

Photoperiodic Control of Seasonal Breeding: A Review

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Abstract

Photoperiod is a powerful synchronizer of seasonal changes in endocrine and metabolic physiology in vertebrates living in tropical to polar zone. The purpose of this review is to study the factors which are involved in the process of photoperiodism in control of seasonal breeding in birds and mammals. The gonadotropin-releasing hormone (GnRH) is crucial in seasonal breeding mammals and birds, whereby under the influence of thyroid hormone, triiodothyronine (T3), it stimulates the anterior pituitary gland to release gonadotropins responsible for maturation of reproductive organs. The process that leads to stimulation of GnRH production differs between birds and mammals. In birds, light is perceived by deep brain photoreceptors and long day induced thyroid-stimulating hormone (TSH) causes local T3 activation. In mammals, light is perceived by the eyes and melatonin which is secreted during the night from the pineal gland regulates TSH. Therefore eyes, pineal gland and melatonin are not essential for regulation of seasonal reproduction in birds. Despite the differences, birds and mammals are subjected to common features i.e. light exposure and TSH during photostimulation. Long photoperiod causes photostimulation followed by photorefractoriness. The latter, has been thought to occur due to the influence of prolactin. The initial gonadal regression which is

encountered during photorefractoriness occurs while there is still releasable GnRH. The timing of photorefractoriness is influenced by food availability, temperature and social factors like songs. The dissipation of photorefractoriness occurs during short photoperiods and is characterized by an increase in hypothalamic GnRH.

Key words: birds, gonadotropin, mammals, photoperiodism, thyroid

Introduction

Photoperiod refers to length of light phase in each day (24h) light-dark cycle, whereas, photoperiodism is the biological process of responding to changes in photoperiod. The latter is a powerful synchronizer of seasonal changes in endocrine and metabolic physiology in vertebrates living in tropical to polar zones (Hazlerigg and Wagner, 2006). In seasonal breeding, initiation is thought to be as a result of gonadotropin-releasing hormone (GnRH) production (Dawson *et al.*, 2001). Production of GnRH occurs in the hypothalamus under the influence of a thyroid hormone, triiodothyronine (T3; Rani and Kumar, 2014).

The GnRH in mammals and birds play a major role in stimulating the anterior pituitary gland to release follicle-stimulating hormone (FSH) and luteinizing hormone (LH; Rani and Kumar, 2014). The LH ensures production of testosterone, estrogen and progesterone in the reproductive organs such as testes and ovaries while FSH is responsible for maturation of reproductive organs (Halford *et al.*, 2009). Hence, the GnRH is crucial in seasonal reproduction (Bentley *et al.*, 2003). The process that leads to stimulation of GnRH production differs between birds and mammals (Rani and Kumar, 2014; Shinomiya *et al.*, 2014). Nevertheless, they are all subjected to common features i.e. the light exposure and thyroid-stimulating

hormone (TSH; Shinomiya *et al.*, 2014). In mammals from light there is involvement of eyes, pineal gland and melatonin to reach actions of the TSH in the pars tuberalis while in birds, the deep brain photoreceptors induce the TSH secretion from the pars tuberalis. Therefore, eyes, melatonin and pineal gland are not essential for regulation of seasonal reproduction in birds (Shinomiya *et al.*, 2014). The purpose of this review is to study the factors which are involved in the process of photoperiodism in control of seasonal breeding in birds and mammals. Further, to point out the similarities and differences in birds and mammals.

Photoreception

Photoreception refers to how the light is received and conveyed to bring about expected output in seasonal reproduction in mammals and birds (Fig. 1). This process is different between mammals and birds (Yoshimura, 2010), and is influenced by light wavelength, colour of the light wavelength, duration and intensity of light (Foster and Follett, 1985; Malik *et al.*, 2004; Sharma and Bhardwaj, 2013; Fig. 1). In birds photoreception occurs at three levels; the deep brain, pineal and eye (Rani and Kumar, 2014). The deep brain photoreceptors are the ones which are believed to mediate seasonal reproduction (Yoshimura, 2010; Davies *et al.*, 2012; Fig. 1). The deep brain photoreceptor, vertebrate ancient opsin (VA-Opsin) mediates the avian photoperiodic response and plays a key role in regulation of seasonal reproduction in birds (Halford *et al.*, 2009; Davies *et al.*, 2012; Fig. 1). Once the light information is received by the deep brain photoreceptors is send to the pars tuberalis of the pituitary gland (Halford *et al.*, 2009; Davies *et al.*, 2012; Fig. 1). However, the precise link between VA photoreception activation of the pars tuberalis is not clear (Halford *et al.*, 2009). Photoreceptors of the eye and pineal gland have been shown that they are not important for the control of

birds' seasonal breeding, since blind and pinealectomized birds show changes in development of gonads (Oishi and Lauber, 1973a; Siopes and Wilson, 1974). Therefore, in birds eyes are not essential for the regulation of seasonal reproduction (Yoshimura, 2010). In mammals there is involvement of eyes and pineal gland, whereby light information is received by the eyes and transmitted to pineal gland via the suprachiasmatic nucleus (SCN) and translated into melatonin secretion patterns (Yoshimura, 2010; Rani and Kumar, 2014; Fig. 1). Melatonin acts on type 1 melatonin receptors (MT1) in the pars tuberalis (Yasuo, 2009; Rani and Kumar, 2014; Fig. 1 & 2). Therefore, the pars tuberalis is the target site for seasonal melatonin signaling (Yasuo, 2009; Fig. 1). Hence, in mammals eyes are essential in synchronization of seasonal and daily biological rhythms, apart from having a role in vision. In both mammals and birds, once the signal is received by the pars tuberalis local production of TSH will be stimulated (Rani and Kumar, 2014; Fig. 1 & 2).

Factors Influencing Photoreception

The light wavelength, colour of the light wavelength, duration and intensity of the light have been found to influence photoreception (Foster and Follett, 1985; Sharma and Bhardwaj, 2013; Malik *et al.*, 2004; Fig. 1). At the same energy levels, the rate of photoperiodic induction was reported to be faster under long wavelength in migratory black-headed bunting (*Emberiza Melanocephala*) (Malik *et al.*, 2004). In chicken the responses of photoperiodism is maximum at the wavelength of 492 nm as it was observed in Japanese quail (*Coturnix coturnix*) (Foster and Follett, 1985). This is supported by the absorbance spectra of two isoforms of VA-Opsin i.e. chicken VA long (cVAL) and chicken VA short (cVAS) having a λ_{\max} at approximately 490 nm (Davies *et al.*, 2012). A greater testicular response was observed in male Brahminy myna (*Sturnus pagodarum*) that were

under complete photoperiod compared to those that were under skeleton photoperiod (Sharma and Berdwaj, 2013). In Brahminy myna photoperiodic response was observed at high light intensities (Sharma and Berdwaj, 2013). However, an increase in light intensity above the threshold did not increase the photoperiodic response (Sharma and Berdwaj, 2013).

The red light was more effective in inducing a photoperiodic response than the green or blue light in Brahminy myna (Sharma and Berdwaj, 2013). This is due to the fact that at equal energy levels, the red light emits larger number of photons than the green or blue light (Sharma and Berdwaj, 2013). Furthermore, the penetration of red light to brain tissue, thereby access to photoreceptors mediating photoperiodic responses is faster than the green or blue light (Sharma and Berdwaj, 2013). Similarly, in blind Japanese quail only the red light at low intensity was effective to elicit gonadal response (Oishi and Lauber, 1973b). Hence, the light wavelength, colour of the light wavelength, duration and intensity of the light determine the photoperiod in birds.

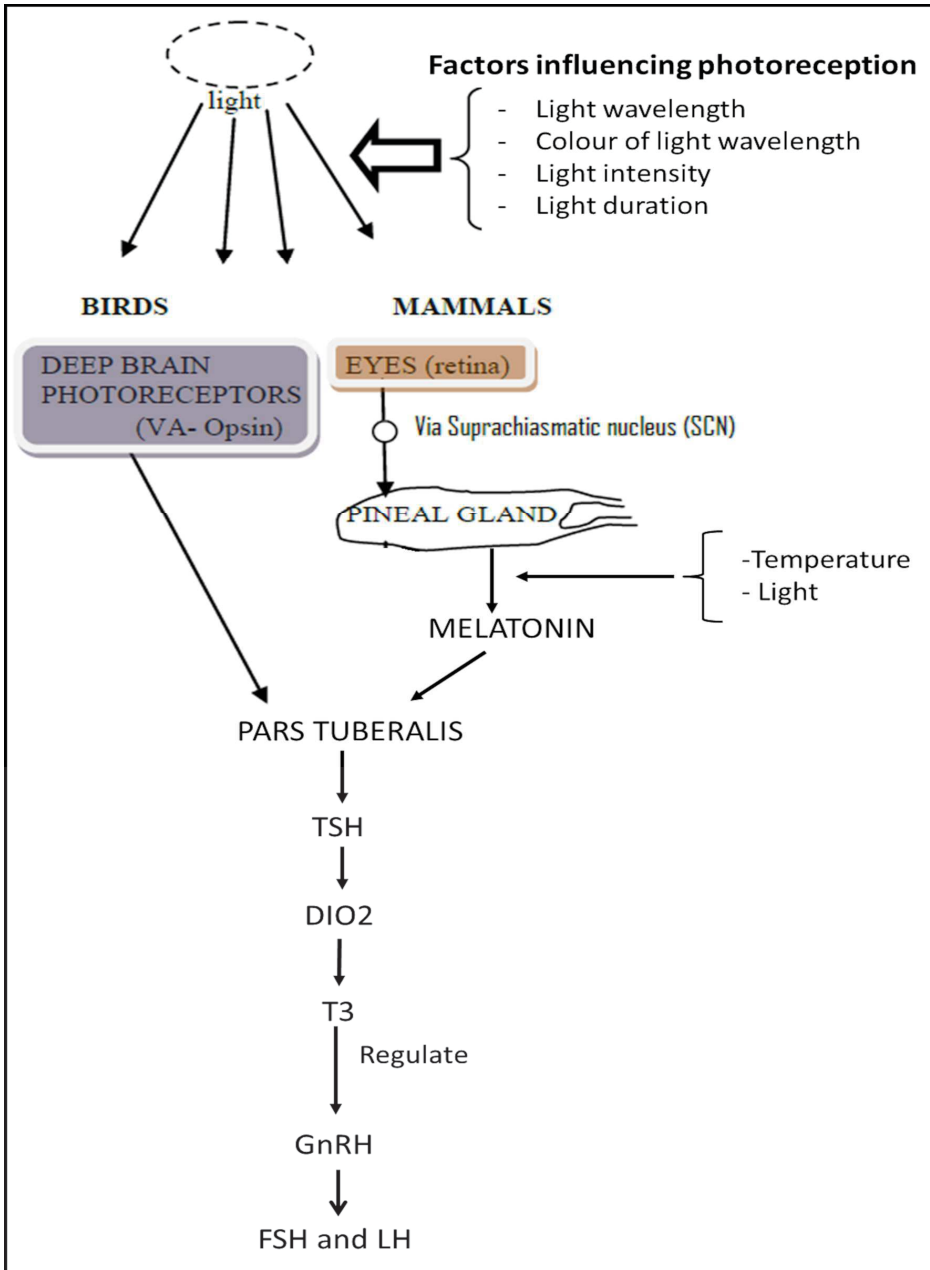


Figure 1: Photoperiodic control of seasonal breeding in birds and mammals. In mammals, light information is received by the eye and transmitted to the pineal gland via the suprachiasmatic nucleus (SCN). The pineal gland secretes melatonin which acts on type 1 melatonin receptors (MT1) in the pars tuberalis of the pituitary

gland. The duration of the nocturnal melatonin signal is the one which regulates secretion of thyroid-stimulating hormone (TSH) from the pars tuberalis. In birds, light information received by the deep brain photoreceptors in the hypothalamus induces secretion of the TSH from the pars tuberalis. In long days the TSH up regulate type 2 deiodinase (DIO2) which convert thyroxine (T4) into triiodothyronine (T3). The T3 induce morphological changes in the gonadotropin-releasing hormone (GnRH) neurons and glial cells to regulate seasonal GnRH secretion and hence gonadotropins i.e. follicle-stimulating hormone (FSH) and luteinizing hormone (LH).

Melatonin

Melatonin which is produced by the pineal gland is very essential in controlling seasonal reproduction in mammals, however, it has been reported to have a little or no importance in controlling seasonal reproduction in birds (Yoshimura, 2010; Fig. 1 & 2). Although melatonin is not seen to be directly involved in regulation of bird's seasonal reproduction, it has been reported to be useful in modulating essential reproductive characteristics such as songs, which are essential in bird's reproduction. Therefore in birds, melatonin is involved with neurological and behavioral aspects of seasonal reproduction (Bentley and Ball, 2000; Fig. 2).

Role of Melatonin

Melatonin transmits photoperiodic signals that regulate reproduction in mammals (Yasuo *et al.*, 2009). Three melatonin receptor subtypes, MT1, MT2 and MT3 have been identified in mammals (Dubocovich and Markowska, 2005; Yasuo *et al.*, 2009). The complete identity of MT3 membrane binding sites as well as the physiological relevance of its binding sites remains to be determined (Dubocovich and Markowska, 2005). It has been found that, the MT1 receptor found in

the pars tuberalis is the one which is responsible for photoperiodic signals (Yasuo, 2009; Rani and Kumar, 2014; Fig. 1 & 2). The MT2 receptors may interfere with the function of MT1 receptors that leads to the decrease in the efficiency of photoperiodism (Yasuo *et al.*, 2009). Melatonin acts on MT1 receptors to cause local release of TSH from the pars tuberalis (Rani and Kumar, 2014; Fig. 1 & 2). Therefore, melatonin is responsible for regulation of seasonal reproduction (Dubocovich and Markowska, 2005) and regulates the prolactin secretion (Johnston, 2004; Fig. 2).

Regulation of Melatonin

Melatonin secretion may result either from modulation of pineal activity by the circadian (i.e. Circadian rhythm is the term used to describe the physiological and behavioral twenty- four hour cycle that most organisms experience) clock in the hypothalamic SCN or from a direct inhibitory action of light during the light phase of the light-dark cycle (Piccione *et al.*, 2013; Fig. 1). In many mammals exhibiting photoperiodism, the secretion of melatonin is under circadian control (Fig. 1), although some mammals such as horses are not under circadian control (Piccione *et al.*, 2013). It is modulated only by the environmental light. In birds, the pineal gland is a self-contained melatonin rhythm-generating system due to the fact that it has an internal clock and photo detectors (Okano and Fukada, 1997; Chong *et al.*, 2000). Melatonin production can be regulated by temperature and light (Max and Menaker, 1992). It has been reported that melatonin production increases in darkness and decreases under light exposure (Max and Menaker, 1992). Increased temperature increases production of melatonin in darkness. Additionally, it also increases the sensitivity of the response to light (Max and Manaker, 1992).

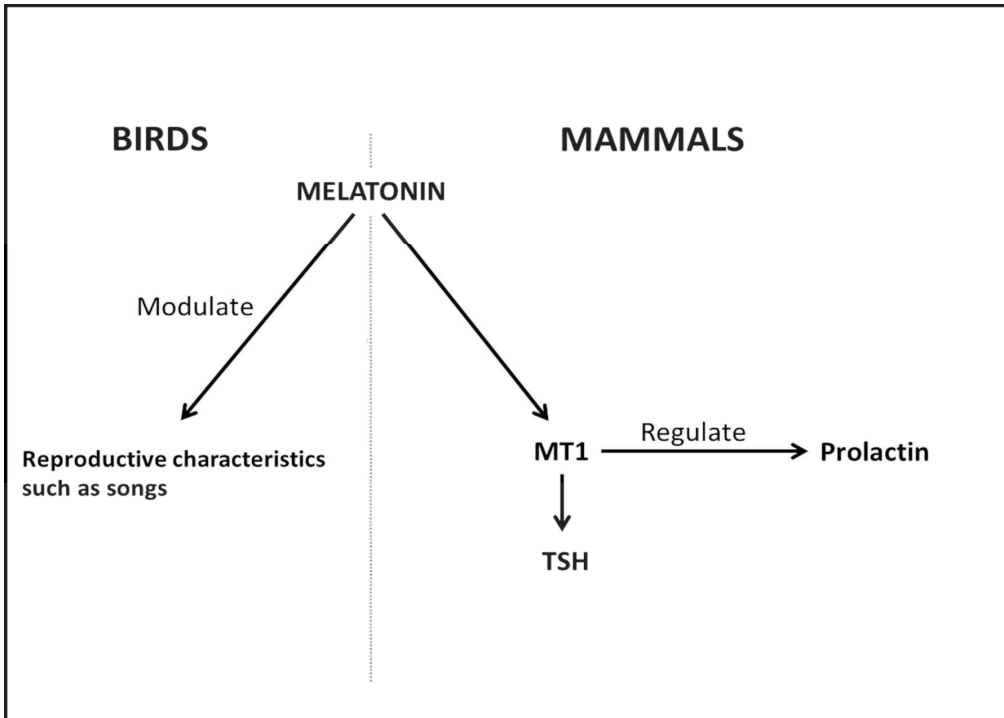


Figure 2: Melatonin in mammals and birds. In mammals, the nocturnal melatonin acts on MT1 receptors to cause local release of TSH from the par tuberalis. Additionally it regulates the prolactin secretion. In birds, melatonin modulates essential reproductive characteristics such as songs.

Thyroid Hormones and Thyroid Stimulating Hormone

The prohormone thyroxine (T₄) is the major form of circulating thyroid hormone and the later regulates reproductive function in mammals and birds (Yoshimura, 2010; 2013). However, triiodothyronine (T₃) is the biologically active thyroid hormone (Yoshimura, 2010; Rani and Kumar, 2014; Fig. 1). Thyroid hormone receptors (TR α , TR β and RXR α) have been reported to be expressed in the median eminence of the hypothalamus (Yoshimura, 2010). Therefore, the target site for the mediobasal hypothalamus T₃ induced under long days is the median eminence (Yoshimura, 2010).

Due to their lipophilic nature, thyroid hormones were long believed to transverse plasma membranes by passive diffusion (Yoshimura, 2013). Currently, it has been established that a membrane transport system for thyroid hormone exists and the organic anion transporting polypeptide (Oatp) family is involved in transporting the T4 (Yoshimura, 2013). Moreover, it has been reported that the gene encoding Oatp1c1 is the most likely responsible for transportation of T4 from the general circulation to the cerebral spinal fluid and from the cerebral spinal fluid to the ependymal cells that lining the ventro-lateral walls of the third ventricle in the mediobasal hypothalamus (Yoshimura, 2013).

The pars tuberalis TSH is a common master factor for regulation of seasonal reproduction in both mammals and birds (Yoshimura, 2010). It is produced by the thyrotrophs in response to light and melatonin in birds and mammals, respectively (Yoshimura, 2010; Rani and Kumar, 2014; Fig. 1). The pars tuberalis TSH stimulates the specialized ependymal cells of the third ventricle, tanycytes, which alter the expression of type 2 deiodinase (DIO2) and type 3 deiodinase (DIO3) enzymes (Halford *et al.*, 2009). Therefore, the levels of pars tuberalis TSH regulate DIO3 and DIO2 enzymes synthesis (Rani and Kumar, 2014). High levels of pars tuberalis TSH in long days up-regulate DIO2, which convert T4 into T3 (Nakao *et al.*, 2008; Yoshimura, 2010; Rani and Kumar, 2014; Fig. 1). Short days up-regulate DIO3, which converts T4 and T3 into inactive reverse T3 (rT3) and 3, 3' diiodothyronine (T2), respectively (Yoshimura, 2010; Rani and Kumar, 2014). The T3 induce morphological changes in the GnRH neurons and glial cells that regulate seasonal GnRH secretion and hence gonadotropins (FSH and LH) secretion from the anterior pituitary gland in mammals and birds (Yoshimura, 2013; Fig. 1). Therefore, the photo-induced increase in pars tuberalis TSH plays a

role in initiation of photo-induced gonadotropins secretion, and it is necessary for maintenance of reproductive activity under continuous long day (Yoshimura, 2010).

Gonadotropin-releasing Hormone

The GnRH regulates reproduction in all vertebrates (Bentley *et al.*, 2003; Fig. 1). The expression of GnRH differs between animals. In rodents, the GnRH development is present from birth to puberty with no inhibition mechanism. In primates, the GnRH development starts perinatally and remains quiescent up to puberty where it develops again. The GnRH is secreted in the hypothalamus and leads to maturation of gonads (Fig. 1). When the synthesis of GnRH is stopped leads to refractoriness and decrease in size of gonads (Fig. 3). The GnRH has also been found to be helpful in controlling and improving breeding in birds such as eggs production. In canaries (*Serinus canaria*) administration of GnRH analogy (lecirelin) was found to cause an earlier significant onset of reproductive activity (Robbe *et al.*, 2008). The action of GnRH can be inhibited by gonadotropin inhibitory hormone (GnIH; Bentley *et al.*, 2003). Other factors like age have been identified to influence the GnRH (Brown *et al.*, 2001). In male Syrian hamsters (*Mesocricetus auratus*) the GnRH mRNA levels showed an aging-related decrease regardless of photoperiod (Brown *et al.*, 2001).

Photorefractoriness

The GnRH-I is the form of GnRH which controls reproductive functions in birds. Moreover, long photoperiods cause photo-stimulation leading to increased GnRH-I secretion, gonadal maturation and breeding (Dawson *et al.*, 2001; Fig. 1). However, breeding ends before the return of short photoperiods and is the consequence of a second effect of long photoperiods i.e. the induction

of photorefractoriness leading to gonadal regression (Dawson *et al.*, 2001; Fig. 3). Therefore, long photoperiod causes photo-stimulation followed by photorefractoriness (Dawson *et al.*, 2001). Photorefractoriness marks an essential aspect in seasonal breeding and occurs when birds do not show response to photoperiod. The absolute photorefractoriness is associated with a marked decrease in hypothalamic GnRH-I, whereas the relative photorefractoriness is not associated with a decrease in hypothalamic GnRH-I (Dawson *et al.*, 2001; Dawson and Sharp, 2007; Fig. 3). In relatively and absolutely photorefractory species, the initial gonadal regression occurs while there is still releasable GnRH (Fig. 3), but for some reason it is not released (Dawson and Sharp, 2007). This may be due to release of a substance which acts at the level of the anterior pituitary gland to antagonize the action of GnRH or development of an inhibitory input to GnRH terminals in the median eminence (Dawson and Sharp, 2007).

The dissipation of photorefractoriness has been reported to occur during short photoperiods and is characterized by an increase in hypothalamic GnRH-I, which is essentially identical to that in puberty (Dawson *et al.*, 2001; Dawson and Sharp, 2007). Various factors have been reported to influence the timing of photorefractoriness such as temperature, food availability, and social factors like songs (Dawson and Sharp, 2007; Fig. 3). Higher temperatures have been reported to advance the onset of photorefractoriness, however the mechanism underlying the temperature effect is unknown (Dawson and Sharp, 2007). It has been suggested that high temperatures may increase prolactin secretion and if prolactin involved in gonadal regression in advance of the decrease in releasable GnRH then it presents a possible mechanism (Dawson and Sharp, 2007; Fig. 3). Thus relative

photorefractoriness has been thought to be due to the influence of prolactin (Dawson, 2005; Dawson and Sharp, 2007; Fig. 3). Prolactin tends to inhibit GnRH release and actions (Dawson *et al.*, 2001). Further, it is good in determining the exact timing of gonadal regression (Dawson *et al.*, 2001; Fig. 3). Prolactin is said to be photoperiodic sensitive and its levels are higher when the gonads start to regress (Sharp and Sreekumar, 2001; Fig. 3). The secretion of prolactin has been shown to be stimulated in long photoperiods and inhibited by short photoperiods (Dawson *et al.*, 2001). However, prolactin is modulated by temperature, whereby prolactin levels have been reported to be higher in increased temperatures compared to low temperatures (Gahali *et al.*, 2001).

Food availability has been reported to influence seasonal breeding and photorefractoriness (Fig. 3), hence breeding activity usually corresponds to periods of food availability (Dawson and Sharp, 2007). Additionally, food supplementation can advance the time of breeding. Restriction of food availability has been reported to cause a significant delay in the onset of photorefractoriness (Dawson and Sharp, 2007).

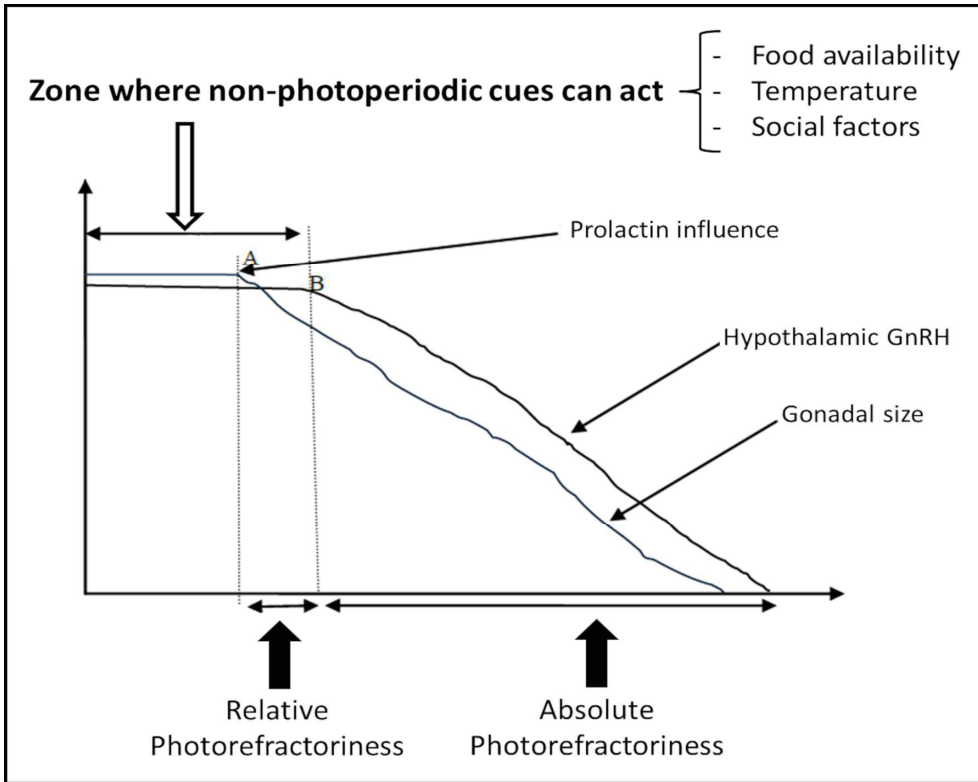


Figure 3: Photorefractoriness. (A) Marks the onset of relative photorefractoriness, whereas (B) marks the onset of absolute photorefractoriness. Note the presence of gonadal regression before the decrease in GnRH level during relative photorefractoriness. Note also the marked decrease in GnRH associated with absolute photorefractoriness.

Conclusion

This review has discussed photoperiodism in seasonal breeding. It has pointed out some essential aspects that are involved in photoperiodic control of seasonal breeding, which includes how light is perceived in birds and mammals, role of melatonin and its regulation, thyroid hormone and thyroid stimulating hormone. Moreover, the study had a brief scope on photorefractoriness.

Various studies showed that, seasonal reproduction is different between mammals and birds. They differ all the way from light perception and essentiality of circadian markers, role of melatonin and much more. All these differences entails that, mechanism of mammals and birds in terms of seasonal reproduction is not alike. However, all of them tend to have common points in terms of regulation of seasonal breeding, such as roles of TSH which tend to be a key player in seasonal breeding in birds and mammals. From this study it shows that photoreception is influenced by the length of the day light, length and color of light wavelength as well as light intensity. This could have an implication in terms of improving reproduction. The use of cheap and easily applicable techniques or methods such as manipulation of photoperiod can be helpful. Long photoperiods can be used to ensure improved reproduction in rabbits and chicken. It is relatively cheaper and non-tedious.

The role of melatonin in regulating seasonal breeding without altering metabolic mechanisms is of great value to mammals. Despite melatonin roles to be exhibited more in mammals, it is clear that its role in birds is still not to be neglected, as melatonin plays the best role in modulating some reproductive characteristics in birds such as songs. Photorefractoriness is shown not to be brought by the onset of short photoperiods but rather by exposure to long photoperiods. Prolactin hormone, temperature and nutrition tend to influence photorefractoriness. The importance of food is also captured, first as to ensure the timing of breeding i.e. its availability provides the clue for when to breed in photoperiodic animals. Secondly, it is obvious that once food factors are regulated in animals, then seasonal reproduction will be improved.

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