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Induction of out-of-season egg laying by artificial photoperiod in Yangzhou geese and the associated endocrine and molecular regulation mechanisms

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ABSTRACT

This study was carried out to induce out-of-season breeding, in the summer, and to achieve high reproductive performance using artificial photoperiod manipulation in the long-day breeding Yangzhou goose. Young geese were subject to a two-phase short-to-long (group A) or a three-phase (long-short-long; group B) photoperiod program February through October. Egg-laying was induced to start similarly in both groups in May, increased to a peak level in July, and then decreased gradually through to October. The peak and post-peak laying rates were higher with the three-phase than with the two-phase program. Plasma progesterone concentrations changed similarly in the two groups, increasing from low levels during the pre-lay periods until the peak laying stage, then decreasing with decline in the egg-laying rate. Plasma T3 concentrations increased from the beginning of the experiment to form the first peak under a short photoperiod, declined to a trough at peak lay and then progressively increased to high levels towards the end of the experiment. Plasma T4 concentrations increased throughout the experiment, showing little response to changes in photoperiod. GnIH mRNA expression level in the hypothalamus steadily decreased from high levels under the short photoperiod to a nadir at peak of lay, but was abruptly up-regulated by over a thousand-fold thereafter. This mRNA expression pattern was also shared by GnIHR, VIPR, TRHR, TSH, and PRL genes in the pituitary gland, and to lesser extent, by GnRH, VIP, and TRH genes in the hypothalamus. Pituitary GnRHR mRNA expression levels changed in a similar manner to that of reproductive activities of geese in both groups. FSH beta subunits mRNA expression levels increased to high levels after day 11 of the long photoperiod, and were higher in group B than in group A at peak laying. LH beta gene expression level was similarly upregulated by photoperiod and was higher in group B than in group A when used the multivariable and two-way analyses of variance. Taken together, photoperiod, through regulation of expression of an array of genes in the hypothalamus and pituitary gland, synchronized stimulation and refractoriness of the reproductive system in Yangzhou geese. The higher out-of-season egg laying performance following the three-phase photo-program treatment was mediated by higher FSH beta and LH beta subunit mRNA expression levels.

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1. Introduction

The great majority of wild animals and birds living in temperate zones are seasonal breeders (Wingfield and Farner, 1993; Dixit and Singh, 2011). This strategy of breeding is a physiological mechanism to cope with the annual changes in the living environment – the young can be born or hatched at the prime times for growth and survival, mostly the warm spring and early summer times that are rich in food supplies (Karsch et al., 1984; Ortavant et al., 1985). It is well established that animals, particularly birds, primarily rely on annual changes in daily photoperiods to regulate seasonality of reproduction and other physiological activities such as food intake, growth, and molting (Dawson et al., 2001; Sharp, 2005; Bédécarrats et al., 2015). The photoperiod, or the length of a day, signals by acting on photoreceptors located in the retina and the deep brain (Mobarkey et al., 2010), directly regulates gonadotropin-releasing hormone (GnRH) pulse generators within the hypothalamus, and acts indirectly through melatonin secretion by the pineal gland and thus gonadotropin-inhibitory hormone (GnIH) secretions (Bédécarrats et al., 2015). GnRH and GnIH, respectively, stimulate and inhibit secretions of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) by the pituitary gland so to activate or inhibit reproductive activities (Bédécarrats et al., 2015). In addition, photo-signals, through stimulation of a subset of photoreceptor cells located in the paraventricular organ (PVO) of the hypothalamus, trigger the release of thyroid-stimulating hormone (TSH) by the pars tuberalis (Nakane and Yoshimura, 2010; Bédécarrats et al., 2015). TSH stimulates the local conversion of thyroid hormone total thyroxin (T4) into triiodothyronine (T3), which may in turn stimulate the release of GnRH-I in the median eminence, which subsequently induces reproductive activation (Nakane and Yoshimura, 2010; Bédécarrats et al., 2015). On the other hand, prolactin (PRL) and its releasing factor vasoactive intestinal peptide (VIP) are also involved in the regulation of seasonal reproductive activities, and their secretions are strongly regulated by photoperiod (Sharp and Blache, 2003). In this aspect, PRL plays both reproduction potentiating and suppressing roles (Li et al., 2011), which may be fulfilled at different levels in the hypothalamo-pituitary-gonadal (HPG) axis (Mobarkey et al., 2010; Bédécarrats et al., 2015), as in the processes of photo-stimulation and refractoriness.

Domestic geese are strongly seasonal breeders with both short- and long-day breeding types (Shi et al., 2008). In modern goose production practices, photoperiod programs (hereafter photo-programs) have been developed to regulate goose reproductive activities to overcome the seasonal breeding obstacle and to achieve year-round production (Sun et al., 2007; Huang et al., 2008; Gumułka and Rozenboim, 2013). Previously, a photo-program, consisting of an 18-h long photoperiod for two-and-a-half months during the winter and spring and a 11-h short photoperiod thereafter, induced out-of-season summer breeding in Magang geese, which produced excellent performance and economic return (Sun et al., 2007; Huang et al., 2008). This long-to-short photo-program included a previously established long photoperiod of 18 h, which is considered to be important for timing the onset and manifestation of reproductive activities in short-day breeding animals (Malpaux et al., 1989). For inducing out-of-season breeding in long-day breeding geese, a simple two-phase photo-program, consisting of a short photoperiod of 8 h followed by a long photoperiod of 11 to 12 h, has been proposed (Buckland and Guy, 2002), the opposite of the photo-program used for the short-day breeding Magang geese (Sun et al., 2007; Huang et al., 2008). However, in both short-day breeding sheep and long-day breeding birds, experience of a preliminary long photoperiod before the short one improved reproduction after the final switch to a long photoperiod (Sweeney et al., 1997; Salvante et al., 2013). Therefore, to develop out-of-season breeding for Yangzhou geese, we compared the effects of a two-phase (short, long) versus a three-phase (long, short, long) photo-program on the timing and efficacy of reproductive activities, as well as on the underlying endocrine and molecular regulatory mechanisms in the HPG axis.

2. Materials and methods

2.1. Experimental design and animals

The animal trial was carried out on Sunlake Swan Farm (119°58′E, 31°48′N) in Henglin Township, Changzhou, Jiangsu Province, China. Two goose barns with automatic programmed lighting and tunnel ventilation with water pad cooling facilities were used to house the geese. Starting January 25, 2015, a flock of 77-day-old Yangzhou geese ($n = 750$, female:male = 4:1) of the same genetic origin were used in the experiment; this flock was divided into two equal groups and each group had three replicates.

Group A was initially exposed to a natural photoperiod until February 28, then to a short photoperiod of 8 h for a duration of 56 days, and then to a photoperiod of 12 h for the subsequent 218 days (Fig. 1A). Group B geese were exposed to the same photo-program as group A, except it began with exposure to a long photoperiod of 18 h for the 35 days from January 25 to February 28 (Fig. 1B). We called days within the 8-h short photoperiod S1–S56 and those in the 12-h long photoperiod L1–L218. The 18-h long photoperiod treatment consisted of natural illumination during the daytime plus supplementary illumination of 80–100 lux by fluorescent tubes at times after sunset and before sunrise. The 8-h short photoperiod was achieved by confining the geese in the barns from 0400 to 0800 h and from 1600 to 2000 h. For the 12-h photoperiod, geese were confined to the barn from 0400 to 0600 h and from 1800 to 2000 h. The daily egg laying rate was calculated as the percentage of totals eggs laid each day over the number of female geese present on that same day.

The birds were fed ad libitum with mixed feed of 12.5% crude protein, and supplemented with green grass whenever possible. Feed was given during the daytime and geese had free access to drinking water provided via drinking troughs. Blood samples from 12 female geese were collected from wing veins into heparinized syringes every 2 weeks. Plasma was separated within 3 h of sample collec-