Regardless of latitude and longitude, a habitat on earth experiences daily and seasonal changes in sunlight (duration, spectrum and intensity), food availability or abundance, climate (temperature, rainfall, etc.) and social factors in their environment (Nelson et al., 2002; Dunlap et al., 2004; Dixit et al., 2014). The two major rhythms of the biosphere are daily and seasonal, relating to the rotation of the earth about its axis approximately every 24 h and the earth’s rotation about the sun approximately in a year (~365 days), respectively. Habitats are diverse with respect to seasonality and in a degree of predictability of this seasonality showing inter- and intra-annual variations. To cope with such variations, organisms possess physiological mechanisms that allow them to temporally coordinate energetically demanding stages in their life, for example, reproductive events with conditions in the environment (Murton and Westwood, 1977; Bronson, 1989; Wingfield and Kenagy, 1991; Shine and Brown, 2008). In seasonal environments, no life cycle can be complete without the means to exploit the favourable season, to avoid or mitigate the unfavourable season and to switch between the two lifestyles in a timely manner. Organisms should, therefore, carefully plan their life history stages in such a way so as to live successfully in a seasonal environment. They exploit the favourable season through growth, development and reproduction and avoid or mitigate the unfavourable season through dormancy or migration. Successful individuals must be prepared for the appropriate seasonal activities when that season arrives. Thus, fitness in seasonal environments is all about timing. Seasonal timings of life-cycle activities like reproduction, moult, hibernation and migration in a given environment require preparations. Hence, fitness is dependent not only upon the optimal time for engaging in season-specific activities but also upon the ability to forecast and prepare for the changing seasons in advance of their arrival (Bradshaw and Holzapfel,
2007). Of all the life-history stages in an organism, breeding is predominantly restricted within a definite time window, to guarantee greater food availability for raising the young and maximize reproductive success (Jacobs and Wingfield, 2000). Thus, appropriate timing of breeding is a challenge and an important component of reproductive success for almost all animals including birds that live in seasonally fluctuating environments. A precise temporal regulation of reproduction is achieved by intricate physiological processes that sense variations in environmental conditions, integrate them with internal information and regulate the reproductive state accordingly (Hau et al., 2008). Seasonality in reproduction and associated events is, thus, a compulsory adaptation for survival in many species. It is represented by the initiation-termination-reinitiation of physiological processes and is species specific (Trivedi, 2005; Singh, 2012). In the life history of birds, some changes are ontogenic i.e. they happen only once in a life time. Birds hatch into nestlings and fledge into juveniles, then they go through a series of life-history changes that repeats every year such as they moult, they may migrate and overwinter. After winter, there is spring migration and then breeding which is followed by moult. Breeding consists of nest building, egg laying, incubation and rearing of the young. Each stage occupies the whole of time available to it so that the temporal overlap between successive stages tends to be minimized. In fact, each of the stages has evolved to occur at the optimum time and the optimum sequence minimizing overlap between successive stages. Thus, annual life-history stages begin and end at optimal times, and do not generally last shorter or longer than the optimal durations (Gwinner, 1996a; Gwinner, 1996b; Dawson, 2008; Budki et al., 2009). Further, all these stages remain in a defined phase relationship and generally center on reproduction (Dawson, 2008) that occurs at the most appropriate time of the year when the food resources in the wild are optimally present and the chances of survival of the young and
parents are maximum (Jain and Kumar, 1995; Deviche and Small, 2001; Dawson, 2007; Singh et al., 2010). Therefore, the timing of actual reproduction is critical for the species. Birds utilise habitats which are different in amplitude and the predictability of environmental factors. They also inhabit different geographical ranges over the course of their lives, resulting in the difference in timing and sequences of their life-cycle stages (Nelson et al., 2001). Most birds generally show tremendous seasonal cycles of recrudescence/regression of their reproductive organs (Balthazart, 1983; Murton and Westwood, 1977; Dixit and Singh, 2011; Dixit and Sougrakpam, 2012) in anticipation of the suitable season for breeding. Also, the time and duration of the favourable season selected for reproduction differ amongst different climatic regions and different ecological groups of birds. The annual breeding cycle is most marked at mid- and high-latitudes, but contrary to earlier widely held view, the species of tropical and subtropical regions are also seasonal breeders (Dixit and Singh, 2011).

Birds, like most other wild vertebrates, show a distinct temporal organization in their reproductive activity. Thus, for most bird species, a precision in time of reproduction is of interesting occurrence. Reproductive organs of the seasonal birds remain quiescent during the non breeding season while they develop and become fully functional at the beginning of breeding season. The morphological changes that birds undergo include body mass and moult while at physiological level; they undergo changes in hypothalamo-hypophyseal gonadal axis (Nicholls et al., 1988; Hahn et al., 1997; Dawson et al., 2001). As these physiological and developmental preparations for reproduction require time, they must be initiated well in advance of the optimum environmental conditions. Lack (1968) commented that “each species of bird has presumably evolved the timing of its breeding so that it raises most offspring” and “laying is normally so timed that young are in the nest when there is enough food for
them to be raised”. It has been observed that most bird species accurately anticipate a favourable season and prepare themselves physiologically well in advance (Helm et al., 2009), thus reproducing around the time when food supply is abundant and survival chances for young are maximum, as mistiming will have severe fitness consequences (Helm et al., 2009) on the young ones. Reproduction is an indispensable part of the life cycle with great environmental dependence (Immelmann, 1971). Birds having annual periodic reproductive season use periodic changes in the environment as predictive information for the oncoming of a favourable season for reproduction. Since physiological preparations for reproduction begin long before the breeding season, the environmental factor selected by an avian species for basic timing of its annual reproductive cycle must have reliable predictive value, so that the physiological mechanisms controlling reproduction may be activated well in advance of the optimal environmental conditions necessary for successful rearing of the young. To achieve successful breeding, most birds use environmental cues like photoperiod, rainfall, food availability etc. to up- and down-regulate the hypothalamic-pituitary-gonadal (HPG) axis. The best studied of such environmental cues is photoperiod, the use of which has been particularly well documented in birds. Typically, increasing day lengths stimulate the activation of the HPG axis in preparation for reproduction (Dawson et al., 2001). Thus, photoperiod is considered to be an ‘initial predictive cue’ to initiate reproductive development (Wingfield, 1983). In some species, photoperiod may be sufficient to induce complete reproductive development. But in the majority of species, additional cues (‘supplementary cues’ and ‘synchronizing and integrating cues’) such as food availability, rainfall, temperature or social interactions are used to fine-tune the timing of completion of reproductive development and onset of breeding (Wingfield, 1983). It has been suggested that temperate zone and high latitude species that exhibit highly seasonal
breeding schedules (which have been the subjects of the majority of studies), rely almost entirely on photoperiod for reproductive timing (Ball, 1993; Sharp, 1996; Hahn et al., 1997; Dawson et al., 2001). However, tropical and low latitude species that exhibit more flexible or opportunistic breeding schedules rely more on non-photonic cues (Wingfield et al., 1992; Hahn et al., 1997, 2008; Scheuerlein and Gwinner, 2002; Perfito et al., 2008). In order to maximize reproductive success, opportunistic species detect and integrate environmental cues in addition to, or independent from, photoperiod into their physiology to initiate breeding (Immelmann, 1963, 1971; Bronson, 1985; Heideman and Bronson, 1994; Hahn et al., 1997; Zann, 1999; Zann et al., 1995). Thus, several environmental factors help in reproductive timing, and important ones include seasonal variations in day length, temperature, rainfall, humidity and vegetation etc. (Immelmann, 1971). Baker (1938) classified environmental factors affecting avian reproduction into two categories: the proximate- and ultimate- factors. The proximate factors help the organisms to select the most appropriate time-window in the year for a seasonal event and the ultimate factors help decide the timing when the actual seasonal event would happen during this time-window. For a critical phenomenon like reproduction, proximate factors provide the information about when the breeding season should be scheduled in nature. This will keep both the sexes physiologically ready, should an opportunity in the environment occur for actual reproduction. Therefore, in the viewpoint of phasing of reproduction, the role of the proximate factor is very important. In timing of avian reproduction, day length acts as the proximate factor, while food, temperature, rainfall etc. act possibly as ultimate factors or supplemental cues. Some ultimate factors that operate in a special situation are competition, nesting conditions, predator pressure and climate change etc (Wingfield et al., 2003; Dixit et al., 2017a).
At all latitudes, birds are exposed to day-to-day variation in light hours, to which they adapt using their endogenous clocks because of their great precision in the timing of various behavioural and physiological events. These systems are innate (endogenous), inheritable and genetic in origin (Aschoff, 1981; Kumar, 2002; Kumar et al., 2004). All eukaryotes and at least some prokaryotes possess this internal, self-sustained circadian clock that regulates daily activities (Dunlap et al., 2004). These endogenous clocks can also be important in timing life history events, but these are generally set by exposure to exogenous factors, e.g. photoperiod as a zeitgeber (Farner and Gwinner, 1980; Gwinner, 1986). These oscillatory systems are synchronized with day and night, and thus, are expressed as daily overt rhythms in the natural environment. When exposed to constant situations (constant dim light, LL_dim or constant darkness, DD), organisms exhibit their endogenous periodicity (Aschoff, 1981) with period (interval between two identical phases) close to 24 hour (24 h), which is referred to as ‘circadian’ (circa- about, dies-day) (Halberg, 1969), or close to one year, which is referred to as ‘circannual’ (circa-about, annum- year). The circadian and circannual rhythms not only interact with outside world, they also interact with other internal rhythms (Singh et al., 2010). In general, seasonal cycles appear regulated involving two mechanisms (Misra et al., 2004): the photoperiodism and circannual rhythm generation. In photoperiodism, the environmental photoperiod (=daily light period) is involved in the generation of seasonal rhythms through induction and termination of physiological processes. Day length interacts with the clock and induces a physiological response. An endogenous clock enables the birds to identify the time when to switch-on (photoinduction) and when to switch-off (photorefractoriness) its physiological mechanisms so that seasonal events occur at the most suited time of the year. The other is the circannual rhythm generation, in which a self-sustained endogenous rhythmicity of about one year times these component events.
Both these mechanisms may not be mutually exclusive and might interact closely as per adaptive needs of the species. However, many investigators believe that the photoperiodism and circannual rhythm generation are evolved as separate mechanisms. A commonly held view is that a photoperiodic species lacks a strong circannual component, and a circannual species lacks a strong photoperiodic component. Part of this widely held assumption arises from studies that (1) show maintenance of the post-reproductive photorefractoriness until a long day photoperiodic bird species is kept under stimulatory long day lengths (Sansum and King, 1976) and (2) show circannual rhythm generation in low latitude and equatorial species that are not considered typically photoperiodic species (Gwinner, 1986). Misra et al. (2004), however, provide data indicating the probability that an endogenous seasonal rhythm underlies photoperiodism in the black-headed bunting (Emberiza melanocephala). This suggests the possibility that photoperiodism and circannual rhythm generation mechanisms coexist in the same photoperiodic species. However, whether absolute photoperiod or change in photoperiod acts directly to control physiology, or if photoperiod acts to synchronize an innate circannual rhythm of life-history changes, is still unclear (Gwinner, 2003; Dawson, 2007).

Birds use reliable environmental cues to anticipate the onset of predictable environmental changes (Dawson, 2008). Of several factors in the environment which the birds are exposed to, the day length is most consistent. As the change in photoperiod is entirely predictable at given latitude, both within and between years, it is used as a reliable cue to time the physiological preparations for three major life-history stages: reproduction, moult and migration (Goldman, 2001). Day length has been shown as a major source of temporal information regulating seasonal responses in a number of avian species inhabiting both mid- and high- latitudes (Jain and Kumar, 1995; Gwinner, 2003;
Hau et al., 2004; Rani et al., 2005; Dawson and Sharp, 2007). Customarily, a bird species that respond to long day lengths is called a long day species and the one that responds to short day lengths is called a short day species. In some avian species, the long day length may maintain the stimulated reproductive status (Nicholls et al., 1988; Chaturvedi et al., 1993). Thus, in most avian species, long daily photoperiods induce gonadal growth followed by regression and development of photorefractoriness while short day lengths by failing to activate hypothalomo-hypophyseal-gonadal axis, do not (Kumar, 1997). In many photoperiodic birds, each period of gonadal growth and function is followed by a rapid collapse of the gonads. Thereafter, a majority of birds enter in a state of unresponsiveness to light during which no known pattern of stimulatory photoperiodic regimes can stimulate their gonads (Farner and Follett, 1966), which has come to be known as photorefractoriness. During this phase, the breeding behaviour ceases, gonads regress and reproductive hormones decline (Dawson et al., 2001). It is a reversible state of unresponsiveness to day length of gonadostimulatory duration terminating seasonal breeding in many species of photoperiodic birds (Wilson, 1989). In nature, it is the primary mechanism by which seasonal reproduction is normally terminated at an appropriate time of year ensuring maximal reproductive success, permitting sufficient time for replenishment of energy stores for post breeding maintenance activity, such as post nuptial moult and preparation for migration (Nicholls et al., 1988). There are two different mechanisms by which photoperiod controls gonadal regression and terminates breeding season: absolute and relative photorefractoriness. Some species exhibit ‘absolute photorefractoriness’ which is characterized by an apparently spontaneous gonadal regression during continuous exposure to long photoperiods and that, following regression, a further increase in photoperiod does not induce renewed gonadal maturation (Hamner, 1968). Gonadal regression in such photorefractory birds begins before the day
length declines. The absolute nature of photorefractoriness is defined by either of the two criteria (Nicholls et al., 1988). First, in species that become absolutely photorefractory, the gonads will regress spontaneously when held on constant long days. In these birds, prebasic plumage moult proceeds with spontaneous gonadal regression without any decline in photoperiod. Second, once gonads have regressed, birds are completely unresponsive to very long days, even to 24 h of light. Gonadotropin levels and gonads are unaffected by even longer days (24L/0D in the extreme) once gonads have regressed and moult is advanced (MacDougall-Shackleton et al., 2006; Hahn and MacDougall-Shackleton, 2008) in these birds. These two criteria have been used interchangeably to characterize the state of absolute photorefractoriness and in many species, both phenomena occur. However, these two phenomena may not be dissociated in some species (MacDougall-Shackleton et al., 2006). On the other hand, some avian species show ‘relative photorefractoriness’ which is characterized by the loss of ability to respond to a stimulatory photoperiod with relatively shorter photophase, but not to the same or longer photophase. In many photoperiodic birds, reproduction is terminated unexpectedly by the rapid collapse of the gonads when days are still long. Relative photorefractory birds require a decrease in the photoperiod to induce gonadal regression, but regression occurs under a photoperiod that is still longer than that which has induced maturation earlier in the year (Robinson and Follett, 1982). Relative photorefractory species can be restimulated on exposure to very long photoperiod following gonadal regression. The gonadal regression in these species occurs when day length declines in nature but still remains longer than critical day length (Kumar, 2001; Dawson and Sharp, 2007). Some birds such as Japanese quail (Coturnix coturnix japonica) and Indian weaver bird, Ploceus philippinus (Anthony, 1970; Robinson and Follett, 1982; Chakravorty and Saklani, 1985) remain in a breeding state under constant long days but
their gonads regress under relatively shorter days. However, most avian species such as white-crowned sparrow, *Zonotrichia leucophrys gambelli* (Blanchard, 1941), European starling, *Sturnus vulgaris* (Dawson and Goldsmith, 1983), house finch, *Carpodacus mexicanus* (Hamner, 1968), brahminy myna, *Sturnus pagodarum* (Kumar and Kumar, 1991, 1993), tree sparrow, *Passer montanus* (Dixit and Singh, 2012; Dixit et al., 2014) and yellow-breasted bunting, *Emberiza aureola* (Dixit and Sougrakpam, 2013; Dixit et al., 2014) exhibit absolute photorefractoriness. Photorefractoriness is terminated by exposing birds either to short days under the laboratory condition or to shortening days of autumn and winter in nature for several weeks so that birds become photosensitive once again to the stimulatory effects of increasing day lengths in spring (Boulakoud and Goldsmith, 1995). Thus, photoperiod plays an important dual role in the precise regulation of both the onset and end of reproduction in seasonally breeding birds (Dawson et al., 2001).

Most bird species need to completely replace their plumage each year, and so a period for moult needs to be included in the annual cycle (Dawson, 2008). Most birds undertake a series of moult during their life span (Trivedi, 2005). Thus, the feathers are periodically shed and replaced. This process of shedding and replacing worn feathers is called moulting and the feather coats worn between moults are called plumages. Avian moult is the periodic replacement of worn feathers and is seasonal, with most passerines moulting once or twice each year. Birds moult their feathers for a variety of reasons: to replace worn feathers, to change colours for crypsis, to change colours for territorial or sexual displays. In many photoperiodic birds, the proximal cue for moult initiation is day length, which has an effect on the hormone levels that ultimately control moult progression. The beginning of the post-nuptial moult is closely related to the time of gonadal regression (Dawson, 2005). Feather production is energetically costly,
increasing the basal metabolic rate by 9-11% in some species (Lindström et al., 1993) and accounts for more than 20% of total body dry weight (Dawson, 2006). The loss and replacement of feathers of moulting birds proceed in a regular sequence on each feather tract. The pattern of moult is most conspicuous in the flight feathers, where moult of the primaries commonly progresses from the wrist outward, and only one or two feathers grow simultaneously (Stresemann and Stresemann, 1966). The most common schedule of moult in birds is the alternation with the breeding because moult, breeding and migration are high energy demanding processes that are essentially mutually exclusive in time (Murphy and King, 1992; Newton and Rothery, 2005; Dawson, 2008); many fascinating adaptive compromises have developed between moult and other phases of the annual cycle (Ashmole, 1968). Therefore, the control of the time and rate of moulting is important in the lives of birds. The physiological basis of the control of the time and rate of moulting and the integration of moult into the annual cycle are of considerable interest, and the discovery remains as a challenge to the comparative physiologist (Dawson, 2008). The quality of a bird's feathers is central to its fitness for many reasons, including predator escape (Swaddle et al., 1999) and influencing mate selection (Fitzpatrick, 1998; Ferns and Lang, 2003; Pryke and Andersson, 2005). Feather quality and moulting efficiency can influence individual energetic expenditures associated with aerodynamic efficiency (Dawson et al., 2000). Further, photostimulation is required to induce moult but it also induces gonadal maturation and regression (Dawson and Goldsmith, 1983; Nolan and Ketterson, 1990). Therefore, it is not clear whether photoperiod has a direct effect on moult, or whether it is a secondary consequence of photoperiodic control of the gonadal cycle and a physiological link between gonadal regression and moult, satisfying the ecological requirement for moult to immediately follow breeding (Dawson, 2008). Many studies have shown that implants of testosterone
can delay, prevent or interrupt moult (Nolan et al., 1992; Dawson, 2004). However, castration has a little effect on the timing of moult in starling (Dawson and Goldsmith, 1984). It is more likely that prolactin is involved. Several studies have investigated seasonal cycles in prolactin in free-living birds and, in each of these, peak prolactin concentrations were found at or just before the start of moult (Dawson, 2006).

Photoperiod seems to regulate the various physiological events associated with migratory phenomenon such as development of a migratory urge (Zugdisposition) which is manifested by fat accumulation, hyperphagia and body weight increase along with Zugunruhe, the migratory restlessness. Migratory birds use lipids as a fuel for the migratory flight (Boswell, 1991). The association of fat deposition with migration in birds has been documented by many workers like King and Farner (1965), Boswell (1991), Rani et al. (2005) and Budki et al. (2008). However, increase in body weight before migration in birds is not always entirely related to an increase in fat storage. Several studies have indicated that the increase in protein levels, notably in the flight muscles, can also occur at this time (Piersma, 1990). Photoperiodic control of premigratory fattening has been observed in a few subtropical migratory visitors in which testicular cycle is photoperiodically controlled (Kumar and Tewary, 1983). On the other hand, fattening is generally lacking in non-migratory birds and if fattening occurs, it is only to a limited extent (Farner and Follett, 1966).

Many species, living in tropics or close to the equator where there is very little or no change in annual photoperiod exhibit clear seasonality in reproductive functions. These observations support the involvement of endogenous circannual rhythm in their control. These rhythms have been experimentally demonstrated in at least 20 species of birds under specific lighting conditions (Gwinner and Dittami, 1990; Guyomarc and Guyomarc, 1995; Cadee et al., 1996; Newton, 2007) suggesting that their annual cycles
of reproduction are controlled by endogenous circannual rhythmicity (Gwinner, 1975). Under seasonally constant environmental conditions, these rhythms persist for several cycles with a period that is usually and slightly different from 12 months. In European starlings, a cycle of reproduction composed of photosensitive and photorefractory phases, continues in constant photoperiod closed to 12 hours (Gwinner, 1996; Dawson, 1997). In birds, the overt expressions of circannual rhythm under constant conditions include seasonal changes in reproduction, body mass, moult and Zugunruhe or the migratory restlessness. Birds that live in habitats where photoperiod is a poor predictor of seasons (equatorial residents, migrants to equatorial/tropical latitudes) rely more on their endogenous clocks than birds living in the places where there is a tight correlation between photoperiod and seasonal events. Such differences in reliance on endogenous clocks may indicate that the annual timing mechanisms are adaptive. The most important temporal cue in the wild and zeitgeber for circannual rhythm is photoperiod. The role of photoperiod in such a temporal scheme is limited where it is used to synchronize the circannual rhythm to the calendar year, but it does not alter the overall temporal course of seasonal programming of the annual event (Budki, 2010). We are not sure if the circadian and circannual rhythms are physiologically distinct and do not overlap. It has been suggested that the circannual clocks are either based upon (i) a de-multiplication (counting) of circadian days (ii) a sequence of interdependent physiological states, or (iii) one or more endogenous oscillators, similar to circadian rhythms (Wikelski et al., 2003). Whether two circa-rhythms can be separated from each other is yet to be established experimentally.

Since the pioneering work of Rowan (1925) that suggests a relationship between photoperiod and avian gonadal cycle, a great deal of attention has been directed towards answering the question: how do the birds measure the length of the day? It has been
suggested that the response system, in most bird species, must have a circadian component related to day length (Follett, 1973; Turek, 1978; Farner, 1980; Follett et al., 1981; Wada, 1983; Turek et al., 1984; Trivedi, 2005; Rani et al., 2005; Ikegami and Yoshimura, 2012; Dixit and Singh, 2012; Singh and Dixit, 2014). Bünning (1963) proposed the involvement of an endogenous daily rhythm in the photoperiodic response mechanisms. This hypothesis involves a circadian (i.e. of about 24 h in duration) component of sensitivity to daily light within the organism as a physiological basis of photoperiodism (Bünning, 1973). According to Bünning, the endogenous circadian rhythm consists of two halves. The first twelve hours is the subjective day or photoinsensitive phase while the latter twelve hours is the subjective night or photosensitive phase. The photogonadal stimulation is the result of direct or indirect, repeated (daily or otherwise) illumination of the photosensitive phase by external photophase. This device functions as a clock to measure the day length. Since then, considerable evidence has been accumulated strongly favouring the involvement of endogenous circadian rhythm in photoperiodic time measurement in many avian species, for example, *Carpodacus mexicanus* (Hamner, 1968), *Carduelis chloris* (Murton et al., 1970), *Passer montanus* (Lofts and Lam, 1973), *Passer domesticus* (Murton et al., 1970; Farner et al., 1977), *Zonotrichia leucophrys pugetensis* and *Zonotrichia atricapilla* (Turek, 1974), *Zonotrichia leucophrys gambelli* (Farner, 1965; Follett et al., 1974), *Coturnix coturnix japonica* (Follet and Davies, 1975; Siopes and Wilson, 1980; Wada, 1981; Follett and Millette, 1982), *Ploceus philippinus* (Singh and Chandola, 1983), *Emberiza bruniceps* (Prasad and Tewary, 1983), *Emberiza melanocephala* (Kumar and Tewary, 1984), subtropical *Passer montanus* (Dixit and Singh, 2012; Singh and Dixit, 2012; Dixit et al., 2017b). As a result, it is now clear that photoperiodic time measurement in majority of the birds is based on a circadian rhythm of responsiveness to
light (Hoffman, 1981; Follett and Follett, 1981; Follett et al., 1981; Turek et al., 1984; Rani et al., 2002; Trivedi et al., 2005; Dixit and Singh, 2016; Dixit et al., 2017b). Thus, in many photoperiodic species, a circadian rhythm of photoperiodic photosensitivity (CRPP) mediates photoperiodic regulation of seasonal and reproductive responses (Follett and Follett, 1981; Turek et al., 1984; Rani et al., 2002; Trivedi et al., 2006; Dixit et al., 2017b). CRPP responds to light in a phase dependent manner (Rani et al., 2005).

There have been numerous subsequent refinements of the Bünning hypothesis. In a more explicit version (Pittendrigh and Minis, 1964; Menaker, 1965; Pittendrigh, 1966) the daily photoperiod has been attributed to play a dual role, i.e. entrainment of circadian rhythm to a 24 h cycle and that of producing photoperiodic response if its duration is sufficient to extend into the photosensitive or more precisely photoinducible phase (Pittendrigh, 1966). Two models have been produced to account the possible ways of functioning of the circadian clock in photoperiodic time measurement (Pittendrigh, 1972): the external and internal coincidence models.

\( a) \) External coincidence model: According to this model, a photoperiodic response occurs due to the direct coincidence between the photoinducible phase of circadian rhythm and the environmental photoperiod. First, light entrains the circadian periodicity in photosensitivity which is presumed to be an endogenous free running circadian rhythm and second, when of sufficient duration extends into the photoinducible phase of the entrained circadian periodicity in photosensitivity, inducing the photoperiodic response.

\( b) \) Internal coincidence model: This model predicts that external light period brings two or more circadian oscillators in a particular phase relationship with respect to one another and results in a photoperiodic response. According to this model, light serves only as the entraining agent without having an active role in inducing a photoperiodic
response. This model suggests that the phase relationship between internal circadian oscillators may vary under different photoperiodic conditions (e.g., a change in the ratio of light to dark) and only under certain conditions (light-dark cycle) will the phase relationship be such that photoperiodic induction shall occur. Long day lengths might establish such a relationship while short photoperiods could maintain the rhythm out of phase with respect to each other. The photoperiodic responses of the majority of birds investigated so far, have been interpreted within the framework of external coincidence model viz. Japanese quails (Follett and Sharp, 1969), golden-crowned sparrows (Turek, 1974), red-headed buntings (Tewary et al., 1982; Prasad and Tewary, 1983), black-headed buntings (Kumar and Tewary, 1984), rosefinch (Dixit, 1987), tree sparrow (Dixit and Singh, 2012; Dixit and Singh, 2014; Dixit et al., 2017b).

The hypothesis that the circadian system is involved in photoperiodic time measurement is supported by the results of different experimental approaches that involve the exposure of birds to a variety of unusual light-dark cycles and the subsequent determination of whether they interpret the light-dark cycle as a long or short day. One of the powerful methods used to test the involvement of circadian rhythm in photoperiodic time measurement is referred to ‘night-interruption’ experiments, in which two light pulses are given in a 24 h light-dark cycle. These light periods consist of a main photophase of a non-stimulatory duration (6-8 h) combined with a dark phase in a 24 h light-dark cycle which is interrupted by a short pulse of light once per cycle at a temporarily fixed point. These two light periods imitate the effect of the corresponding long light period. The first light period, called the entraining light pulse (E-pulse) and given early in the subjective day, “entrains” the CRPP, so that the photoinducible phase ($\Phi_i$) begins at some “fixed” hours later in the day (Ball and Balthazart, 2003). These experiments were designed on the assumption that despite the quality of light being
provide is similar at all times, its quantitative effects on gonadotropin secretion vary depending on where it falls in a 24 h cycle.

Exclusive studies have been done on the circadian rhythm and its characteristics by eminent workers in many vertebrates including birds (Zimmermann, 1966; Daan and Pittendrigh, 1976; Pittendrigh and Daan, 1976; Pohl, 1977; Aschoff and Pohl, 1978; Gwinner, 1981; Marimuthu et al., 1981; Berthold and Querner, 1982; Berthold, 1984; Chandrashekar, 1985; Binkley, 1990; Kumar, 2002; Singh et al., 2002; Malik et al., 2004; Rani et al., 2005; Doyle and Menaker, 2007; Dixit and Singh, 2011; Cassone and Westneat, 2012; Dixit and Sougrakpam, 2012; Dixit et al., 2017b). Birds show well defined circadian rhythmicity. They are unique among vertebrates having distinct physiological and behavioural features that change with the change of season. The daily patterns of the activity-rest cycle under natural and artificial photoperiodic conditions together with changes in the daily circadian activity behaviour have been widely studied in several birds as a measure of adaptation to day-night environment (Gwinner, 1975; Daan and Aschoff, 1975; Pohl, 1977; Poesel et al., 2006; Kumar et al., 2007; Dixit and Singh, 2014, 2016; Dixit et al., 2017b). Day length is also the strongest predictor of circannual variation in activity duration (Singh et al., 2014) and is used as a major source of temporal information by many vertebrate species in regulation of their seasonal responses. Daily rhythms of locomotor activity are perhaps one of the most conspicuous and easily measurable behavioural parameters in birds. The daily changes in the pattern of short-term behavioural functions such as locomotor activity are influenced by seasonal changes in day and night cycle (Ramenofsky et al., 2008). Therefore, general activity of a bird within its cage is used as a measure of the response of the circadian system (Singh, 2013). Locomotor activity in birds has been identified as one of the important parameters to reveal the seasonal variability in phase association between activity (internal) and time
cues (external) in both captive and free living conditions (Marimuthu, 1984). Rhythm in locomotor activity is most commonly used to unravel features of the biological timing. This is because the locomotor activity is one of the most reliable markers of the circadian system recorded as a measure of the response of the circadian system (Daan and Aschoff, 1975; Malik et al., 2004). The onset, offset or mid points of activity can be used as reliable reference points to characterize the period, amplitude and phase of the circadian rhythm (Daan and Aschoff, 1975).

The solar cycle causes extreme changes of light intensity and wavelength in the environment from day to night, and many organisms have become specialised for locomotor activity at a particular phase of the 24 h day. The effects of wavelength and intensity of light on the clock have been found to be phase dependent in the red-headed bunting (Rani and Kumar, 2000). Such phasic effects can be seen in skeleton photoperiods in which light is applied discretely at different circadian phases (Rani and Kumar, 1999). It is known that the properties of a daily light-dark cycle that are important to time keeping processes are its period or cycle length, phase or timing of dawn and/or dusk, the photoperiod or duration of light per day, the intensity and wavelength of incident light. Light exerts its effects via one or all of its three significant variables or characteristics: the duration, intensity (quantity) and wavelength (spectral distribution, spectral composition) (Kumar, 2002). 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 light spectrum, besides duration. This has not been investigated in much detail in birds. These light characteristics change during the day as well as during the season of the year and affect the behaviour of birds as evident in black-headed bunting (Kumar et al., 2000; Rani et al., 2001), quail (Oishi and Lauber, 1973), broiler chickens (Prayitno et al., 1997)
and domestic chickens (Miklosi et al., 2002). They have also been found to influence reproductive functions in some birds (Wolfson, 1959; Rani and Kumar, 2013, 2014; Malik et al., 2014).

Apart from duration, the wavelength and intensity (irradiance) of daily light also influence the photoperiodic responses in birds (Rani et al., 2002). Many researchers have reported light wavelength as an important aspect of light. Light is just one portion of the various electromagnetic waves flying through space. The electromagnetic spectrum covers an extremely broad range, from radio waves with wavelengths of a meter or more, down to x-rays with wavelengths of less than a billionth of a meter. The visible portion occupies an intermediate position, exhibiting both wave and particle properties in varying degrees. Irradiance is a measure of radiometric flux per unit area or flux density. Irradiance is typically expressed in w/cm$^2$ (watts per square centimeter) or w/m$^2$ (watts per square meter).

The visible spectrum of light is composed of seven colours of the rainbow (VIBGYOR) having a wavelength of 400-700 nm, starting from violet to red, where violet and blue corresponds to short wavelengths, green and yellow to mid-wavelengths and red to long wavelengths. The white light is a mixture of the colours of the visible spectrum. Black is a total absence of light. The circadian and seasonal photoperiodic responses in few birds have been found to be affected by the spectral composition of daylight (Rani et al., 2002). Few studies have examined the effects of varying spectral composition of light on circadian processes. In mammals, action spectra for entrainment in pocket mice (Gordon and Brown, 1971) and in rats (McGuire et al., 1973) were found to resemble the spectral sensitivity function for rhodopsin, with a single peak in the blue-green region of the visible spectrum. In the flying squirrel, phase response curves (PRCs) for 15-min light pulses of red (620 nm), green (500 nm) and white light are all similar,
except that the amplitude of the PRC for green light exceeds that for red (DeCoursey, 1988). Some previous studies have suggested the role of light wavelengths in photoperiodic responses of birds (Bissonnette, 1932; Ringoen, 1942; Benoit and Ott, 1944; Ishibashi and Kato, 1951; Oishi and Lauber, 1973; Kumar and Rani, 1996; Kumar et al., 2000; Rani and Kumar, 2000; Malik et al., 2004, 2014; Yadav et al., 2015). The effects of light wavelengths on egg laying have also been investigated to improve performance in turkeys (Leighton and Potter, 1969; Gill and Leighton, 1988; Levenick and Leighton, 1988; Felts et al., 1990; Hulet et al., 1992), laying chickens and broilers (Max et al., 1995; Rozenboim et al., 2004; Bailey and Cassone, 2005; 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 by studies on black- and red-headed bunting (Kumar and Kumar, 1995; Kumar and Rani, 1996; Kumar et al., 1996; Rani et al., 2001; Misra et al., 2004; Malik et al., 2004, 2014; Rani et al., 2005). There is a critical light energy level (threshold) for photoperiodic induction, which in the natural environment is achieved by the combination of duration, intensity and wavelength of the daily light period. The wavelength and intensity (irradiance) of daily light influence the endogenous time keeping system such that the circadian output is synchronized to best time-of-day and/or time-of-year (Aschoff, 1981).

Another important variable of light is its intensity. Light intensity has significant effects on the photoperiodic seasonal responses of birds. The effects of a range of light intensity on various reproductive functions have been studied in house sparrow (Bartholomew, 1949; Menaker and Eskin, 1967; Menaker et al., 1970; Underwood and Menaker, 1970), white-crowned sparrow (Farner, 1959), domestic duck (Benoit, 1964),
domestic turkey (Nestor and Brown, 1972) and Japanese quail (Oishi and Lauber, 1973; Wilson and Siopes, 1976; Siopes and Wilson, 1980; Follett and Millette, 1982). Further studies using different combinations of light intensity and period suggest that both play significant roles in the initiation of gonadal growth and development in birds (Kumar and Kumar, 2004; Rani et al., 2007; Budki et al., 2009). It was also found that photoperiod-induced seasonal responses tend to have light intensity thresholds (Menaker, 1971; Oishi and Lauber, 1973; Kumar, 1986, 1988; Kumar and Rani, 1996). Though, the duration of photoperiod has been an important factor in determining the seasonal responses, the light intensity could be a potent zeitgeber in affecting the seasonal response as it changes across the year in both tropical (that occur as a result of changing cloud cover associated with the dry and rainy seasons) and temperate zones (that occur as a result of change in the day length). Light intensity has been assigned a greater role in regulating reproductive activities in the species inhabiting lower latitudes. Though the species living in the equator are capable of responding to photoperiod, they are unlikely able to detect slight changes in day length in their habitat (e.g. for equatorial Ecuador, Moore et al., 2005). Therefore, they need and are suspected that these species utilize seasonal variations in other photic environmental information such as light intensity (Gwinner and Scheuerlein, 1998). When equatorial African stonechats were exposed to a constant photoperiod (12.25L: 11.75D) with bi-annual variations (alternating low- and high-intensity) in light intensity during the day, they showed gonadal and moult rhythms which were synchronized with the light intensity cycle (Gwinner and Scheuerlein, 1998). Control birds exposed to the same photoperiod but a constantly high daytime light intensity did not synchronize and showed variable responses. Also, stonechats may respond to low light intensity as a predictive cue for rainfall (Gwinner and Scheuerlein, 1999). These findings suggested that equatorial birds can use the photic information to
predict seasonal variations in the environment by measuring light intensity (Hau et al., 2008). Light intensity can also modify the reproductive responses of birds under the same photoperiod (Bissonette, 1931; Bartholomew, 1949). Its seasonal variations could amplify slight variations in photoperiod and thus, facilitate their detection in near equatorial habitats. Wikelski et al. (2000) reported that gonads of spotted antbirds from Panama start growing during the early part of the year when light intensity is maximum, thus, indicating their ability to amplify the small increase in photoperiod that occurred at that time. Further, in a study on starlings, both photoperiod and light intensity were found to integrate to change the perception of day length and the birds exposed to particular photoperiod with a low light intensity interpreted it as being shorter than the same photoperiod with a higher light intensity (Bentley et al., 1998). These findings suggest that light intensity may act as a circannual zeitgeber and that the light intensity and day length may act synergistically. It is important to mention here the “Aschoff’s Rule” which states that as constant light intensity increases, tau (τ) lengthens for nocturnal species and shortens for diurnal species (Aschoff, 1960).

Although photoperiod is the primary zeitgeber, other environmental factors do have significant synchronizing influence on the circadian system and seasonal timing. Seasonal activities often appear linked with the changes in environmental photoperiod, although cues like changes in food supply and temperature can influence the timing of a seasonal event (Gwinner and Dittami, 1985; Gwinner and Dittami, 1990; Wingfield and Farner, 1993; Jain and Kumar, 1995; Hau, 2001; Deviche and Small, 2001; Dawson, 2005, 2008; Hahn and MacDougall-Shackleton, 2008; Verhulst and Nilsson, 2008; Tokolyi et al., 2011; Burger et al., 2012; Schaper et al., 2012; Caro et al., 2013). These cues provide ‘essential supplementary information’ and ‘synchronizing and integrating information’ (Wingfield, 1980; Wingfield and Kenagy, 1991) for fine adjustment of life-
cycle stages to the particular ecological circumstances of birds. They also include mild weather, the availability of nest sites and stimulatory social interactions (Lewis and Orcutt, 1971; Bluhm, 1985; Wingfield and Kenagy, 1991), which can trigger territorial behaviour, nest building and final stages of yolk accumulation. Lots of information and evidence have been accumulated about how non-photic cues such as temperature, food availability, nest sites and social interactions act as zeitgebers in the synchronization of circannual rhythms (Mrosovsky, 1977, 1978, 1986; Gwinner and Scheuerlein, 1998; Gwinner, 2003) can affect the timing of the onset and the end of reproduction (Goldman et al., 2004). It is presumed that these non-photic cues work as complementary and modifying factors (Hau et al., 2004; Helm et al., 2006) for the day length and light intensity induced harmonization of seasonal periodicities. Lack (1950) proposed that the birds breed at the appropriate time along the annual time scale when there is plenty of food in its neighbourhood, and the ambient temperature is optimum. It was later supported by Berthold (2001), who suspected that birds make physiological and behavioural adjustments to ensure that breeding occurs at the most appropriate period of the year. It is now known that cycles of temperature (Hoffman, 1968; Rajaratnam and Redman, 1998; Herzog and Huckfeldt, 2003; Torti and Dunn, 2005), food availability (Boulos et al., 1980; Aschoff, 1987; Mistlberger, 1994; Hau and Gwinner, 1996, 1997; Kumar et al., 2001; Davidson and Menaker, 2003) and social cues (Vishwanathan and Chandrashekar, 1985; Mrosovsky, 1988; Mrosovsky et al., 1989; Scott et al., 2007) also play roles in the synchronization of circadian functions in many vertebrates including birds and these factors along with reproductive experience, vegetation of the habitat and the stress factors affect the timing of reproduction (Moore, 1982, 1983; Visser and Lambrechts, 1999; Grieco et al., 2002; Breuner and Hahn, 2003; Salvante and Williams, 2003). Food availability may influence gonadal growth and development in
several avian species (Wingfield and Farner, 1993; Hau et al., 2000; Kumar et al., 2001; Scheuerlein and Gwinner, 2002; Bhardwaj and Anushi, 2004). To adjust the timing of their reproduction with the maximum food availability, birds proximately respond to a specific set of environmental predictive cues (Murton and Westwood, 1977). These factors tend to modify and/or supplement the photoperiod induced responses (Scott et al., 2007). The degree to which these non-photic factors affect the physiology of breeding depends on the species as well as the environment considered (Hau et al., 2000; Hau, 2001).

While photoperiod plays an important role in seasonal timing (Dawson et al., 2001; Dixit and Singh, 2011; Dixit and Sougrakpam, 2012), it cannot account for the annual variation in reproduction. Also, for most species, the increase in biomass of their food resource is temperature dependent. Temperature has increased at a very high rate over the past decades because of global warming and it correlates with seasonality which is a complex phenomenon (Parmesan and Yohe, 2003; Buckley and Foushee, 2012). Climate change affects population dynamics, distribution ranges and life-cycles of organisms worldwide (Stenseth et al., 2002; Parmesan, 2006). Consequently, climate change is likely to advance the time of peak food availability. If birds rely entirely on photoperiod to time breeding, the peak in food availability may have already passed by the time young require it. There is evidence that this is happening (Visser et al., 2004). It is common for non-tropical avian species to limit reproductive activity to the time of year when temperatures are relatively mild and the necessary food resources are present (Baker, 1938; Perrins, 1970; Wingfield, 1983). It has been observed that certain avian populations, such as great tits (Parus major) nesting in the Netherlands are shifting the timing of reproduction as the temperature increases (Visser et al., 1998, 2006). The impact of global change on natural populations has been studied in the reproductive
timing of song birds in relation to their invertebrate food supply (Crick et al., 1997; Torti and Dunn, 2005; Visser, 2008; Gienapp et al., 2008; Both et al., 2009). Suomalainen (1937) was the first to investigate the effect of temperature on timing of reproduction in birds and since then many more researchers have addressed this question (O’Connor, 1978; Perrins and McCleery, 1989; Nager and van Noordwijk, 1995; van Noordwijk et al., 1995; McCleery and Perrins, 1998; Meijer et al., 1999; Visser et al., 2003; Salvante et al., 2007; Schaper et al., 2012; Caro et al., 2013; Shiao et al., 2015). The effects of temperature on parameters affecting timing of reproduction like temporal patterns in circulating hormones (Jones, 1986; Silverin and Viebke, 1994; Wingfield et al., 2003; Dawson, 2005; Perfito et al., 2005; Silverin et al., 2008; Kumar et al., 2010) or gonadal size (Dawson, 2005; Perfito et al., 2005, Silverin et al., 2008; Singh et al., 2011) have been established in studies on some avian species while investigation on others produced more inconsistent results (Suomalainen, 1937; Farner and Wilson, 1957; Silverin and Viebke, 1994; Wingfield et al., 1996; Dawson, 2005; Perfito et al., 2005). It is suggested that temperature affect timing directly, as seen by modified activity patterns and behaviour in response to changing thermal conditions (DeCoursey, 1960; Vivanco et al., 2010). In addition, the temperature could affect timing by modifying the underlying circadian period length. But the proximate mechanisms that precede the behavioural response to temperature cues are still poorly understood (Dawson, 2007; Visser et al., 2009). Although attempts were made to assess the role of temperature on photoperiodically induced gonadal maturation, the results showing positive and negative effects are inconclusive (Spencer and Bryant, 2002; Wingfield et al., 2003) and need further investigation.

It is a well-known fact now that day length plays an important role in the regulation of seasonal breeding in a majority of birds (Hau, 2001; Trivedi et al., 2006).
Thus, there must be mechanisms for the input and interpretation of day length and for the endocrinological output that affects the expression of seasonal phenotypes (Bradshaw and Holzapfel, 2010). Seasonal changes in reproductive activities are correlated with the gonadotropin hormone (GTH) secretion (Ubuka et al., 2003). The mechanisms as explained in chicken where the rate and degree of gonadal maturation is ultimately determined by the rate and secretion of gonadotropin-releasing hormone I (cGnRH-I) and possible antagonistic effects of gonadotropin inhibiting hormone (GnIH; Bentley et al., 2003; Ukena et al., 2003) and/or prolactin (Dawson and Sharp, 1998; Sharp and Blache, 2003). cGnRH is a decapeptide synthesized in the cell bodies of specialized neurosecretory neurons. It passes down the axon of these neurons and is secreted in the median eminence at the base of the hypothalamus, from where it passes via a blood portal system to the pituitary gland. After reaching to the pituitary, cGnRH-I stimulates the synthesis and release of two gonadotropic hormones namely, luteinizing hormone (LH) and follicular stimulating hormone (FSH). These two hormones once released into the circulation cause gonadal growth and maturation. The activity of cGnRH-I neurons is primarily controlled by photoperiodic information received from encephalic receptors integrated in some way with a circadian clock. As the photoperiod increases, it causes conversion of thyroxine to triiodothyronine (Yasuo et al., 2005) and this to some extent (Takagi et al., 2007) leads to an increased secretion of cGnRH-I (Yamamura et al., 2006). Among recent advances in physiological basis of photoperiodism is the implication of mediobasal hypothalamus (MBH). Studies on Japanese quail have suggested that MBH is an important center controlling photoperiodic responses (Meddle and Follett, 1997). The expression of the gene encoding type 2 iodothyronine deiodinase (DIO2) in the MBH, that catalyses intracellular deiodination of thyroxine (T4) prohormone to the active 3, 5, 3’-triiodothyronine (T3), is induced by light in Japanese
quail. Intracerebroventricular administration of T₃ mimics the photoperiodic response, whereas the DIO2 inhibitor iopanoic acid prevents gonadal growth. These findings demonstrate that light induced DIO2 expression in the MBH may be involved in the photoperiodic response of gonads in Japanese quail (Yoshimura et al., 2003). The involvement of local thyroid hormone conversion within the MBH in the regulation of seasonal reproduction has subsequently been confirmed in tree sparrow (Nakao et al., 2008). Furthermore, it has been reported that pars tuberalis of the pituitary gland relays photoperiodic information to the MBH (Nakane and Yoshimura, 2010). TSH from pars tuberalis appears to act retrogradely on TSH receptors in the tanyocytes to induce DIO2 expression via the TSH-receptor-cAMP signalling pathway (Nakao et al., 2008). In addition, chronic administration of TSH into the third ventricle of quail, in short day, induces expression of DIO2 and full testicular growth. This suggests that the TSH from pars tuberalis is a master factor regulating seasonal reproduction in birds (Nakane and Yoshimura, 2010). Thus, the light information detected by opsin-5-expressing cerebrospinal fluid (CSF) contacting neurons in the paraventricular organ (PVO) is transmitted to pars tuberalis (PT) to induce thyroid stimulating hormone (TSH) expression. TSH from PT retrogradely acts on TSH receptor in the tanyocytes to induce DIO2 expression. DIO2 converts prohormone thyroxine (T₄) to bioactive 3,5,3’-triiodothyronine (T₃). Long day induced T3 in the MBH not only causes morphological changes in the nerve terminals and glial processes that contain gonadotrophin-releasing hormone (GnRH), but also induces GnRH secretion causing release of gonadotropins (LH and FSH) from anterior pituitary that induce gonadal growth and functions (Nakane and Yoshimura, 2010). Photoperiodically induced secretion of cGnRH-I secretion may be modulated by non photoperiodic information from other neural inputs. Thus, the conversion of thyroxine to triiodothyronine may act as a long photoperiod signal. This
may ultimately down regulate cGnRH-I synthesis as bird become photorefractory. It is to be mentioned here that long day length stimulates GTH secretion in quail (Follett, 1976), white-crowned sparrow (Wingfield and Farner, 1980), tree sparrow (Wilson and Follett, 1974), canaries (Nicholls, 1974), duck (Balthazart et al., 1977) and starling (Dawson and Goldsmith, 1983) etc. Increasing levels of gonadal steroids in blood serum regulate important physiological changes and behaviours associated with reproduction (Wingfield et al., 1999) such as secondary sexual behaviours and secondary sexual characteristics that may include bill and plumage colour etc. and spermatogenesis (Follett and Robinson, 1980; Ball, 1993; Wingfield and Farner, 1993). The gonadal steroids affect GTH secretion by a negative feedback loop (King et al., 1989; Dunn and Sharp, 1999) thereby suppressing LH and FSH secretion and gonads regress.

The overall process of reproduction in birds can be explained in a simple way as in the following: stimulating environmental (day length) or internal (circannual rhythms) cues increase the production and secretion rates of gonadotropin-releasing hormone (GnRH), the vital protein hormone that functions like an on/ off switch for an entire endocrine cascade that eventually activates the reproductive organs and results in their seasonal gonadal growth (Ball and Hahn, 1997; Ball and Bentley, 2000; Dawson et al., 2001; Sharp, 2005). The median eminence of the hypothalamus releases GnRH which then travels via the portal blood system to the anterior pituitary where it induces the release of two gonadotropins- follicle stimulating hormone (FSH) and luteinizing hormone (LH). These two hormones act together to stimulate the growth and maturation of the ovary in female and the testes in male birds. The gonads will then increase the production of sex steroids such as estradiol and testosterone, which act on receptors in the brain to promote the expression of reproductive (song, courtship, copulatory) and aggressive (song, territory defence) behaviour. Once the HPG axis has been stimulated
by long days, other environmental/ supplementary cues such as ambient temperature, food abundance, social factors along with reproductive experience, vegetation of the habitat and the stress factors affect the timing of reproduction (Moore, 1982, 1983; Visser and Lambrechts, 1999; Grieco et al., 2002; Breuner and Hahn, 2003; Salvante and Williams, 2003) and can further stimulate or inhibit its seasonal growth and overall functioning (Wingfield and Kenagy, 1991; Wingfield et al., 1992; Ball, 1993; Schoech et al., 2004; Voigt et al., 2007). These types of cues allow the animal to fine-tune the timing of reproduction to the local environment (Perfito et al., 2004).

Male and female birds differ in many aspects of reproduction in relation to physiology, morphology and behaviour, however, very little is known about possible sex differences in response to environmental cues that control the timing of seasonal breeding. While male reproductive fitness typically varies more as a function of sexual selection, female reproductive fitness typically varies more as a function of fecundity selection (Ball and Ketterson, 2008). Thus, for females, variation in the precision of the timing of egg laying is likely to have more serious fitness consequences, while for males, variation in the timing of recrudescence of the male testes and accompanying territory establishment and courtship is likely to have more serious fitness consequences (Ball and Ketterson, 2008). From the proximate perspective, sex differences in control of reproduction could be regulated via the response to photoperiod or in the relative importance and action of supplementary factors (such as temperature, food supply, nesting sites and behavioural interactions) that adjust the timing of reproduction so that it is in step with local conditions (Ball and Ketterson, 2008). Questions such as ‘what is the adaptive significance for males and females to respond differently to the same cue or to respond to different cues altogether?’ can be addressed by ultimate causes while questions such as ‘How do males and females differ in the environmental cues they
respond to and in the nature of their response?’ can be explained by proximate causes.

Another question arises here as to what cues a particular sex will most likely respond to. For example, there is evidence that males and females both respond to photoperiod, but there may well be secondary cues that are salient in this regard in a sex-typical fashion.

The ability of photoperiod alone to induce full gonadal growth is different between males and females in many seasonally breeding species is clear (Ball and Ketterson, 2008). Greater the similarity in the reproductive behaviour of the sexes, greater is the similarity in the supplementary cues that males and females will use to time the onset, prolongation and termination of reproduction (Jacobs and Wingfield, 2000; Moore et al., 2005). Conversely, the more divergent the role of the sexes in reproduction, the less similar the cues should be (Ball and Ketterson, 2008). Although, the females have been paid less attention by the workers, there is evidence that the female reproductive system is also stimulated by long days in spring, is interesting (Trivedi et al., 2006; Dixit and Singh, 2011). Furthermore, the majority of the investigations on the effects of photic and non-photonic cues on avian reproduction and related functions have been limited to studies on males (Dolnix, 1975; Farner, 1980; Dixit, 2002). An extensive study to investigate their roles in the regulation of seasonal responses in female birds is scanty or rather lacking (Dixit and Singh, 2012). Synchronizing male and female reproductive development within pairs (Jacobs and Wingfield, 2000; Moore et al., 2005) is a prerequisite for a bird to breed successfully. Therefore, it is considerably reasonable to perform serial and thorough experiments involving photic and non-photonic cues on both the sexes in order to reveal the mysteries of environmental control of reproduction in birds.

The importance of photic and non-photonic cues in controlling reproduction and associated events are recognized in the birds that breed at higher latitudes (between 40°-70° N) (Farner and Wingfield, 1980; Dawson et al., 2001; Rani et al., 2002; Trivedi et al.,
2006; Bradshaw and Holzapfel, 2007; Hau et al., 2008; Dixit and Singh, 2011; Malik et al., 2014). The fact that birds inhabiting both high and low latitudes can discriminate even small changes in photoperiods (Trivedi et al., 2006), suggests that they necessarily represent adaptations by inhabiting different photoperiodic environments. The North-East region offers significantly different environmental conditions compared to the other parts of India, and this could be advantageous in making comparative studies and to enable us to address evolutionary aspects of regulation of seasonal cycles in birds. Also, less is known about the importance of day length and associated factors in control of reproduction of seasonal breeders at low latitudes, e.g. in tropics and subtropics. In the tropics and subtropics, it is generally believed that the annual variation in day length is too small to provide birds with reliable cue for the timing of seasonal events (Farner and Lewis, 1971; Kumar, 1997; Hau, 2001; Hau et al., 2008), and has been speculated to be of little use in triggering the reproductive and metabolic activities of the birds of these zones (Immelmann, 1971). Although, the literature on avian photoperiodism has become voluminous, most of it pertains to mid- and high- latitude breeders. However, few experimental investigations on low latitude seasonal breeders have been carried out and it has been found that some tropical and subtropical avian species possess photoresponsive mechanisms and are photoperiodic (Hau et al., 1998; Styrsky et al., 2004; Trivedi et al., 2006; Dixit and Singh, 2011; Dixit et al., 2014), leading to a tentative conclusion that day length has a more pronounced role in control of reproduction and related functions in the tropical and subtropical birds as well than has been assumed (Tewary and Kumar, 1982; Tewary and Dixit, 1986; Hau et al., 1998). Therefore, one has to be careful before minimizing or denying the importance of day length in reproduction and related events in birds inhabiting low latitudes. Further, the photoperiodic response itself is expected to be the target of selection in the present
scenario of the global environmental change (Coppack and Pulido, 2004). Ultimately, selection favours those birds that possess mechanisms, permitting them to respond to reliable proximate cues that predict impending relevant changes in the environment (Baker, 1938). Also, various characteristics of the natural light-dark (LD) cycle, viz. the amplitude of light and darkness, the length of the photoperiod and the duration of twilight vary systematically with the season. These changes can provide a reliable cue to organisms to adapt to changes in the environment. Therefore, it is interesting to study how changing LD cycles time seasonality in the biological clock characteristics observed in outputs as an overt short term and long term physiological and behavioural functions in the tropical and subtropical birds.

Birds are immensely valuable study systems because they show a dramatic seasonal reorganization in physiology, morphology and behaviour (Follett, 1984; Dawson, 2002). Further, since birds have excellent clock system, they can be the excellent model of research to understand the biological timing in vertebrates (Kumar, 2005). Although there has been a spurt of activity to identify cellular and molecular events related to vertebrate clock including the birds (Kumar, 2005), the biological questions at phenotypic levels have been consistently overlooked. It is known that the environment influences the down-stream mechanisms significantly such that behavioural and physiological functions are induced at “the appropriate time”. Therefore, it remains important to know how endogenous timekeeping mechanisms are tuned to changing environment so that an organism can live in its surrounding in the most profitable way. Breeding strategies in birds are highly complex and diversified, and so they might be using variations in timekeeping systems for their optimal survival. Thus, a study on birds would provide a novel input, particularly useful to understand how different environmental cues interact and synchronize endogenous timekeeping system to produce
strategies adopted by a vertebrate species for its survival in the wild conditions. Studies under artificial light and temperature conditions will throw some light on regulatory mechanisms used to schedule breeding at the appropriate time of the year. Investigations addressing whether temperature affects physiological responses to increasing photoperiod during spring are scanty. Therefore, it is logical to perform more experiments on different species to ascertain the role of temperature on the photoperiodic regulation of reproduction and associated events in birds. Also, it is useful to study the role of light intensity and wavelength in species that live in tropics and subtropics where light and temperature conditions are relatively different than those in the temperate regions. It is considerably reasonable to perform serial and thorough photoperiodic experiments on both the sexes in order to validate the generalization regarding the photoperiodic system of a bird species. North-East region offers significantly different environmental conditions compared to the other parts of India, and this could be advantageous in making comparative studies and to enable us to address evolutionary aspects of regulation of seasonal cycles in birds. Therefore, it would be interesting to study the roles of photic (duration, intensity and wavelength) and non-photic (temperature) cues in timing the seasonal breeding and associated functions in both the sexes of the tree sparrow, *Passer montanus* that occupies both low- and high- latitudes and adapts well to the laboratory conditions.

**The present thesis**

The present study was undertaken to address the role of photic and non-photic cues in the regulation of circadian and seasonal reproductive and associated responses in the tree sparrow (*Passer montanus*), a resident bird, inhabiting North-East part of India (Shillong: Lat. 25°34’N, Long. 91°53’E). An attempt has also been made to assess if temperature plays a modulatory role in photoperiodic responses in this species. In
particular, the emphasis is placed on studying seasonal responses of the tree sparrow under artificial photoperiodic and temperature conditions in both short and long term experiments. The experiments included in this thesis center mainly around three main objectives: (i) to determine the effects of three different properties of light: period, wavelength and intensity in regulation of seasonality in gonadal size, bill colour, feathers moult and body weight, (ii) to investigate the involvement of an endogenous circadian rhythm in timing photoperiodic responses, (iii) to study the effects of different light intensities and wavelengths on various circadian characteristics and (iv) to know whether temperature modulates photoperiodic seasonal responses.

The thesis begins with the general introduction that gives an overview of the topics included in the thesis. The general materials and methods include general procedures that are common to most experiments. The thesis ends with general conclusion and references. All the investigations carried out are organised into following four chapters and the experiments are dealt under sub-headings as follows:

Chapter I: Photoperiodic time measurement and photoentrainment of circadian activity rhythm

This chapter includes experiments to investigate the involvement of an endogenous circadian rhythm in photoperiodic time measurement during initiation of gonadal growth and functions and also to study the photic entrainment of circadian activity rhythm.

Chapter II: Effects of different wavelengths of light on circadian and seasonal responses

This chapter includes following three experiments designed to investigate the effects of different wavelengths of light on seasonal and circadian responses: (i) Effects
of different wavelengths of light on seasonal responses (ii) Entraining and inducing effects of different wavelengths of light on reproductive and related responses (iii) Effects of different wavelengths of light on circadian characteristics of activity rhythm.

Chapter III: Effects of different intensities of light on circadian and seasonal responses

In this chapter, following experiments were performed using novel experimental protocols to study the effects of different intensities of light on seasonal and circadian responses (i) Effects of different intensities of light on seasonal responses (ii) Influence of different light intensities on the entraining and inducing properties of light in gonadal and body weight responses.

Chapter IV. Effects of different temperature conditions on photoperiodic seasonal responses

In this chapter, seasonal responses were studied in different temperature conditions under constant photoperiods to investigate if temperature modulates photoperiodic seasonal responses.