Circannual rhythms in birds

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Abstract

Circannual rhythms are shown to mediate a wide range of seasonal and annual processes and help the animals to plan these events at most favourable time of the year. They are self-sustained biological oscillations with a period close to 12 months and are entrained by both photic and non-photic cues. The understanding of the circannual rhythm would help us know the temporal adaptation in animals. The present review outlines the basics of circannual rhythms, its interaction with environmental factors, differences between the two mechanisms that regulate seasonal responses in organisms i.e. photoperiodism and circannual rhythm, and also present some experiments which have demonstrated circannual rhythm in reproduction, migration and molt behaviour of birds.

Key words: circadian, circannual, photoperiodism, spotted munia

Introduction

Organisms anticipate the changes in their environment on daily basis to optimise the resource utilization and maximise their reproductive fitness. Most commonly observed are the adaptations in daily activities, which are readouts of time-of-day. These activities are under circadian (*circa* = about; *dian* = day) control. The circadian rhythms are ubiquitous, exist in almost all forms of life (Aschoff, 1981) and have a period of about 24-hours (Hastings et al., 2003). Besides daily activities, the long lived animals also adjust their physiology and behavior according to the seasonal changes in the environment which are mediated by the circannual (*circa* = about; *annum* = year) timekeeping system (Gwinner, 1996; Kumar et al., 2010; Rani and Kumar, 2013). Similar to circadian clock, the circannual clock is a self-sustained, endogenous, oscillatory system which has a period of about 12 months under constant conditions (Gwinner, 1986; Gwinner, 1996). The circannual clocks improve the ability of the animals such as long distance migrants and hibernating mammals to respond to appropriate seasonal cues and ignore the environmental fluctuations (Shine and Brown, 2008). Thus, it gates a seasonal event at appropriate time of the year, since a mistiming will delay the event until the arrival of favourable time next year (Miyazaki et al., 2006). In general, the circannual rhythms are relatively weaker oscillations with larger individual variations in their circannual periods. The difference between circadian and circannual rhythms may be related to the selection pressure onto the two endogenous systems (Hazlerigg and Loudon, 2008).

The species exhibiting circannual rhythmicity are shown to inhabit a range of habitats; from highly seasonal (temperate region) to almost constant (tropical region and deep sea) environment (Andersen and Keafer, 1987). Therefore, the diversity in circannual patterns could be the result of adaptation to diverse environments (Wingfield et al., 1992). The circannual rhythms may persist for many years under different environments e.g. constant light-dark schedules, constant dim light and in exceptional cases even under naturally changing day length OR may dampen rapidly in amplitude and require a recurring seasonal signal for sustained rhythmicity (Holberton and Able, 1992; Gwinner, 1996). This forms the basis of categorization of annual rhythms into truly circannual (Type II) or the one displaying a mix of endogenous and exogenous characteristics (Type I) (Mrosovsky, 1978; Lincoln et al., 2006).

It is argued that circannual events are the manifestation of circadian rhythms. This is because the circadian rhythms involvement has been shown in photoperiodic birds and mammals in the initiation and termination of seasonal gonadal response (Kumar and Follett, 1993; Kumar, 1997). However, various evidences rule out the involvement of circadian clocks in generation or expression of circannual rhythms (Dark et al., 1985; Pant and Chandola-Saklani, 1992; Kumar et al., 2004; Rani et al., 2006; Budki et al., 2012, 2014). Unlike circadian clocks, the circannual clocks have not been described yet at anatomical, physiological and molecular levels.

Interaction between circannual rhythms and environmental factors

The long lived animals, and birds in particular show different life history stages (LHSs) at different times of the year. The scheduling of these LHSs depends mainly on changes in the day length (photoperiod). Day length is considered as reliable temporal information by a number of avian species inhabiting both mid and high latitudes (Jain and Kumar, 1995; Kumar, 1997; Rani et al., 2005; Hahn and MacDougall-Shackleton, 2008) as it does not vary significantly at given latitude both within and between years. Also, the environmental information other than the photoperiod (non-photic cues) such as food, temperature, rainfall etc. may synchronize the timing of seasonal responses; however, they mainly act as supplementary and modifying cues (Farner and Follett, 1966; Helm et al., 2006). The importance of different environmental cues is different for temperate and tropical birds e.g. photoperiod is the most effective *Zeitgeber* (*zeit* = time; *geber* = giver) for temperate birds but in tropics, where, photoperiod remains almost constant across the year, the change in light intensity, food availability or temperature, could act as *Zeitgeber*. However, which one would entrain the circannual rhythms is still yet to be resolved.

Birds from the tropics show particularly robust circannual rhythmicity as has been demonstrated by classical experiment on the African stonechat (*Saxicola torquatus axillaris*), where, the circannual rhythms in molt and reproductive traits continued for more than 10 years under constant 12.25L:11.75D (light:dark) conditions (Gwinner and Dittami, 1990; Gwinner, 2003). Such rhythmicity was also observed in those stonechats that never experienced other photoperiods (Gwinner, 1991, 2003). The birds that reproduced successfully under constant photoperiodic conditions and their offsprings that were hatched under same conditions, equally displayed the circannual rhythms (Gwinner, 1996). Moreover, circannual rhythm expression under a wide range of photoperiodic conditions has been documented in the spotted munia, a tropical species (*Lonchura punctulata*; Chandola-Saklani et al., 2004; Budki et al., 2012, 2014). These and other studies (summarized in Gwinner and Dittami, 1985 and Rani and Kumar, 2013) suggested that tropical environments may indeed favor a robust circannual regulation of lifehistory stages (LHSs).

Photoperiodism vs. circannual rhythms

Birds show great precision in the timing of various behavioral and physiological events that are mediated by their endogenous time-keeping device(s), called “clocks”. The day length interacts with these clocks and induces seasonal responses. Thus, the seasonal responses appear to be regulated by two mechanisms: the photoperiodism and circannual rhythm generation (Misra et al., 2004).

In photoperiodism, the photoperiod is involved in generation of seasonal rhythms through induction and termination of physiological processes. The interaction of clock with photoperiod helps the bird to switch on (photoinduction) and switch off (photorefractoriness) its physiological mechanisms, which allows the seasonal events to occur, at most suited time of the year. When the daily light coincides with the photoinducible phase (φi) of the endogenous clock (Kumar and Follett, 1993), that usually falls ~12 hours after sunrise in a long day breeder, it is read as a “long day” and results in photoperiodic induction. Failure of such coincidence during winter months, with daily light <12 h per day, is read as “short day" and results in no response (Kumar and Follett, 1993). Once, the stimulation, for e.g. of gonads has occurred, the birds undergo spontaneous regression. This is known as photorefractoriness. Thus, the photoperiodic birds alternately exhibit two phases during the year: the photosensitive phase, when they respond to increasing day lengths and undergo gonadal maturation and the refractory phase when they are insensitive to stimulatory effects of the long days and undergo gonadal regression (Kumar, 1997). The decreasing day lengths in winter terminate photorefractoriness, and birds regain their photosensitivity.

The other mechanism is the circannual rhythm generation, in which a self-sustained endogenous rhythmicity of about a year times these component events (Gwinner, 1981; Chandola et al., 1985; Budki et al., 2012, 2014). The circannual clock interacts with the day length in timing the seasonal events (Bradshaw and Holzapfel, 2007) and photoperiod determines the seasonality in species that are living in highly seasonal environment such as at higher latitudes (Misra et al., 2004). The evidences suggest that the circannual rhythms and photoperiodism (photoperiod plays a role in the annual timing) are mutually inclusive processes.

Circannual rhythms in tropics

The endogenous circannual rhythms have been experimentally demonstrated in more than twenty migratory and resident bird species from both tropical and temperate regions. Most of the studies have focussed on the role of circannual clocks in regulation of reproduction, migration and molt (Gwinner, 1986; Gwinner and Dittami, 1990; Holberton and Able, 1992; Cadee et al., 1996).

The first robust avian circannual rhythm was reported in migratory behaviour and moult of the willow warbler (*Phylloscopus trochilus*) (Gwinner, 1968). The warblers kept under constant photoperiod and temperature conditions showed persistent rhythms in migratory restlessness (*Zugunruhe*) and moult for up to 3 years (Gwinner, 1977). Subsequent studies were done on African stonechat (*Saxicola torquata axillaris*) which provided the most compelling evidence for the existence of circannual rhythms (Gwinner, 1996). This suggested the longevity of circannual clock in an individual (Berthold, 1978; Gwinner, 1986).

In general, photoperiod is considered as the most important time cue (*Zeitgeber*) for synchronization of circannual rhythms. Since, changes in photoperiod in the tropical regions are subtle, it was not considered as *Zeitgeber* for a very long time. However, a group working on spotted antbirds (*Hylophylax n. naevioides*) showed that these birds are able to respond to the changes in photoperiod as small as 17 min and initiate their gonadal growth (Hau et al., 1998; Beebe et al., 2005). Subsequently, other studies on tropical birds such as spotted munia showed that these birds are also sensitive to small changes in photoperiod (Chandola-Saklani et al., 2004). This could be useful in anticipating the arrival of rainy season and timing of breeding (Hau et al., 1998). In tropical region, the photoperiodic changes are subtle, but the rainy season is very prominent. The cloud cover during rainy season changes the daylight intensity which could be used as time cue as shown by a study on African stonechats (Gwinner and Scheuerlein, 1998). The stonechats under constant photoperiod when exposed to changing daylight intensity mimicking the annual pattern of rainy and dry seasons were able to synchronize annual reproduction and molt pattern.

At the equator, regular but synchronous variation in sunrise and sunset time provide another reliable photic signal which remains consistent between years (Gwinner and Dittami, 1985). Recently, African stonechats have been shown to use the sunrise and sunset as a *Zeitgeber* to synchronize their circannual rhythms. Interestingly, the spotted munia is capable of reacting to increments of 1.5 min for 15 days in photoperiod by advancing gonadal growth, but do not respond to absolute long or short photoperiods (Chandola-Saklani et al., 2004). This suggests the importance of sunrise and sunset in synchronization of the annual events at tropics. Possibly, the twilight transitions in spectral composition of light are of some importance which needs to be answered.

Circannual rhythms in spotted munia

Spotted munia (*Lonchura punctulata*), is a passerine finch (family: Estrildidae), widely distributed throughout the Indian subcontinent. They are seasonal breeders with breeding season extending between June and October (Ali and Ripley, 1974; Thapliyal, 1981). They are photosensitive, but are not categorized as a typical photoperiodic species because they can respond to very short photoperiods such as 1 or 3h light per day as well (Chandola et al., 1975). However, it may still use light in the synchronization of its annual gonadal cycle, as shown by the effects of small increments of 1.5-2 min daily light periods in the time around the vernal equinox (Chandola-Saklani et al., 2004). Spotted munia have been reported to show both circadian and circannual rhythms (Bhatt and Chandola, 1985; Pant and Chandola-Saklani, 1992; Budki et al., 2012, 2014). They show circadian rhythm of locomotor activity and circannual rhythms in body mass, food intake and testicular growth-regression cycles under constant light-dark cycles (Chandola et al., 1982; Bhatt and Chandola, 1985).

A recent study on tropical spotted munia from our laboratory, addressed the question whether endogenous mechanism of annual breeding cycle (i.e. the timing and duration of gonadal phases in a year) is based on circannual rhythms and also if sexual differences exist in their circannual rhythms (Budki et al., 2012). Munia of both sexes kept in 12L:12D, 24L:24D and LL at light intensity ~22lx for more than two years at constant temperature (18±1°C) showed repeated testicular growth-regression cycle and molt similar to that in nature. Munia exhibited sex-dependent differences in circannual periods; in females, ovarian growth-regression cycle exhibited large period variations (~10-13 months) as compared to males' testicular growth-regression cycle (~11months). Also, gonadal recrudescence-regression phase was longer in males than in females. Females showed relatively more variations in both frequency and pattern of body plumage molt as compared to males. Therefore, it is suggested that annual breeding cycle in spotted munia is regulated by the self-sustained circannual rhythms, which probably interact with the annual photoperiodic cycle to synchronize it to the calendar year.

In another study on the same species it was demonstrated that circadian rhythm is not involved in circannual rhythm generation (Budki et al., 2014). Birds exposed to different period of light:dark (LD) cycles (T-cycle) with identical light (12h) but different dark hours, such that T16 (12L:4D), T21 (12L:9D), T24 (12L:12D) and T27 (12L:15D), or continuous light (LL, 24L:0D) for 21 months at ~18°C showed two circannual cycles of gonadal growth-regression and molt regardless of the light conditions as that of wild birds. This further confirmed the involvement of circannual rhythms in the regulation of seasonal responses in spotted munia (Bhatt and Chandola, 1985; Budki et al., 2012). This also supported the idea that seasonal physiology is not a direct response to the prevailing photoperiod and suggested that circadian rhythms are not involved in the timing or generation of the annual breeding cycle in the spotted munia.

Perspective

Even after 3 decades of circannual rhythms demonstration (Gwinner, 1986), it is still intriguing how such long term events with time constant are managed by the living system. The circannual rhythms are the readouts of seasonal changes in the environment therefore, it would be important to study the mechanistic basis of circannual rhythms to understand the seasonal physiology in organisms. This may have relevance in understanding the effect of climate change on circannual rhythm disruption and its effect on well being of different species including human.

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