A (VA) include the maintenance of the normal visual function of animals, the integrity of epithelial tissue, growth performance, immunity, egg production and quality, and antioxidants effects (Khan et al., 2023). The NRC (1994) recommended a nutritional requirement of 4000 IU/kg of VA for breeding ducks and geese. However, researchers generally believe that this requirement represents the minimum for the animal body and may not achieve optimal effectiveness. A study found that the addition of 8 000 to 12 000 IU /kg of VA to the breeding Yangzhou geese diet could improve egg quality, reduce lipid peroxidation products, and improve the antioxidant capacity of the eggs (Dai et al., 2019). This suggests that these dosages might be the appropriate level of VA addition in the breeding geese diet. Additionally, VA can be transferred from maternal to offspring through eggs. The growth and development of offspring were affected by the amount of VA added to the maternal diet. Dietary VA supplementation in breeding Yangzhou geese significantly affected the early growth performance, antioxidant index, tissue VA content of the goslings, immune organ weight, the immune organ index and immunoglobulin content in goslings (Liang et al., 2019; Yang et al., 2020). Taken together, supplementing maternal diet with12,000 IU/kg VA and offspring diet with 9,000 IU/kg VA is conducive to gosling growth.

Vitamin D (VD) participates in regulating calcium and phosphorus metabolism, facilitating bone calcification and eggshell formation process, and plays an essential role in the reproductive processes of poultry (Keane et al., 2017; Hrabia et al., 2023;). It can be produced endogenously from 7-dehydrocholesterol in the skin upon exposure to ultraviolet radiation b (UVB). However, with the development of the modern poultry farming industry, birds have shorter exposure to sunlight, causing lower synthesis of VD in their body. Consequently, supplementing sufficient VD in the diet is very necessary. There are four forms of VD, namely VD_3 (also known as cholecalciferol), 25-OH-D_3 (the primary storage and transport forms in animals), 1,25- $(OH)_2$-D_3 (the active form), and VD_2. Dietary VD_3 supplementation during the laying period of breeder geese significantly increased the number of qualified eggs, enhanced eggshell quality, elevated serum T and P_4 concentrations, and improved serum antioxidant enzyme activities, and a combination of 400 IU/kg VD_3 and50 μg/kg 25-OH-D_3 supplementation yielded the optimal effects (Zhang et al., 2023). However, feeding pullets an excessively high VD_3 content resulted in reduced growth and decreased laying hens performance (Wen et al., 2019). For Lohmann White laying hens, additional VD supplementation, regardless of forms (VD_2, VD_3, and 25-OH-D_3), had no significant impact on egg production and quality (Adhikari et al., 2020). These findings indicate that the dosage and effectiveness of different VD forms may vary among different poultry breeds and age groups.

Vitamin E (VE) is essential for human and animal reproduction (Evans and Bishop, 1992). However, poultry cannot synthesize sufficient VE and thus needs to obtain it from the diet to meet body requirements (Khan et al., 2012). The supplementation of VE is crucial in the antioxidant process as it protects cellular membranes from reactive oxygen species and prevents the formation of free radicals (Niki, 2014). The beneficial effects of dietary VE on egg laying, and antioxidant capacity in laying hens have been investigated (Jiang et al., 2013). In the late laying period of Jiangnan White breeding geese, both VE deficiency and an excessive dose (2000 IU/kg) hampered reproductive performance and

Table 4
The effects of essential trace elements on the reproduction response of breeding geese were summarize.

Breeder	Age	Treatment	Optimum level	Significant effects	References
Wulong	34 weeks	Mn	24. 27 −32.91 mg/kg	Suitable Mn supplementation improved the reproductive performance, eggshell quality, serum total antioxidant capacity and FSH content.	Wang et al., 2019a
Wulong	46 weeks	Mn BS	30 mg/kg 5×10^9 CFU/kg	Inclusion of suitable Mn and BS provided the optimal effects on production performance, egg quality, antioxidant capacity, and intestinal structure.	Wang et al., 2020a
Breeding geese	34 weeks	Zn	65-70 mg /kg	Zn supplementation has the beneficial effects on reproductive performance, serum indices, yolk color and Haugh unit.	Shi et al., 2019
Wulong	45 weeks	Zn BS	45 mg/kg 5×10^9 CFU/kg	A combination of supplementations with Zn and BS has positive effects on the reproductive performance, egg quality, antioxidant, nutrient digestion and absorption and intestine health.	Fan et al., 2022
Wulong	46 weeks	Fe BS	60 mg/kg 5×10^9 CFU/kg	Using Fe in combination with BS in diet effectively improved the reproductive performance, eggshell quality, nutrient digestibility, antioxidant status, and hematopoietic function.	Zhang et al., 2020c
White Koluda	3 years	Se VE	0.3 mg/kg 100 mg/kg	Supplemental dietary Se and VE simultaneously improved both the ganders' response to manual semen collection and semen quality.	Jerysz and Lukaszewicz, 2013

reduced antioxidant capacity, whereas a 200 IU/kg VE supplementation resulted in optimal reproductive capacity, such as improved qualified egg rate, fertility, hatchability, plasma reproductive hormones levels (i.e., FSH, E_2, and P_4), and follicular development, mainly achieved by enhancing antioxidant capacity and immune status (Fu et al., 2022). However, in this study, four dietary VE levels (0, 40, 200, and 2000 IU/kg) were tested, and the range between 40 and 200 IU/kg was excessively wide. Therefore, future research should conduct on determine the precise VE requirement during the late laying period.

Vitamin K (VK), also known as hemostatic vitamins, includes VK1, VK2, and VK3, with VK3 requiring artificial synthesis. VK plays an important role in the blood clotting and bone mineralization processes (Shiraki et al., 2015). VK synthesis in the gut is extremely limited and unable to meet the body's requirement (Wang et al., 2019b); thus, appropriate dietary supplementation is necessary. Dietary VK3 supplementation in Wulong breeding geese, particularly at the optimal dosage of 10.0 mg/kg, enhanced reproductive performance, egg quality, and antioxidant capacities (Hao et al., 2023). Similarly, dietary VK supplementation in aged laying hens improved laying performance (Fernandes et al., 2009), and the combination supplementation of vitamins A and VK3 had interactive effects on eggshell quality, yolk color, and antioxidative ability of the eggshell gland (Guo et al., 2021). Table 5 summarizes the effects of dietary fat soluble vitamins supplementation on the reproductive performance of breeding geese.

Research on water-soluble vitamins mainly centers around B vitamins, which comprise a group of vitamins, such as thiamine (B_1), riboflavin (B_2), niacin (B_3), and biotin (B_7), etc. Vitamin B_1 (VB_1) plays an important role in the growth, development, and metabolic processes of animals. Given it short storage duration in the body before being rapid excretion, maintaining adequate levels of VB_1 requires a regular dietary intake. A deficiency in vitamin B1 can lead to disease and even death (Polegato et al., 2019). Experimental results have shown that adding appropriate levels of vitamin B1 to animal feed has a positive effect on the body. For instance, adding 2 mg/kg VB_1 to the diets of Wulong breeding geese significantly contributes to increasing reproductive hormone levels, improving intestinal tissue development, and enhancing intestinal immunity during the egg laying period (Li et al., 2023).

Vitamin B_3 (VB_3), is an important B vitamin that can promote animal fat metabolism, alleviate stress, improve productivity, and prevent diseases in early research results (MacKay et al., 2012; Jiang et al., 2014). Niacin is one of the naturally forms of VB_3. The addition of niacin has been shown to regulate lipid metabolism, and enhance the meat quality and intramuscular fat content in 5 to 16 week Wulong geese (Zhang et al., 2021a). Dietary supplemental niacin also has impacts on laying performance, as laying hen fed 66 or 132 mg/kg supplemental niacin produced more eggs than those fed 22mg/kg (Leeson et al., 1991). When niacin was added to the diets of breeding geese, the feed to egg ratio during the laying period reduced, whereas the eggshell thickness and eggshell strength improved, and some serum biochemical indicators changed (Wang et al., 2020b). This study suggested that the dietary niacin supplemental level for breeding geese during laying period is 40 mg/kg, with the dietary total niacin content being 69.16 mg/kg.

Choline, also referred to as vitamin B4 (VB_4), is a composition of the major phospholipids in cell membranes and is involved in the formation of acetylcholine for neurotransmission. It is essential for very low density lipoprotein secretion and hepatic fatty acid transport to eggs in laying hens (Dong et al., 2019). Adding appropriate amounts of choline into feed can enhance production capacity and improve the quality of livestock and poultry products. Choline supplementation has positive effects on egg production and egg mass in hens fed flaxseed containing diets (Beheshti Moghadam et al., 2021). Regarding breeding goose, an optimal choline level of 600 mg/kg not only significantly improved the laying rate, but also increased the qualification rate, hatching rate and shell strength of breeding eggs, and the mechanism by which choline affects production performance may involve positive or negative

Table 5
The effects of dietary fat soluble vitamins supplementation on the reproductive performance of breeding geese.

Breeder	Ages	Treatment	Optimum level	Significant effects	References
Yangzhou	180 d	VA	8 000~12 000 IU /kg	VA supplementation improved the egg quality, reduced the lipid peroxidation products, and improved the antioxidant capacity of the eggs	Dai et al., 2019
Yangzhou	180 d	VA	12,000 IU/kg in the maternal diet and 9,000 IU/kg in the offspring diet	Supplementing the maternal and offspring diet with VA increased weight gain, immune organ weight, the immune organ index, immunoglobulin content and antioxidant capacity in goslings.	Liang et al., 2019; Yang et al., 2020
Wulong	34 weeks	VD	400 IU/kg 50 μg/kg	Feeding vitamin D_3 plus 25-OH-D_3 gave optimal effects on the laying rate, eggshell quality, serum hormone levels and serum antioxidant function	Zhang et al., 2023
Jiangnan White	48 weeks	VE	200IU/kg	Both VE deficiency and high-dose VE (2000 IU/kg) reduced reproductive performance, whereas a dose of 200 IU/kg VE achieved optimal fertility, possibly through enhancing antioxidant capacity and immune status.	Fu et al., 2022
Wulong	82 weeks	VK_3	10.0 mg/kg	VK_3 supplementation enhanced the production performance, egg quality, vitamin K-dependent proteins, and antioxidant properties.	Hao et al., 2023

feedback regulation within the HPG axis, as it directly elevates serum hormone levels (P_4, T, and E_2) (Li et al., 2022c). However, dietary choline levels of no more than 700 mg/kg were sufficient to maintain egg production and egg quality in laying hens, while 1500 mg/kg was adequate for laying quails (Zhai et al., 2013; Olgun et al., 2022). Based on the results of these studies, the addition of choline has a certain impact on the reproductive performance of geese. However, the optimal level of choline addition differs significantly from the research results in other poultry. This variance may be related to factors such as choline purity, poultry species, or feeding patterns.

Vitamin B_5 (VB_5), also known as pantothenic acid, can be transformed into coenzyme A and acyl-carrier protein, participating in fatty acid metabolism reactions. It also plays important roles in the oxidation of carbohydrates and proteins in the body. Deficiency of VB_5 can induce various symptoms, such as a decline in animal immunity, growth retardation, ataxia, dermatosis, inhibited antioxidant capacity, and even mortality (Tang et al., 2020; Hrubša et al., 2022). In one-to four--week-old Wulong geese, dietary addition of pantothenic acid significantly affected the growth performance, slaughter performance, lipid metabolism, and antioxidant function, and the optimal supplemental level was 15.50 mg/kg (Wang et al., 2016). Regarding breeding geese during the laying period, dietary addition of VB_5 was beneficial for improving the qualified rate, fertilization rate, hatching rate, eggshell strength, healthy chicks rate and antioxidant capacity, and the suitable supplemental level was found to be 15 to 20 mg/kg in this study (Liu et al., 2021b).

Biotin, also referred to vitamins B_7 and H, is an essential nutrient for both humans and animals, and acts as an antioxidant in the body (McMahon, 2002). Biotin is crucial for normal embryonic development and the hatchability rate in broiler breeders (Whitehead et al., 1985). However, another study showed that although dietary supplementary biotin increase egg production and fertility rate, it has no effect on hatchability and chick quality in broiler hens (Daryabari et al., 2015). In breeding geese, diets supplemented with an appropriate amount biotin (0.2-0.3 mg/kg) can improve the egg qualification rate, fertilization rate, average egg weight, and eggshell strength, and also affect serum P_4, LH, E_2, and FSH levels; nevertheless, it has no effects on hatchability (Sun et al., 2024). These discrepancies in the effect of biotin on hatchability might be due to differences in experimental conditions, such as animal breed, age, and biotin dosage.

Vitamin B_{12}, also known as cobalamin (Cbl), is the sole vitamin in animals that contains metallic elements. Vitamin B_{12} palys a pivotal role in DNA synthesis and methylation in view of the fact that it can transfer methyl groups. It also has a proven antioxidant effect by scavenging of free radicals and reducing oxidative stress

(Halczuk et al., 2023). For young geese (5-15 week), adding 0.01mg/kg of vitamin B12 to their feed achieved the optimal effect on final body weight and average daily weight gain, mainly through its antioxidant effect (Long et al., 2018). In addition, it impacts reproductive performance. Dietary vitamin B_{12} supplementation can improve the laying performance and egg quality of Wulong geese during the laying period, regulate the serum biochemical indices, and enhance the antioxidant capacity. Under the conditions of this experiment, the suitable supplemental level of vitamin B_{12} is 25.0 μg/kg (Tan et al., 2024). Another study found that dietary vitamin B_{12} (25.0 μg/kg) and folic acid (2.0 mg/kg) act synergistically to improve the fertilization rate of breeding eggs, eggshell quality, serum reproductive hormone contents and antioxidant capacity of breeding geese during the laying period (Zhao et al., 2024).The increased laying rate and egg number might be attributed to the involvement of vitamin B_{12} in the methionine cycle in the body, as homocysteine obtains a methyl group from folic acid and converts to methionine with the help of vitamin B_{12}. Eventually, the increase in methionine content leads to an increase in egg production. The relevant research on the effects of adding water soluble vitamins to feed on the reproductive performance of breeding geese is presented in Table 6.

Table 6
The effects of dietary water soluble vitamins supplementation on the reproductive performance of breeding geese.

Breeder	Ages	Treatment	Optimum level	Significant effects	**References**
Wulong	34 weeks	VB_1	2 mg/kg	Addition of vitamin B_1 improved the serum reproductive hormone contents, promoted the development of intestinal tissue, and optimized the cecal flora structure.	Li et al., 2023
Wulong	34 weeks	VB_3	40 mg/kg	VB_3 supplementation reduced the feed to egg ratio, improved the eggshell thickness and eggshell strength, and changed the contents of some biochemical indicators in serum.	Wang et al., 2020b
Wulong	34 weeks	VB_4	600 mg/kg	Adding VB_4 improved the laying rate, the qualification rate, the hatching rate, the shell strength and protein height of breeding eggs, and the content of serum P_4, T, and E_2.	Li et al., 2022c
Wulong	34 weeks	VB_5	15~20 mg/kg	Addition of VB5 was beneficial for improving the qualified rate, fertilization rate, hatching rate, eggshell strength, the healthy chicks rate and antioxidant capacity.	Liu et al., 2021b
Wulong	34 weeks	VB_7	0.2~0.3 mg/kg	Supplemented with appropriate level of VB_7 improved the egg qualification rate, fertilization rate, average egg weight, and eggshell strength, as well as affected serum P_4, LH, E_2, and FSH levels.	Sun et al., 2024
Wulong	34 weeks	VB_{12}	25.0 μg/kg	VB12 supplementation improved the laying performance and egg quality, regulated the serum biochemical indices, and enhanced the antioxidant capacity.	Tan et al., 2024; Zhao et al., 2024

Others

The addition of other feed additives to the commercial breeder stock also improve reproductive performance and semen quality. For instance, feeding diets containing different levels of parsley significantly increase semen volume, sperm concentration, normal viable sperm and the semen quality factor; however, the proportion of abnormal sperm and acrosomal abnormalities were significantly reduced in local Iraqi ganders (Al-Daraji et al., 2011). In Hortobágy White geese breeder, supplementation with compound micronutrients in their drinking water improved egg production, but did not affect fertility and hatchability (Janan et al., 2015).

Daidzein, an isoflavone phytoestrogen, at an appropriate dose, increases egg weight and fertility in female Zhedong White geese, but has no significant effect on the number of eggs and hatchability, which are achieved by affecting serum hormone levels and regulating gene expression in the HPG axis (Zhao et al., 2013). On the contrary, in Bilgoraj gander, dietary higher levels of phytoestrogens decrease ejaculate volumes and the normal spermatozoa proportion; although the fertilization rates remains unaffected (Opalka et al., 2008). These results emphasize the importance of dosage when adding such substance to the diet.

Enteromorpha, a large green seaweed rich in seaweed polysaccharides and polyunsaturated fats, is highly suitable for use as animal feed. Dietary supplementation with *Enteromorpha* powder significantly increased egg production, laying rate, and egg weight and exerted its antioxidant effect in Zi geese during the late laying period (Ma et al., 2020). Additionally, *Enteromorpha* powder supplementation increased the serum levels of E_2 and ovarian PRL concentration in female Zi geese (Ma et al., 2021).

Arginine is regarded as an essential amino acid for animals owing to the low activity of the key enzymes involved in its synthesis (Geng et al., 2011). Dietary arginine supplementation had significant effects on the egg production rate in broiler breeders and enhanced the antioxidant capacity of hens, their eggs, and their offspring (Duan et al., 2015). Similarly, a recent study reported that dietary arginine improved the laying performance, egg weight and antioxidant capacity of laying Wulong geese, with the recommended optimal dosage being 1.02 % (Chen et a., 2023b).

To date, compared with studies on chickens, research regarding the regulation of reproductive performance through dietary nutrition in breeding geese remain lacking. Furthermore, there is no unified standard for the nutritional requirements and feed formulation of breeding geese, which has become one of the key issues impeding the development of the goose industry.

Hormone immunoneutralization to improve reproductive efficiency

Some hormones or factors can inhibit reproductive performance. However, through the hormone immunoneutralization technique, these inhibitory effects can be inhibited or attenuated. Immunized of certain hormones to animals will produce corresponding antibodies that can inhibit or attenuates the physiological functions associated with those hormones, and the application of active immunization of recombinant hormones has successfully promoted the reproductive performance of turkey hens (Ahn et al., 2001), broiler breeder hens (Satterlee et al., 2002), and geese (Chen et al., 2020).

Inhibin (INH) immunization

INH is secreted by the GCs of ovarian follicles in females and Sertoli cells in the male testes (Ying, 1988). INH can block FSH secretion in pituitary gland without affecting LH synthesis and release. It thus plays a modulatory role in follicular growth, atresia, and steroidogenesis (Knight, 1996). In Yangzhou ganders, active immunization of the INH α-subunit promoted testicular weight and Sertoli cell development through the regulations of HPG axis gene expressions (Akhtar et al., 2019). However, Akhtar et al. also found that INH immunization disrupted germ cells and testicular histology, and impaired spermatogenesis in Akhtar et al. (2021b). The potential molecular mechanisms and apoptotic pathways require investigation in future research. In female Zhedong geese, INH immunization was found to stimulate LH hormone secretion, and rescue recruited follicles from atresia, accordingly shorting the broody duration intervals, and decreasing the broodiness rate (Zhang et al., 2021b).

Anti-Müllerian hormone (AMH) immunization

AMH has inhibitory activity on the sensitivity of FSH. Thus, it plays a crucial role in ovarian follicular development. however, studies on its biological functions in birds are scarce (Wojtusik and Johnson, 2012; Hayes et al., 2016; Yang et al., 2019b). High expression of AMH mainly occurs during the broodiness period and is also a significant factor related to avian broodiness (Johnson et al., 2009).

In our previous study on broody Zhedong White geese, we found that active immunization against AMH improved yolk deposition, accelerated the development potential of the ovarian follicle, upregulated FSH gene expression and secretion, and led to an increase in egg production by one to two eggs in two consecutive laying-incubation cycles (Chen et al., 2020). However, whether AMH immunoneutralization can have impacts on broodiness behavior remains unravel. Another study showed that immunization against AMH could increase LH hormone levels, regulate follicle development, shorten the broody duration intervals, and decrease the broodiness rate in Zhedong White geese (Zhang et al., 2021b). In humans, serum AMH level is an important marker of Sertoli cell development (Fujisawa et al., 2002). To date, AMH active immunization is underreported in ganders, thus necessitating exploration.

Follistatin (FST)immunization

FST was initially isolated from the follicular fluid of cattle and pigs due to its ability to repress FSH secretion (Robertson et al., 1987; Ueno et al., 1987). Subsequently, FST mRNA was detected in the small follicles of the hen ovary and in the rooster testes (Davis and Johnson, 1998). When *in-vitro* cultured GCs were stimulated by FSH, FST expression was significantly downregulated (Du et al., 2018). This indicates the existence of FST in the goose ovary and the antagonistic relationship between the FSH and FST. FST can neutralize the bioactivity of activin, and the balance between activin and FST is crucial in the development of pre-hierarchical follicles (Lin et al., 2003).

Our recent study demonstrated that active immunization against FST improved the developmental potential of ovarian pre-hierarchical follicles in Yangzhou geese, the egg-laying rate increased after primary immunization, and the average number of eggs was 10.6 for the immunized geese vs. 7.7 for the control geese (Chen et al., 2022b). This represents the first report, to our knowledge, suggesting that FST may also be significant in regulating egg production. However, immuno-neutralization of FST did not obviously change the *FSH* mRNA expression in the pituitary gland, which is contrary to the conventional cognition that FST inhibits FSH secretion in birds. Hence, this phenomenon requires further investigation.

Leptin (LEP) receptor immunization

LEP is a white adipocyte-derived peptide hormone, which regulates bone mass, appetite, and energy metabolisms (Yadav et al., 2009). The functions of LEP are mediated by its receptors (LEPRs). In addition, some studies have revealed that LEP significantly influences reproduction and fertility (Casabiell et al., 2001; Zhang and Gonge, 2018).

When *in vitro*-cultured goose GCs were treated with LEP, it was found that LEP is involved in the development of goose ovarian follicles and steroid hormone secretion, which were attributed to its interaction with its receptor (Hu et al., 2014). Immunization against LEPR in egg-laying hens down-regulated the expression of genes that regulate follicular development and interrupted egg laying [211] (Lei et al., 2014). These results indicate the agonistic activity of LEP/LEPR in female reproduction.

In males, exogenous LEP negatively affects sperm quality, and impairs integrity of blood-testis barrier in mice and rats (Haron et al., 2010; Wang et al., 2018). To explore the function of LEP protein in male birds, Yangzhou ganders were subjected to LEPR immunization, and the results demonstrated that LEPR immunization significantly inhibited prepubertal testicular development and testosterone synthesis, and using *in vitro*-cultured testicular Leydig cells further verified these results (Lei et al., 2021). Therefore, at a high concentration, LEP exerts an adverse effect on testicular development and steroidogenesis.

PRL immunization

In poultry, PRL plays a crucial role in starting and maintaining broody behaviors, as well as regulating hormone secretion and reproductive activities. PRL is regarded as the primary factor inducing avian broodiness, as its plasma levels elevate during the broodiness period. Based on this, recombinant-derived PRL has been used to immunize broody-prone poultry to prevent the occurrence of broodiness (Sharp, 1997). Reportedly, immunization with recombinant PRL inhibited broody behavior and promoted laying performance in turkeys and laying hens (March et al., 1994; Crisóstomo et al., 1997). After Magang geese were active immunization with PRL, their broody behavior weakened, and the final clutch size subsequently increased (Liu et al., 2009). For Zhedong white geese, which are characterized by strong brooding, immunized against PRL shortened the broodiness duration and increased the egg production by an average of 1.34 eggs (Zhang et al., 2021b). However, the increase in egg laying after PRL immunoneutralization usually occurs under a short photoperiod. These above results indicate that active immunization against PRL can be used as a technical method to improve egg-laying performance of geese, and a second immunization may be necessary.

ARTIFICIAL INCUBATION TECHNIQUE TO IMPROVE REPRODUCTIVE EFFICIENCY

Egg hatching is the final stage in breeding poultry production and has a significant influence on their reproductive performance. With the intensification and scaling of poultry production, artificial incubation of eggs has been widely used to improve laying performances. Currently, chickens are the predominant domestic fowls. As a result, machine incubation technology has been designed primarily on the basis of research and practices related to the incubation of chicken eggs (Buys, et al., 1998; Elibol and Brake, 2006). However, owing to the larger and heavier size of goose eggs than those of chicken, the hatchability fertile goose eggs is much lower than that of chicken eggs, and thus, the ideal incubation outcome is not achieved. Hence, apart from regulate the incubation conditions including temperature, humidity, and ventilation, the development of more developed incubators and advanced studies of novel incubation techniques are essential for achieving better hatchability and gosling quality in goose production.

Egg turning

During the incubation process, egg turning is necessary for stimulating the development of the yolk sac membrane, promoting blood circulation, and accelerating the absorption of nutrients from the yolk (Deeming, 1989; 2009). It also prevents improper adhesions of the embryo to the inner shell membrane during embryonic development (Cutchin et al., 2009). The absence of or inadequate egg turning often causes mortality during incubation. The typical and optimal flipping angle is set at 45° once an hour during chicken eggs incubations.

Our recent studies have showed that increasing the turning angle from the conventional 45° or 50° to 60° or 70° significantly improves the hatchability of fertile goose eggs (Dai, et al., 2017; Guo, et al., 2021a). The improved hatchability can be attributed to the more efficient utilization of the lipids in the yolk throughout embryogenesis (Guo et al., 2021b). A further study revealed that incubation under a wider angle of egg turning also improves the hatched gosling quality and growth rate, and the primary effective mechanism is through upregulating gene expression and somatotropic hormones secretion, thereby promoting embryo and gosling development (Guo, et al., 2023). Therefore, incubating goose eggs with the egg turning angle at 70° can significantly benefit the poultry industry economically. The next approach is to conduct related studies on a variable angle turning method during the incubation period.

Photostimulation

In commercial hatcheries, fertile poultry eggs are typically incubated in the dark. However, under natural incubation conditions, eggs occasionally receive daylight exposure when the hens leave the nest to search for food and drink. Considering the higher photosensitivity of birds compared to mammals (Prescott and Wathes, 1999), light may also be a significant environmental factor determining the hatching outcomes of artificial incubation (Tona et al., 2022).

Photostimulation during chicken egg incubation exerts significant influences on embryo development, hatchability, hatching time and post-hatching growth performance (Rozenboim et al., 2004; Tong et al., 2018; Wang et al., 2021b), especially when the light source is monochromatic green LEDs. Light exposure during the incubation of broiler chicks may favor their adaptation to new environments (Archer et al., 2009). To date, research on providing light during incubation has mainly been carried out on rapidly growing broilers or high-yield laying hens.

Our latest study has demonstrated that fertile goose eggs incubated under 12 h of monochromatic green light have better embryonic development and hatching results and a shorter hatching time compared to those incubated in 24 h of darkness (Chen et al., 2022b). In addition, the growth-promoting effects of monochromatic green light on embryos are associated with the regulation of energy metabolism in the liver and myogenic regulatory factors in muscle. Moreover, the heart index (heart weight / embryo weight × 100) at 13 and 16 embryonic ages in the green light group were significantly higher than those in the dark group individuals, and *GATA*4, *GATA*5, *Sma*d4, and *GHR* were identified as candidate genes for goose embryonic heart development through transcriptomic analysis of the heart tissue (Chen et al., 2024). Our preliminary research has also revealed that green light stimulation during the incubation period improves chorioallantoic membrane angiogenesis in goose embryos (Yan L, unpublished observations). These studies provide a theoretical basis for the application of green light in goose egg hatching. However, the photoreception and recognition mechanism of green light during the goose embryo stage remain unknown, and thus we are currently investigating this issue.

Incubation temperature, relative humidity and ventilation

Incubation conditions such as temperature, humidity, and ventilation can also influence embryonic development and hatchability (Decuypereand and Bruggeman, 2007, Tona et al., 2022). For most poultry species, the optimum incubation temperature ranges between 37°C and 38°C. Both a low temperature and a very high temperature negatively affected hatchability by increasing embryo mortality, and reduced chick quality (Yildirim and Yetisir, 2004; Maatjens et al., 2017). The evaporation of water from the embryo to the external environment during the incubation phase is inevitable. However, incubating chicken eggs at a higher or lower relative humidity both damage embryonic development and hatching performances (Van der Pol et al., 2013). Additionally, there might be an interaction of temperature and relative humidity on hatchability.

Ventilation can ensure that the oxygen and carbon dioxide in the commercial egg incubator are maintained at ambient levels for embryonic development. Insufficient ventilation may cause hypoxia (low O_2), and hypercapnia (high CO_2). Their impacts on embryonic development mainly depends on the stage of the embryo development and the levels of O_2 and CO_2 at which the embryo is exposed to (Zhang and Burggren, 2012; Özlü et al., 2019).

Unfortunately, to date, there is almost no research have been conducted on the optimal temperature, humidity, and ventilation for the hatching process of goose eggs.

These incubation factors are mainly referring to chicken eggs and modifying slightly.

Variable temperature and humidity were used during goose egg incubation (Guo et al., 2021a; Chen et al., 2022a). Nevertheless, due to the fact that goose embryos are much larger than chicken embryos, they need to use their lungs to breathe and expel a large amount of heat during the later stage of hatching, therefore, ventilation should be strengthened.

Egg cooling

Chick embryos may live under the stress from excessive production of heat during the latter stage of egg incubation (Tullett, 1990). Egg cooling during the incubation to relieve the stress caused by excessive production of metabolic heat is suggested. Cooling eggs refers to the process of incubating eggs in the middle and later stages, turning off the electric heating or opening the incubator door to dissipate the residual heat inside the incubator. Egg cooling allow the embryo to obtain more fresh air, which is beneficial for embryo development.

Particularly, goose eggs are heavy and have a high fat content in yolk, which lead to high oxygen demand in the embryo, as a result, more physiological heat were releases during the later stages of hatching. In addition, the ratio of egg weight to eggshell surface area is larger than that of chicken eggs, and the eggshell is thicker (Liu, 2021). Therefore, only by cooling the egg can goose embryos dissipate heat, and effectively lowering the temperature of the embryo. Otherwise, excessive heat generated during the hatching process will cause the death of goose embryo. The cooling time for goose eggs is usually after 12 days of incubation. Conventional operations of egg cooling include open the door of the incubator or pull the egg rack truck directly out of the incubator until the temperature drops to 35 ℃. Additionally, 37 ℃ warm water was sprayed on the surface of the eggs not only helps dissipate heat, but also brittle the eggshell for later pecking the shell.

Conclusion and perspectives

The production capacity of breeding geese is constrained by their poor reproductive performance, manifested as breeding seasonality, broodiness, and poor semen quality, which hinder the development of goose industry. Given the high demand for poultry meat and its importance, a comprehensive understanding of the reproductive characteristics of geese and the methods of reproductive regulation is a crucial area of investigation. Initially, an overview of endocrine mechanism of goose reproduction is presented. Subsequently, this review summarizes the reproductive characteristics of geese that contribute to their poor reproductive performance. By manipulating the reproductive properties of geese, it is possible to enhancetheir reproductive performance. This can be accomplished through various developed methods, such as artificial lighting control, nutrition supplementation, immunoneutralization techniques, and artificial incubation technology. However, studied on and expansion of these strategies should continue, as achieving optimal effects requires diverse range of approaches.

Additionally, future developments and areas for further research should cover several crucial areas. First, it is essential to efficiently formulate differentiated artificial illumination programs for both long- and short-day breeding geese. This can be achieved by identifying reliable photoperiodic regimens, light spectrum, and light intensity. Second, the nutritional requirements and feed formulation of breeding geese are blank, which severely restricts the standardized production of the goose industry. Therefore, further investigations are needed into the effects of nutrients such as metabolic energy, protein, lysine, methionine, calcium, phosphorus, vitamins, trace elements, and linoleic acid in the feed of breeding geese on laying performance, physiological and biochemical indicators, and functional gene regulation. Lastly, goose researchers and practitioners should place greater emphasis on improving the reproductive performance of ganders. The integration of these potential techniques will generate novel directions in the field of breeding geese, and greatly benefiting the poultry industry and consumers. It also provides a theoretical reference for fully tapping into the reproductive potential and production performance of goose.

Disclosures

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work. There is no professional or other personal interest of any nature or kind in any product, service or company that could be construed as influencing the content of this paper.

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