



Photoperiodic Supervision and Adaptability in Avian System

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ABSTRACT

Photoperiodism is a prime selective force and in response to photoperiod and other supplementary environmental cues, birds exhibit behavioral and physiological responses. Birds have developed specialized temporal programming for the adaptation to their activities during 24-h of periodicity. To maintain the successful survival of progeny, they use both environmental cues and endogenous cycles in the suitable time window of the year. These timing mechanisms commonly involve an internal molecular oscillator which we called as 'clock' (s) that is 'entrained' to the environmental cycle. They express their endogenous cycles in physiology and behavior by receptor mechanisms responding to appropriate environmental signals ('Zeitgeber', i.e. time-giver) that allow anticipation of the seasons. Birds can respond to environmental stimuli in 3 key ways: disperse, adjust through phenotypic plasticity, or adapt through genetic changes. In this article, we discussed the significance of ecological factors affecting bird's physiology and behavior. Furthermore, the migratory songbird's performance along with downstream proceedings about these factors and their adaptive approaches towards nature's circuitry.

Keywords: Photoperiodism, Photoperiod, Birds, Environmental stimuli, Cues

Periodic changes in environmental cues and photoperiodic responsiveness:

Photoperiod is the chief environmental cue for synchronizing the circadian clocks (Kumar, 1997; Trivedi *et al.*, 2006) and is a dominant constituent in providing periodic information about the environment to the birds (Kumar *et al.*, 2010). Prominently, the photoperiodic environment acts as *Zeitgeber* (Zeit = time, geber = giver) for the synchronization of endogenous clocks, and this environmental *zeitgeber* influences circadian and circannual clock (s) controlling functions. Apart from photoperiod, the temperature is a powerful entraining agent for circadian rhythms (Takahashi *et al.*, 2012).

Circadian (circa = about; dies = day) and circannual (circa = about; annum = year) rhythms are the two foremost considered rhythms. The circadian rhythm measures close to a 24-h day, and the circannual rhythm measures close to a year. Birds need to adapt their physiology and behavior to these regular cycles in their environment (Kumar *et al.*, 2010). As changes in environmental cues like temperature,

day length, availability, and quality/quantity of food affect bird's physiology and behavior so because of this, they possess the instinctive strategy to track their time in changing environmental surroundings (Williams and Karasov, 2015).

In synchrony, birds have evolved a mechanism to time their breeding phase with a suitable period when environmental conditions are optimal for their young ones (Bentley, G.E. 2010). Likewise, the ability to stay away from breeding during the less suitable period is also important just to keep a check on energy expenditure, time, and resource availability (Foster *et al.*, 1987). Birds possess a complex timekeeping system which responds on both daily and seasonal bases and exhibit biochemical, physiological, and behavioral patterns that are species and niche-specific (Cassone *et al.*, 2017). They can measure day length throughout the year and during the photosensitive period; their neuroendocrine system can respond to long photoperiod. As a result, at this time physiological cascade includes a dramatic increase in

gonadotropin secretion resulting in gonadal growth and related behavioral responses. The status of sensitivity in birds to long day length is photosensitivity and response is known as photostimulation (Perfito *et al.*, 2008).

Variables of temporal information:

There are predictive daily and/or seasonal changes in day length, temperature, food availability, humidity, nutritional state, and social cues (Cassone *et al.*, 2017). These environmental variables are grouped into proximate and ultimate cues based on their role in the regulation of circadian and seasonal cycles. Proximate and ultimate cues are required to an animal for appropriate adjustment of its physiology, morphology, and behavioral response. Proximate cues help in deciding the constructive time window (season), while the ultimate cues lead to the culmination of the physiological event at the most profitable time during the defined season (Bentley, 2010).

Alteration in day length provides the most reliable source of chronological information about the changing environment. This has been adopted by birds for synchronizing reproduction, molt, and migration with a 'favorable time window'. On the other hand, the timing of life-history stages is also affected by temperature, rainfall, food abundance, and social stimuli, but provides only short-term predictive information. These supplementary cues serve for fine-tuning the rate of gonadal growth and the best timing of breeding with local phenological conditions. Migratory songbirds encounter complex photoperiodic conditions throughout the year, in which day length acts as a synchronizer, entraining endogenous circannual rhythms of gonadal maturation, molt, and nocturnal migratory activity. The seasonal cycle of a migratory bird can be divided into two phases in which short and long days exert different effects on the timing of life-cycle events (Pulido *et al.*, 2007). Apart from all these factors and signals, many songbirds illustrate adaptive responses to migrating through a moving flow in an air medium. These responses are fine-tuned to the air travel capabilities concerning the wind currents around them. Magically, migrants are expected to have evolved mechanisms for anticipating favorably directed flows and flight altitudes. Researchers demonstrated that in many songbirds moving directions during flight were undoubtedly influenced by wind flow. They do not wait to fly only on nights with the most favorable winds but they habitually travel on nights with crosswinds and opposing winds too (Chapman *et al.*, 2016).

Chronometers or timekeepers within animals:

Biological rhythms are generated at the molecular level through auto-regulatory positive and negative feedback

loops of the core clock genes on a daily and seasonal basis. In every organism, clock genes (CGs) are candidate genes that control life-history events (Paibomesai *et al.*, 2010). The machinery that allows the organism to anticipate imminent daily changes is termed the 'circadian clock'. The 24-h rhythm generated by this circadian clock is motivated by a set of clock genes (Magnone *et al.*, 2005). It acts as a bioregulator of reproductive activity through the mediation of the central nervous system, hypothalamus, adenohypophysis, and the pineal gland, and this regulatory pathway is coined as photoperiodism (Vasantha and Vasantha, 2016). This phenomenon is coupled to diverse functions i.e., morphological, metabolic, immunological, and reproductive adaptations. These all run definitively to cope with calendar changes throughout the season (Kumar *et al.*, 2010). The seasonally changing environmental conditions set a 'suitable time window' for appropriate behavioral actions such as breeding, migration, or hibernation. This 'time window' is determined by other factors, of which the most appropriate in the context of climate change are 'climatic factors' (Charmantier and Gienapp, 2013).

Circadian clock system and the mechanism beyond the photostimulation:

The avian circadian clock system is a 3-component system that includes the retina, suprachiasmatic nucleus (SCN), and the pineal gland. This clock system is located in separate structures but functionally connected and works in a specific manner. Circadian union in the avian system is a multifaceted arrangement of multiple pacemakers. The dynamics by which these pacemakers couple at the physiological/biochemical levels indicate that the SCN influences pineal oscillators via sympathetic inhibition of melatonin biosynthesis (Cassone *et al.*, 2017).

The conceptualized clock is an input-pacemaker-output system. In this hierarchical system input is the receptive unit. This unit may reside within or outside the structure that contains the oscillator. The centrally placed pacemaker generates oscillations with a precise cycle (Kumar *et al.*, 2004). In long-day breeding birds, approaching spring and increasing summer day length induces synthesis and release of gonadotropin-releasing hormone (GnRH) from neurons in the preoptic area (POA) of the brain. This stimulates the pituitary for the secretion of gonadotropins; luteinizing hormone, (LH), and follicle-stimulating hormone, (FSH), resulting in gonadal recrudescence. Under long days, light-activated deep brain photoreceptors induce TSH β (thyroid-stimulating hormone beta) transcription in the pars tuberalis, PT. This in turn activates type 2 deiodinase (*DIO2*) synthesis

in the ependymal cells of the mediobasal hypothalamus (MBH), resultant T4 converts inactive T3 and results in the GnRH synthesis and release from the POA. In short days increased synthesis of type 3 deiodinase (*DIO3*) for the conversion of T4 and T3 into inactive reverse T3 (rT3) and diiodothyronine (T2), respectively, which results in the inhibition of GnRH synthesis. When birds are exposed under long and short days there has been found the shifting of genes encoding these two thyroid activating enzymes i.e. *DIO2* and *DIO3* which in turn responsible for the synthesis of GnRH and GnIH (Srivastava *et al.*, 2015) (Figure 1). Studies have shown the mediobasal hypothalamus (MBH) as the photoperiodic induction site, by identifying the molecules reinforcing the long-day treatment effect (Rastogi *et al.*, 2013).

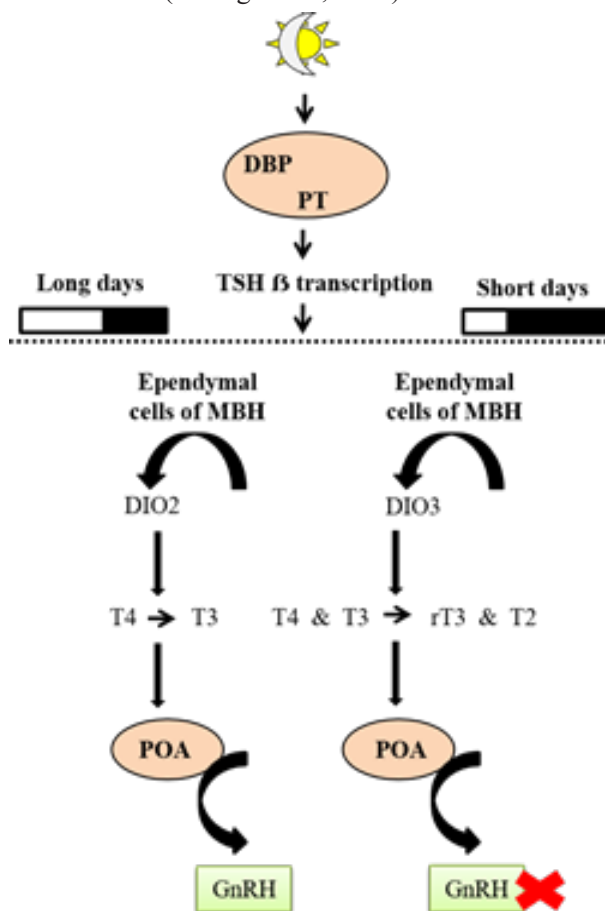


Fig. 1: A hypothalamic response under long and short days showing thyroid hormone signaling (Yoshimura *et al.*, 2003; Nakao *et al.*, 2008; Srivastava *et al.*, 2015)

The environmental light-dark cycle is generated by endogenous clocks or timekeepers. The clocks (s) are self-sustained and continue to be expressed in overt functions even in the absence of input from the environment. These clocks coordinate systematically the passage of time in synchrony with the periodic environment from molecular

through cellular and systems levels (Kumar *et al.*, 2010).

At the molecular point, clock and *bmal1* (positive-feedback loop), period and cryptochrome (negative-feedback loop), expression constitute a circadian clock and show signs of daily oscillations within the core circadian tissues in birds. This clock system functions together and generates daily time. Circadian oscillations are generally produced by transcriptional–translational negative feedback loops. This coordination is organized in the positive (*clock* and *bmal1* genes) and negative limbs (*period* and *cryptochrome* genes). An additional loop formed and stabilized orphan nuclear receptor (NRs) *rev-erba* which supports the negative limb of the feedback loop (Kumar *et al.*, 2010, Stevenson *et al.*, 2017). These NRs are a family of conserved transcription factors (TFs). In response to various environmental stimuli, these TFs regulate gene transcription and expression of genes important for an organism’s development, homeostasis, and metabolism. Recently, heme was identified as the ligand for the orphan receptors REV-ERBa/b, the well-known regulators of the circadian clock and lipid metabolism. Also, recent advances have recognized two nuclear receptor subfamilies (orphan subclass), the REV-ERBs and the ‘retinoic acid receptor-related orphan receptors’ (RORs), as critical regulators of the circadian clock with significant roles in lipid homeostasis. The RORs, recognize the same DNA binding sites as the REV-ERBs and are often coexpressed in the same tissues as the REV-ERBs (Solt *et al.*, 2011). In the circadian clocking system, this REV-ERBa appears as a link between the two limbs. CLOCK and BMAL1 proteins drive the expression of *per*, *cry*, and *rev-erba* genes within the nucleus. In turn, PER and CRY (represented by PERIOD [*per*] and CRYPTOCHROME [*cry*]) proteins down-regulate their expression and that of REV-ERBa by suppressing the action of CLOCK/BMAL1. The absence of REVERBa protein de-represses *bmal1* and possibly clock genes. Later, CLOCK/BMAL1 proteins reinitiate a new cycle of ~24 h. Briefly, a transcription complex of different clock proteins is formed during activation and inhibition (Kumar *et al.*, 2010, Stevenson *et al.*, 2017) (Fig 2).

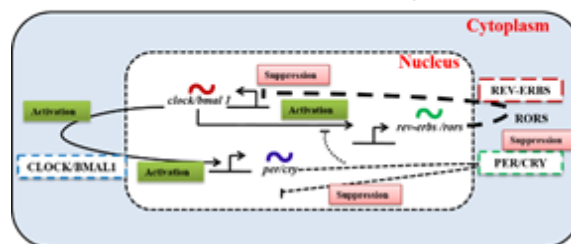


Fig. 2: Molecular circuitry for the avian circadian clock (The data have been adapted from Kumar and Singh 2005; Kumar *et al.*, 2010; Stevenson and Kumar 2017).

Migratory runners take a trip on the migratory route:

Migration is one of the greatest spectacle events. If not all, most birds reproduce seasonally, and many of them are engaged in twice-a-year long-distance migrations between wintering and breeding grounds. During spring migration many diurnal songbirds fatten and gain in body mass, perform a migratory flight, and exhibit gonadal growth and development (Rani *et al.*, 2006). Night migratory birds i.e. buntings during their migratory journey migrate several thousand kilometers at night to reach their wintering grounds in late autumn and breeding ground in late spring. However, during non-migratory seasons, these birds are active during the day and inactive at night. In migratory seasons, they remain active during the day but undergo a profound shift in their night-time behavior: birds fly at night and take less rest during the journey. When these birds are held in captivity under experimental conditions, they exhibit intense activity at night likewise in the wild; this is called migratory restlessness or *Zugunruhe* (Malik *et al.*, 2014). Also, pieces of evidence have been shown that in diurnal migratory songbirds i.e., warblers (*Sylvia*) the temporal pattern of *Zugunruhe* reflects the pattern of the actual migration (Rani *et al.*, 2006). Likewise, during the migratory phase (*Zugunruhe*) of their LHSs, a day-time active non-migrating bunting changes to leading night-time activity. While it is day-active during the non-migratory phase, it eats in the day and consumed food in the day and replenishes fuel stores used during the dark phase of the circadian period. Therefore, it is predictable that the liver exports nutrients during night fasting. Consequently, all exercises in the form of these behavioral and physiological transitions between the LHSs result from dynamic and energetic regulation of cell-autonomous circadian clocks and key biochemical pathways (Gupta *et al.*, 2020).

Migratory songbirds utilize different stopover sites in appropriate areas during migration. They necessitate selecting a specific time of night i.e. within-night decision to resume a migration. These departure decisions are mutually affected by a certain combination of intrinsic and extrinsic factors, i.e., departure cues. These cues which in turn largely determine the speed of migration (Packmore *et al.*, 2020). Further, at stopover sites, migrating birds spend more time and energy than they do in the migratory journey. The reason behind that, refueling rate is the foremost determinant of stopover duration. Those factors that affect refueling, have great potential to influence migration speed and their success. Food quantity and quality, intra- and interspecific competition, arrival condition, and predation risk are primary factors

that affect refueling rate. Behavioral and physiological differences among individual birds may also play a lead role (Seewagen *et al.*, 2013).

During spring migration, to reach their breeding areas, trans-Saharan passerines must cross two large ecological barriers i.e. the Sahara Desert and the Mediterranean Sea. During flights, migrants have to deal with a particular physiological situation, since they have to fast, even up to several days, despite very high energy demanding conditions. Data based upon literature shows that the energy used for flight is mainly derived from fat stores. A previous study on Ventotene Island (Italy), suggested that nectar is an ideal first food for birds with a reduced digestive capacity because monosaccharide does not have to be digested because they are absorbed directly. The nectar utilization is allowing birds to obtain water and energy at stopover sites in a short time as nectar is easy to find and quick to digest. Also it has been documented that in Europe, nectar consumption has been observed in migrants landing at stopover sites on Mediterranean islands. Nectar-feeding by trans-Saharan passerines has also recently been described at oases in the Sahara Desert (Cecere *et al.*, 2011).

However, many anthropogenic activities in the climate and atmosphere have globally affected ecological processes. Resultant the spatiotemporal occurrence of the main annual cycle events i.e., breeding, wintering, molting, and migration have shifted in migratory birds (Schmaljohann, 2019).

Living by the calendar Act:

Annual cycle of the photoperiod along with other ultimate factors is a major geophysical cue, acts to entrain and synchronize the circannual rhythm to the precise 365-day periodicity of the Earth's year. Organisms use both an endogenous calendar and a day length-measuring mechanism to adjust physiological state precisely to the seasons (Lincoln *et al.*, 2006). Biological activities like migration, hibernation, reproduction, and molt are achieved by adjusting the period of endogenous clocks to the annual change in the photoperiod. In complex vertebrates, the zygote potentially carries circannual timer genes into all progeny cells and tissues which support the concept of a 'clock-shop'. In this clock-shop, cell-autonomous long-term rhythms are generated in each tissue, orchestrated by a central circannual pacemaker system, and by this, they show seasonal recurrence of biological activities. This is analogous to the circadian timing system organization. For the circannual timescale, specialized thyrotroph cells located in the pars tuberalis (PT) of the pituitary gland and adjacent tanycyte cells located in the ependymal wall of the third cerebral ventricle of the brain act as putative

a bird's survival as sustained maladaptation can lead to extinction. As only adaptation will allow birds to persist in nature, such predictions will allow a better assessment of possible threats of climate change to biodiversity. Also, we would argue that studies on birds seem to specify the complexity of the circadian organization found in other non-mammalian vertebrates.

ACKNOWLEDGMENTS:

The authors thank reviewers for their assistance during the course of this article preparation. Financial assistance from UGC-BSR Fellowship (F. No. 25-1/2014-15 (BSR) / 7-109/2007/ (BSR) is gratefully acknowledged.

Conflict of interest:

The authors have no conflict of interest.

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