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Photic and nonphotic cues in regulation of seasonal reproduction in birds

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Abstract

The present review documents the recent advances on the roles of photic and non-photic cues in regulation of seasonal reproduction and associated functions in birds. Annual variation in day length is the most consistent and reliable cue in timing life history stages including reproduction, molt and migration in most birds. Other environmental factors such as temperature, rainfall, availability of food and social interactions etc. are essential supplementary factors used to supplement and/or modify the timing of reproduction. Increasing day lengths of spring and summer trigger hypothalamus-pituitary-gonadal (HPG) axis to secrete gonadotropins, which cause gonadal growth and development and induce endocrine gonads to secrete sex steroids that mediate cellular processes and control development of accessory sex structure, secondary sexual characters like bill and plumage colour and reproductive behavior. Photoperiod also plays an important role in the regulation of fat deposition, feathers molt and migratory immune responses. Apart from its duration, the other photic characters like intensity and wavelength together with some non-photic cues play crucial roles in overall timing of avian reproductive cycles.

Keywords: Photoperiod, Avian, Reproduction, Molt, Seasonal.

1. Introduction

Seasonality involves initiation, termination and reinitiation of physiological processes. It is an important adaptation for survival and is exhibited by many wild species. It ensures the occurrence of seasonal events at the most appropriate time of the year when the environmental factors are most conducive. Birds exploit favorable season by reproducing and avoid or mitigate unfavorable season by migrating or becoming refractory. In nature, they are exposed to changes in different environmental factors that influence their biological functions. Most critical among these functions is the timing of reproduction, a scheme that causes reproductive activity to occur during the period that assures minimum stress on the adults and maximum probability for survival of young and parents (Dixit and Singh 2011, 2020). Most birds reproduce seasonally in order to coincide the birth of young ones when food and shelter are optimally present. They also exhibit seasonality in some other physiological and behavioural functions including migration, molt, bill and plumage coloration and hormone levels, etc. (Dawson, 2007;

Dixit and Singh, 2011). The precise temporal regulation of reproduction is achieved through intricate physiological processes that sense variations in environmental condition, integrate them with internal information and regulate the reproductive state accordingly (Hau *et al.,* 2008). Thus, reproduction being an important part of life cycle greatly depends on environment (Immelman, 1971).

Successful individuals should be fully prepared for appropriate seasonal activity when that season arrives. Thus, fitness in a seasonal environment is all about the timing. There are optimum times to start and stop reproduction, molt and migration which are important life history events in annual cycles of most birds. As all the above events in life cycle of an avian species require preparation, therefore, fitness in a seasonal environment depends not only on the occurrence of seasonal events at the appropriate time in a year but also on the ability of the birds to anticipate and prepare for the favourable seasons in advance of their arrival. Thus, like most other wild vertebrates, birds also show a distinct temporal organization in their reproductive activity (Dawson *et al.,* 2001). The time and duration of the favourable season selected for reproduction differ among different climatic regions and different ecological groups of birds. Many environmental factors help birds in timing of seasonal reproduction and related events in their life history. The predictability of these factors is crucial as the birds need to make necessary physiological preparations before the onset of each life history stage (Dawson, 2008). It is important that the environmental factor selected by bird for control of its annual reproductive cycle must have reliable predictive value. The amplitude and predictability of environmental factors differ in different habitats of birds. These factors also differ in the geographical ranges occupied by them during their life span causing differences in timing and sequence of stages in their life-cycle. Various environmental factors have been classified into two categories by Baker (1938): the proximate and ultimate factors. The proximate factors help birds to select the most appropriate time window in the year for a seasonal event and the ultimate factors help decide the timing of actual seasonal event within this time window. The proximate factors provide the information when the breeding season should be scheduled in nature. This keeps both the sexes physiologically ready to avail any opportunity in the environment for reproduction. Thus, the role of proximate factor is very important with respect to timing of reproduction. The day length plays the role of proximate factor, while food, temperature, rainfall, etc. act possibly as ultimate factors or supplemental cues in control of annual reproductive cycle in majority of birds (Dixit and Singh, 2011). Some ultimate factors including nesting conditions, climate change, competition, predator pressure, etc. influence reproduction under special circumstances (Wingfield *et al.,* 2003). Many birds from both temperate as well as tropical and subtropical regions including India, therefore, use annual cycle of changes in photoperiod as calendar to time their reproductive and associated physiological and behavioural functions (Kumar *et al.,* 2004). The role of day length has been well recognized in the birds that breed at mid and high latitudes (Dawson *et al.,* 2001; Hau *et al.,* 2008). However, because of small annual variations in day length at lower latitudes, it is generally considered less suitable (Hau, 2001) and other nonphotic indicators such as temperature, rainfall, social factors have been given much importance (Perfito *et al.,* 2008). However, despite little annual variation in tropical and subtropical regions, many avian species have been reported to be photoperiodic (Dixit *et al.,* 2017).

2. Photic cues in control of avian reproduction

The endogenous oscillators involved in control of reproduction are sensitive to certain environmental cues (Daan and Aschoff, 2001). Light is a primary environmental signal that can affect the period of circadian oscillation in birds and thus entrain its physiology and behaviour. Because the light environment varies both in terms of intensity and spectrum, it is logical to expect that endogenous clocks regulating daily and seasonal responses will be sensitive to both the light intensity and spectrum, besides its duration. Birds experience incremental shifts in the length, spectrum and intensity of day-to-day light in nature. Light exhibits its influence on reproduction of most birds by all or any combination of above three characteristics viz. duration, intensity and wavelength (Kumar, 2002).

2.1 Photoperiod

Of all the environmental factors to which the birds are exposed to photoperiod is the most reliable and consistent environmental cue in controlling avian reproduction (Dawson *et al.,* 2001; Dixit and Singh, 2020). Daily and seasonal changes in illumination on earth surface is due to earth's rotation on its axis and its revolution round the sun, respectively. The day length away from equator changes with season and the light intensity at any given time changes with weather even at the equator. The annual variation in day length at a given latitude remains fairly constant for several years. This constancy makes day length a potent environmental factor for birds to rely on in timing physiological preparations for reproduction and related events. Day length not only changes with the season but it also changes with the latitude. Therefore, birds show latitude and season dependent photoperiodic adaptations in their reproductive responses (Dixit and Singh, 2014). Photoperiod is known as the initial predictive cue for initiating reproductive development in most birds (Wingfield, 1983). Following Rowan's (1925) groundbreaking study on Slate-colored Juncos (*Junco hyemalis*), several investigations evidenced the importance of day length as a major source of environmental information in programming seasonal reproduction (Dawson and Sharp, 2007). Day length is predictable and provides reliable environmental information in regulation of reproductive cycles of the birds inhabiting both mid and high latitudes (Hau *et al*., 2008). Studies on sexual cycles of some Indian birds reveal that they correspond to the seasonal changes in day length (Thapliyal and Tewary, 1964). Various investigations on birds that breed in spring/summer months at high latitudes and overwinter in India including blackheaded bunting, redheaded bunting and rosefinch and also on Indian resident species like common myna, yellowthroated sparrow, tree sparrow, house sparrow, and baya weaver reveal that they are responsive to day length. These birds can be placed into following categories based on their responses to artificial photoperiods: (i) those that exhibit gonadal development only under ultrashort day lengths (0.25 to 6 h) but fail to respond to the customary long and short days (8 to 24 h) for example Spotted Munia (Thapliyal *et al.,*1975; Chandola *et al.,* 1976) (ii) gonadal development occurs under long as well as short (8 to 24 h) days, e.g. Blackheaded Munia (Thapliyal and Saxena, 1964; Pandha and Thapliyal, 1969; Chandola *et al.,* 1973) (iv) short days (9L/15D) can stimulate gonadal development, however, pituitary function can be induced by long days as well, e.g. Lal Munia (Tewary, 1967) and (iv) long days (15L/9D) induce gonadal development while short days (below 9 h light/ day) fail to do so. Long daily photoperiods induce gonadal growth followed by regression and development of photorefractoriness in photoperiodic birds while short daily photoperiods fail to induce above events (Dixit and Singh, 2011). Thus, the seasonal responses in photoperiodic birds cycle between photosensitivity and photorefractoriness. The initiation of gonadal growth is a long day phenomenon while the termination of photorefractoriness and consequent recovery of photosensitivity is a short day phenomenon. Thus, both long and short days are important for photoperiodic regulation of annual reproductive cycles in them, although the birds use them for different purposes. The critical day length for a photoperiodic response is species specific and is a consequence of adaptation for breeding at specific time at particular latitude (Tewary and Dixit, 1986). The threshold photoperiods for initiation of gonadal growth lie between 10 and 11 h in tree sparrow (Dixit and Singh, 2011); 11–12 h in blackheaded bunting (Mishra and Tewary, 1999), weaver bird (Singh and Chandola, 1981), yellowbreasted bunting (Dixit et al., 2014) and between 12 and 13 h in rosefinch (Tewary and Dixit, 1983), redheaded bunting (Prasad, 1983), and yellowthroated sparrow (Tewary and Dixit, 1986). The rates of gonadal growth in these birds also change with changing photoperiods. The photosensitivity and initiation of reproductive events remain associated with the increase in gonadal growth and functions such as increase in sex steroids: testosterone and estradiol 17-β in male and female birds, respectively. Gonadal growth and development, in photoperiodic birds, are accompanied by increase in synthesis and release of hypothalamic gonadotropin releasing hormone (GnRH), pituitary gonadotropins (Leutenizing hormone, LH and follicle stimulating hormone, FSH) and gonadal steroids (testosterone and estradiol 17-β) and decrease in synthesis and release of hypothalamic gonadotropin inhibitory hormone (GnIH) and reverse is true during gonadal regression and photorefractoriness (Dixit and Singh, 2013; Dixit and Byrsat, 2018). Most photoperiodic birds cease to respond to the light stimulus upon long-term exposure to long day length (Bentley *et al.,* 1998). This total loss of sensitivity to long days is known as absolute photorefractoriness (Dawson and Sharp, 2007). It has adaptive significance as it restricts reproduction to best suited portion of the year, provides sufficient time for replenishment of energy stores for post reproductive events like molt and preparation for migration (Dixit and Singh, 2012). Gonads involute and become quiescent in photorefractory birds as the negative feedback mechanism operate to decrease the synthesis and release of GnRH from hypothalamus thereby suppressing pituitary gonadotropin and gonadal sex hormones secretions causing gonadal involution (Chandola *et al.,* 2004; Dixit and Singh, 2012). Restoration of responsiveness to increasing day lengths (photosensitive) of spring and summer does not occur until photorefractory birds experience decreasing day lengths of autumn and winter in nature or short day lengths in laboratory conditions (Dixit and Singh, 2012). However, there are some birds that do not show phorefractoriness until they experience decreasing day lengths in nature like Japanese quail, *Coturnix coturnix japonica* (Robinson and Follett, 1982) and Indian weaver bird, *Ploceus philippinus* (Chakravorty and Saklani, 1985). This is known as relative photorefractoriness.

Apart from reproduction, birds show distinct seasonality in several other morphological, physiological and behavioural functions related to reproduction such as feathers molt, body fattening, bill and plumage coloration, hormone levels, song production etc. (Dawson *et al.,* 2001). Feather loss can impede flight efficiency (Swaddle *et al.,* 1999), hence good-quality feathers are important for survival. Feathers need to be replaced every year as they wear out. Therefore, feathers are regularly removed and replenished by new feathers through a high energy consuming process called molt. Most passerine birds molt seasonally and once or twice (pre and post nuptial molt) in a year. Reproduction and molt are generally phased at different times in a year as both are energy intensive phenomena (Dixit and Singh, 2011). Molt generally coincides with gonadal regression. However, it is not decreasing gonadal steroids but increase in prolactin during gonadal regression that perhaps regulates molt (Dawson, 2005). It is still not clear whether photoperiod has a direct impact on the molt or molt is a consequence of photoperiodic induction of gonadal regression and its physiological interaction with molt (Dawson, 2008). Photoperiod controls different physiological activities linked to migratory phenomena such as *hyperphagia*, increase in body mass as a result of fat build-up (Zugdisposition), and migratory restlessness or *zugunruhe* (Robart *et al.,* 2018). Photoperiodic induction of body fattening is important for bird migration as the stored fat is a rich source of energy and sustains long migratory flights (King, 1968). However, photoperiodic control of fattening is minimal or nonexistent in non-migratory birds as they have uniform availability of food across the year and any accumulation of fat in them may hamper their flight activities (Dixit and Singh, 2011). Photoperiodically induced secretions of sex-hormones control various developmental and behavioral responses related to breeding cycles of birds such as appearance of secondary sexual characters like changes in bill and plumage color, development of accessary sex structures and a display of reproductive behaviors like establishment of territory, song production, mate selection, nest building etc. (Dixit and Singh, 2011). Immune system is very important in fight against various infections and pathogens. It is reported that photoperiod and temperature take part in regulating the lymphoid organs like thymus, spleen and other parameters of the immune system in mammals (Demas *et al.,* 2003) and these factors have also been speculated to play such roles in birds. Study on lymphoid organ and responses to the mitogen Con A in jungle bush quail (*Perdicula asiatica*) indicates that minor variations in daylength may disturb the immune system by effecting existing levels of melatonin and sex hormones (Verma *et al.,* 2017). The Long days in summer months cause high secretion of sex hormones that in turn are responsible for reproductive activity but decrease the immune status as steroids inhibit immunity (Singh and Haldar, 2005). Short days improve immune function in a state of energy-compromising conditions (Nelson and Drazen, 1999). This is done by repression of sex steroids and prolactin by the melatonin hormone. Thus, the neuroendocrine and immune system can be correlated to seasonal variations in day length.

2.2 Light Intensity

One of the critical components of light with a major impact on the photoperiodic seasonal responses of birds is the light intensity. It plays significant influence on photoperiodic seasonal responses of birds. Various intensities of light have been reported to influence reproductive activity in house sparrow (Menaker *et al.,* 1970), white-crowned sparrow (Farner, 1959), domestic duck (Benoit, 1964), domestic turkey (Nestor and Brown, 1972) and Japanese quail (Follett and Millette, 1982). Further, studies involving different combinations of light intensity and period suggest that both play significant roles in initiation and development of gonads in birds (Budki *et al.,* 2009). Furthermore, photoperiod-induced seasonal responses tend to have light intensity thresholds (Kumar and Rani, 1996). Light intensity could be a potent zeitgeber in affecting seasonal responses as it changes across the year in both tropical and temperate zones. It has been assigned a greater role in control of reproduction in the birds inhabiting lower latitudes. Although equatorial species have the ability to respond to photoperiod, they are unlikely to detect slight changes in day length prevailing at these latitudes (Moore *et al.,* 2005). Therefore, it is believed that these species utilize seasonal variations in other light parameters such as light intensity (Gwinner and Scheuerlein, 1998). There are reports suggesting that the equatorial birds can monitor seasonal variation in photic information by measuring light intensity (Hau et al., 2008).

2.3 Light Wavelength

The visible spectrum of light consists of seven colors of the rainbow (VIBGYOR) having a wavelength of 400-700 nm, starting from violet and ending to red. Violet and blue colour correspond to short wavelengths, green and yellow to mid-wavelengths and red to long wavelengths. The white light is mixture of the colours present in the visible spectrum while black is total absence of light. The spectral composition of daylight has been found to affect the circadian and seasonal photoperiodic responses in some birds (Rani *et al.,* 2002). Some investigations examining the effects of varying spectral composition of light have revealed the role of light wavelengths in photoperiodic responses of birds (Malik *et al.,* 2014; Yadav *et al.,* 2015). The effects of light wavelengths on egg laying have also been investigated to improve performance in turkeys (Hulet *et al.,* 1992), laying chickens and broilers (Halevy *et al.,* 2006; Zhang *et al.,* 2014). The importance of wavelength of light in control of photoperiodic responses in a long day species was recognized by studies of Oishi and Lauber (1973) and Foster *et al.* (1985) on Japanese quail. Also, the role of wavelength of light in regulation of both circadian and seasonal responses have been shown in studies on black- and red-headed bunting (Misra *et al.,* 2004; Malik *et al.,* 2004, 2014; Rani *et al.,* 2005).

3. Nonphotic cues in control of avian reproduction

The birds of same latitude breed at different times in different habitats, and in the same habitat between different years (Caro *et al.,* 2005). This suggests that apart from day length, other factors such as food availability, social factors, and ambient temperature can fine tune the initial, general reproductive response to photoperiod (Wingfield *et al.,* 1991). The non-photic cues such as temperature, rainfall, food abundance and social stimuli etc. may modulate the exact time of breeding within the time window fixed by photoperiod or may affect the timing of photoperiodic window for reproductive activities. The above factors provide only short term predictive information and can modify and/supplement the photoperiod induced responses (Scott *et al.,* 2007). Photoperiod as a proximate factor has been studied extensively for initiating seasonal reproduction in birds, while the use of other non-photic environmental factors like temperature (Parmesan, 2007; Wingfield *et al.,* 1992), rainfall (Sekercioğlu *et al.,* 2012; Hau, 2001), humidity (Hau *et al.,* 2004), food availability (Both and Visser, 2001) etc., in the regulation of reproductive function and in rare cases associated events is less well understood. Various studies recognize these cues as ultimate factors which help to decide the timing when the actual seasonal event would take place during the time window and supplement as well as modify the period of reproduction in birds. Variation in any one or more of these environmental factors may affect the timing of reproduction in birds. Therefore, it is essential to understand the role of non-photic cues in avian reproduction and its associated events.

3.1. Temperature

Temperature is one of various environmental factors that can influence the process and timing of avian reproduction directly by changing patterns and behaviour or indirectly by interfering with photoperiod and changing its effect (Parmesan, 2007; Dawson and Visser, 2010). The effect of ambient temperature on seasonal reproduction in birds differs among species and within the population of same species. Thus, the issue of whether temperature influences the timing of reproduction remains unanswered (Dixit *et al.,* 2018). There is evidence in some, but not in all species of birds, that the time of egg-laying varies with spring temperature (Torti and Dunn, 2005). It is less clear whether this is a consequence of a direct effect of temperature on photoperiodically induced gonadal maturation. Although attempts have been made to assess the role of temperature on photoperiodic induction of gonadal growth, the results, showing positive or negative effects, were inconclusive (Wingfield *et al.,* 2003; Spencer and Bryant, 2002).

The breeding seasons of many birds have been found to shift in response to rise in global temperature (Walther *et al.,* 2002; Parmesan, 2006). Those birds that adapt to the changing temperature survive and reproduce successfully while those exhibiting rigid life-history stages may perish (Visser *et al.,* 1998; Coppack and Pulido, 2004). There may be shift in breeding schedules of many tropical birds in response to change in spring temperature (Dixit *et al.,* 2018). There may be advancement of the breeding season in these birds or they may produce lesser offspring due to decreased reproductive rate resulting in population decline (Wormworth and Sekercioğlu, 2011). There are studies suggesting that the birds' egg-laying dates are partly decided by the past ambient temperatures (Visser *et al.,* 2003; Salvante *et al.,* 2007). This is important as the bird's fitness is related to its ability to match reproduction with the short period of temperature-dependent arthropod abundance (Visser *et al.,* 2006). Visser *et al*. (1998) reported that the egg-laying date did not advance in the Dutch population of great tits (*Parus major*) over a period of 23 year period though the selection for early laying was intensified. The seasonal increase in temperature has been reported to fine-tune laying dates in great tits, while they remain unaffected by mean temperature and daily temperature variation (Schaper *et al.,* 2012). The effects of temperature on reproductive activities have been studied in some other avian species and it was found that high temperature fail to induce gonadal maturation in starlings (*Sturnus vulgaris*) and white-crowned sparrows (*Zonotrichia leucophrys gambelli*); however, low temperature delays the development of photorefractoriness in starlings (Dawson, 2005). The above findings, showing both positive and negative effects of temperature on gonadal development, are inconclusive (Spencer and Bryant, 2002; Wingfield *et al.,* 2003). The studies involving causal effects of temperature on seasonal timing of reproduction and related events are crucial in resolving mystery of the biological consequences of climate change (Caro *et al.,* 2013). The day length and temperature cycles are inseparable in nature. Therefore, it is reasonable to believe that the timing and duration of seasonal responses are possibly regulated by day length as well as temperature rather than by day length alone. Furthermore, temperature should also be considered as a predictor of future environmental conditions, in addition to its role as an environmental cue that constrains homeostasis through energetic challenges to the birds (Caro *et al.,* 2013).

3.2. Rainfall

Rainfall is another critically important environmental factor modifying the timing of avian reproduction both directly and indirectly. Inland water birds such as ducks are highly dependent on precipitation to withstand their wetland habitats while tropical species often have fixed breeding seasons related to predictable periods of rainfall (Wikelski *et al.,* 2000). Thus, any alteration in pattern of rainfall has major consequences for these species. Many birds inhabiting Himalayan regions and arid zones start breeding immediately after the first summer rainfall, the timing of which is unpredictable. Nest building in some species starts immediately with the onset of rain (Immelmann, 1973), which shows that the reproductive system by now was fairly mature to respond so quickly to the changes in the surrounding. Zebra finch is an opportunist breeder (Bentley *et al.,* 2000). This species although being a seasonal breeder in predictable habitats breeds opportunistically in arid zones where rainfall pattern is irregular. The gonadal growth is controlled by day length in Rufous-winged sparrow (*Aimophila carpalis*), but the exact timing of breeding occurs in response to rainfall within the breeding window (Deviche *et al.,* 2006). A similar response is exhibited by other species such as canaries (*Serinus canarius*) which is photoperiodic (Storey and Nicholls, 1976) but breeds in response to rainfall (Leitner *et al.,* 2003). Thus, rainfall acting as a supplementary cue ultimately fine tune the onset of breeding (Wikelski *et al.,* 2000). Many researchers are uncertain of the primary physiological mechanism i.e. the nature of the cue associated with rainfall and also how it interrelates with reproductive physiology. The cue may not be the rainfall itself, but any combination of factors associated with rainfall or consequences of rainfall i.e. the arrival of rain brings about changes in vegetation leading to an improved food supply, the environment is cleaned from dust particles allowing more ultra violet light to reach on earth, the landscape changes from brown to green etc.

3.3. Food Availability

Availability of food, upon which young ones depend, is an important ultimate factor that controls the timing of breeding (Lack, 1968). Food can also act as a proximate factor (Perrins, 1970) because females require sufficient food for the production of eggs. Reproduction in birds can be affected by providing supplement food (Davies and Deviche, 2014). Some studies have shown that egg laying dates in some birds advances if provided with supplemental food and this advancement is normally within the range of few days (Reynolds *et al.,* 2003). In starlings, the egg laying days can be advanced by 5 days on providing supplemental food (Kallander and Karlsson, 1993) and food restriction delays egg laying in captive birds (Meijer and Langer, 1995). In spotted antbirds (O'Brien and Hau, 2005) and wild canaries (*Serinus canaria*) (Voigt *et al.,* 2007), the testis development can be enhanced by food in the absence of photostimulation. Some species such as Crossbills (genus *Loxia*) breed opportunistically at any time of the year when there is sufficient amount of food available. However, the gonadal growth and regression, in this species, are regular seasonal events and the opportunism is mainly limited within this primary seasonality (Deviche and Sharp, 2001). Crossbills possess a long breeding window within which breeding can occur but the exact time of breeding within the window depends upon the food availability. Moreover, breeding does not occur even though food availability is maximum outside this breeding window during gonadal regression and molt (Hahn, 1995). However, food restriction has little or no significance on birds in which gonadal maturation is controlled by photoperiod (Meijer, 1991). Ovarian growth advances in tricolored blackbirds (*Agelaius tricolor*) upon providing live grasshoppers but the effect is not seen in the case of males (Payne, 1969). Few researchers are of the opinion that there exists no correlation between testicular growth and appropriate food items or food restriction (Vleck and Priedkalns, 1985). Thus, the food availability has a greater role as ultimate factors in control of avian reproduction. However, it also acts as proximate factor in special circumstances.

3.4 Social cues

Social cues related to reproduction help in communicating information about the reproductive state and availability and quality of potential mates and help in initiating reproductive process by mate selection, territorial establishment, courtship and clutch initiation. However, some social cues retard gonadal development and egg laying by acting negatively. Due to the multimodal sexual signals, the demonstration of social cues in many experiments conducted on gonadal development and lay is more varied and distinguished than for other kinds of non-photic cues. There are different experimental manipulations which include: inclusion and exclusion of potential partner (Perfito *et al.,* 2015), manipulation of partners reproductive state (Watts *et al*., 2016), intragroup manipulation of social status (Brouwer *et al.,* 2009), presentation of recorded song stimuli on behalf of potential mates (Chmura *et al.,* 2017) or a social group (Setiawan *et al.,* 2007), devocalization (Cheng, 1992) and inclusion or hindrance of visual cues (Meijer and Langer, 1995). Experiments conducted on female birds revealed that the presence of a sexually mature partner enhances follicular maturation (Perfito *et al.,* 2015) and shortens the time of clutch initiation (Crino *et al.,* 2017). However, the presence of male fail to affect the ovarian regression (Silverin and Westin, 1995). Further studies throw light on the characteristics of a partner that initiate gonadal development in females. Matthews (1939) and Stevenson *et al*. (2008) reported how gonadal growth can be influenced by the visual stimulus of a male. Gonadal growth and egg-laying can also be advanced by providing additional stimuli such as song tapes (Morton *et al.,* 1985) and the presence of mate (Shields *et al.,* 1989). In canaries it is seen that heterospecific and conspecific songs enhance follicular growth (Bentley *et al.,* 2000) but between the two, conspecific song is more effective stimulus. There occurs enhancement of gonadal growth in female rock doves when males specifically direct courtship song towards her (Friedman, 1977). Brockway (1965) suggested that the male budgerigar's "soft warble" vocalization can act as an effective way to promote egg laying in females. In female canaries, longer-higher quality vocalizations can result in nest building and formation of larger clutches (Kroodsma, 1976).

4. **Conclusion and Perspective**

Reproduction is the part of life cycle with great environmental dependence. Various photic and non-photic environmental factors help birds in precise timing of their seasonal reproduction when resources in the wild are optimally present and chances for survival of offspring are maximized. The proximate factor like day length, acting as a reliable and predictable cue, helps birds to choose the most appropriate time window for seasonal reproduction; however, the non-photic cues such as ambient temperature, rainfall, food availability and social factors etc. acting as ultimate factors help decide when precisely the actual breeding should occur in the photoperiodic window. The predictability of environmental factors keeps the birds physiologically ready before the favorable season arrives. The integration of environmental factors and neuroendocrine components regulates the physiological, developmental and behavioral responses related to seasonal reproduction in birds. There is paucity of data on sex-dependent and latitudinal variations in environmental control of avian seasonal reproduction opening up new avenues of research in the field. New experiments designed to focus on molecular mechanisms and physiological pathways are needed to reveal the complete story.

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