Avian Migration: Relation to Their Endogenous Circadian and Circannual Rhythm.

Aditi Ghosh, Ipsita Maity, Pinakiranjan Chakrabarti

[Department of Zoology, Vijaygarh Jyotish Ray College, Biojoygarh, Kolkata]

Abstract: Endogenous circadian and circannual clocks are best studied in migratory bird species as these phenomena are responsible for the initiation of periodical migration particularly during autumn and spring. The timing of migration is very important in birds specifically those who spent their winter close to the equator where the environment is fairly constant. In nocturnally migrating birds, alteration in the circadian signals leads to the development of its nocturnal activity. Here melatonin plays an important role as its secretion pattern often affects the general circadian system so that the migratory birds adjust faster to the new condition after a long flight.

Key words: Circadian Rhythm, Circannual Rhythm, Migration, Birds.

Introduction

Biological rhythms and the endogenous clocks are fundamental properties of nearly all living organisms, ranging from cyanobacteria to humans. These biological rhythms are functionally tied to environmental cycles. The daily 24-hour cycle of day and night imposes a rhythmic cascade of positive and negative selective pressures on nearly all organisms on earth. Migrations of birds are conspicuously rhythmic phenomena. Migration occur at certain seasons and certain times of day and thus are manifestations of an approximately annual (circannual) as well as an approximately diurnal (circadian) rhythmicity. Both of these rhythms reflect basic adaptations to environmental cycles and serve as biological clocks to cope with the annual and daily fluctuations in external conditions. Circannual and circadian rhythms play integral roles in both the timing of migratory behaviour and the capacity for orientation during migration. Annual and daily clock of migratory birds provide two types of orientation mechanism- orientation in time and orientation in space controlled by separate processes. In this review we will concentrate on two- circadian rhythm, circannual rhythm and their relation with bird migration.

Bird migration and its Importance

In birds, migration means two-way journeys—onward journey from the 'home' to the 'new' places and back journey from the 'new' places to the 'home'. This move-ment occurs during the particular period of the year and the birds usually follow the same route. There is a sort of 'internal biological clock' which regulates the phenomenon. Migration is more or less regular, extensive movements between their breeding regions and their wintering regions. There are many ecological implication of migration. The food resources of some regions would not be adequately exploited without moving populations. The sequence of migratory movement is closely integrated in the annual cycle of ecosystems characterized by productivity fluctuations. Migratory behaviour concerns only species located at specific trophic levels (zones of food availability) where maximal fluctuations occur both in breeding areas and in wintering regions. Migrant birds avoid equatorial forests where productivity is constant throughout the year, and food surpluses do not occur. They do congregate in savannas where productivity varies with the seasons. Such a coordinated sequence is particularly apparent in the case of birds migrating from the northern Arctic regions to tropical winter regions; both life zones are characterized by broad fluctuations in productivity. Migration, then, has considerable ecological significance. It enables fast-moving animals to exploit fluctuating resources and to settle in areas where life would not be tenable for animals incapable of rapid travel. On the other hand, peaks of food production would be unexploited without the periodic presence of migratory populations.

Circadian Rhythm and Biological Clock That Control Migration

Circadian rhythms are physical, mental, and behavioural changes that follow a 24-hour cycle. These natural processes respond primarily to light and dark whereas biological clocks are organisms' natural timing devices, regulating the cycle of circadian rhythms. They're composed of specific molecules (proteins) that interact with cells throughout the body. A master clock in the brain coordinates all the biological clocks in a living thing, keeping the clocks in sync. In vertebrate animals, including birds, the master clock is a group of about 20,000 nerve cells (neurons) that form a structure called the suprachiasmatic nucleus, or SCN. The SCN is in a part of the brain called the hypothalamus and receives direct input from the eyes. In many bird species locomotor activity occurs exclusively in the light portion of the light: dark (L: D) cycle. In autumn and spring, however, the seasons corresponding to natural migratory activity, the birds exhibit additional locomotor activity at night. Under constant condition the period of the rhythm is longer or shorter than 12 months attesting to its endogenous circannual nature. Similar to the annual repetition of migratory activity, its diurnal recurrence is also under the control of an endogenous circadian clock. In bird migration both the annual and the daily pattern of the 'migratory drive' that expresses itself in nocturnal activity and in a series of concomitant physiological and behavioural changes are primarily based on endogenous (circannual and circadian) clock mechanisms.

Molecular Basis of Circannual and Circadian Mechanism

Circadian rhythms are regulated by a highly conserved set of genes, collectively called "clock genes", whose products are believed to dynamically interact to elicit rhythmic patterns of transcription, translation, biochemical and physiological processes, and behaviour. In birds the central core of this gene network can be broadly characterized as "positive elements" *clock* and *bmal1* and "negative elements" *Period 1 (Per1), period 2 (per2), period 3 (per3)* and cryptochromes, *cryptochrome1(cry1)* and *cryptochrome 2 (cry2).* In contrast to mammals, birds do not express a *per1* and have been shown to only express only per2 and per3. *Clock* and *bma11*are transcribed and then translated in the cytoplasm, where they dimerize and re-enter the nucleus and activate transcription of the negative elements through the activation of E-box promoter elements. The *pers* and *crys* in turn are transcribed and translated in the cytoplasm, where the PER proteins are targeted for proteosomal proteolysis by a series of protein kinases, most notably casein kinase 1å (CK1å) and CK1ä. This process slows the accumulation of the cytoplasmic PER and thereby increases the period of the molecular cycle. In the cytoplasm, PER and CRY proteins form oligomers that re-enter the nucleus and interfere with the CLOCK/BMAL1-mediated activation. A secondary cycle involving two genes containing E-box promoters, *ReverbA* and *rorA*, amplify the cycle by activating and inhibiting *bma11* transcription respectively. Disruption and/or knock-out of these genes' action has profound effects on the expression of circadian rhythms in birds.

Physiological Basis of Circannual and Circadian Mechanisms

In vertebrates including birds, pineal gland –a unpaired appendage of brain produce a hormone Melatonin which mediate the adaptation to the day night(light: dark L:D) cycle of the environment. Melatonin is secreted only during night. Two major role of melatonin are first, melatonin is involved into circadian system. The retinal and the pineal clocks control their circadian output via melatonin rhythm. Thus absence of melatonin leads to arrhythmicity. Second, melatonin is critical for photoperiodic system and operates accordingly. A high amplitude melatonin increases the self-sustainment of clocks and decreases their susceptibility to the photoperiodic noise. Similarly reduced melatonin amplitude decreases the self- sustainment of the clocks and facilitating the adjustment of the circadian system to changing zeitgeber conditions. In birds the circadian system is highly complex as it composed of several independent clocks. Each clock has its own input and output pathways

Melatonin can also provide seasonal signals with higher levels in the fall and winter months and lower levels in the spring and summer correlating to the changing hours of daylight. Melatonin in birds mediates the entrainment of circadian activity rhythms, and thus helps to time hatching of eggs and facilitate migration. Twice a year, signals provided by the circannual clock mechanism cause alterations in the circadian system leading to the development of nocturnal activity. The changes in the daily pattern of locomotor activity resulting in the development of Zugunruhe are associated with concomitant changes in the diurnal pattern of melatonin secretion.

Onset of Migration and Directional Changes

Circannual rhythms have been convincingly shown to provide important stimuli triggering the onset of migration in both autumn and spring. This timing function of circannual rhythms is particularly evident and of high biological significance in birds wintering close to the equator. In these regions, photoperiod is constant over the year and other environmental factors such as temperature, precipitations and food abundance are too variable from one year to the next to be suitable for serving as external timing cues. In such birds with equatorial wintering grounds, processes preceding or accompanying spring migratory restlessness (e.g. winter moult and spring migratory fattening, respectively) are also under circannual control. Many species of migratory birds, including sparrows, finches and warblers, maintained in captivity under natural photoperiodic conditions spontaneously exhibit two bouts of migratory behaviour in which normally diurnal birds express nocturnal activity called *Zugunruhe* or "migratory restlessness" at the same times of year that coincide with natural migration. Drastic reductions of migratory restlessness caused by severe interference, e.g. exposure to complete darkness at night, exposure to a combination of complete darkness at night, high humidity and rain, reduction of food intake to levels slightly below those required for the maintenance of fat-free body mass. Although all of these treatments reduced nocturnal activity, the birds did not compensate for the reduced activity during the intervals following treatments. Zugunruhe is controlled by a time programme that is little affected by a bird's actual performance or its energy turnover. When birds are maintained for more than a year in a constantly equinoctial photoperiod (LD 12:12), they express two bouts of *Zugunruhe* approximately 6 months apart, strongly indicating an internally generated temporal program produces these migratory behaviours. Circannual rhythms might control not only the timing of the onset of migration and the timing of changing migratory direction but, in addition, the temporal course and the duration of the migratory flight. The internal clock may thereby provide the distance component required for 'vector navigation', a process in which direction and distance are integrated such as to bring the animal to its specific goal. By endogenous control of flight duration, the birds would arrive at their wintering area even if they possessed no more than directional information.

Timings and Other Factors Influences Migration

Migratory birds, in addition to being confronted with problems of spatial orientation, have to solve various problems of orientation with respect to time. The success of their migrations depends, among other factors, upon proper timing of the onset and end of their daily and seasonal migratory activity. Environmental changes in day length are of overwhelming significance for the timing of migrations in birds. Many bird species have been shown Subsequently to depend strongly on environmental changes in photoperiod for the timing of their migratory activities. Photoperiodic induction, however, cannot be the only mechanism, many bird species breeding in the temperate zones migrate to regions close to the equator and thus winter in environments in which seasonal changes in photoperiod are of small magnitude. Nevertheless, these birds depart in spring very precisely at the appropriate time for their homeward migration. Factors other than photoperiod seem to induce migratory behaviour in these birds. However, in many equatorial regions, none of the more obvious environmental factors, such as temperature or precipitation, is likely to be the releaser of spring migration because these factors either vary within a narrow range or so irregular that they could not account for the very precise departure of the birds. It has been speculated, therefore, by Rowan and others that these birds may be equipped with an endogenous timing mechanism that makes their temporal orientation independent of environmental information. The only environmental factor known to be capable of changing the time course of the programme is photoperiod.

Photoperiod synchronizes the circannual rhythms and, by doing so, it also affects the programmes that depend upon the basic clockwork. The circannual mechanism frequently responds to photoperiod in a functionally adaptive way. Two major effects have been described for the long-distance migrating garden warbler (reviewed in Gwinner, 1989*a*, 1996) (1) The onset and the end of the post-juvenile moult and the onset of autumn migratory restlessness are advanced by short photoperiods. This accelerating effect of short photoperiods in summer is important for young birds that have hatched from late clutches and, hence, grow up under shorter photoperiods than young hatched from earlier clutches. To be able to leave the breeding grounds in time, the birds from late clutches must start migration and complete the preceding processes of development at an earlier age. (2) The end of autumn migratory restlessness, the onset and end of the winter moult and the onset of spring migratory restlessness are advanced by long photoperiods. This accelerating effect of long photoperiods in winter is of high adaptive value because it truncates autumn migration in individuals that happen to have been carried too far into the southern hemisphere by their endogenous time programme. At the same time, it enables these birds to initiate spring migration earlier. This is probably necessary for them to reach their breeding grounds in time, i.e. not later than conspecifics that have spent the winter further north. While long photoperiods advance the onset of spring migratory restlessness and the associated onset of gonadal recrudescence, the acceleration is usually relatively small (Gwinner *et al.*1988*a*). This slow response to long photoperiods guarantees that the reproductive system of warblers that have crossed the equator during their autumn migration is not instantaneously activated by the increasing photoperiod of the southern hemisphere spring (Gwinner, 1987).

Avian Navigation:

One of the one of the greatest mysteries associated with birds is their ability to navigate over great distances with remarkable accuracy during semi-annual migrations or even in their day to day navigations within their home ranges. There are many theories about avian orientation and navigation, including sensitivities to barometric pressures, olfactory cues and the Earth's magnetic field. These are neither mutually exclusive nor unrelated. One of the most enduring ideas is the sun compass or time-compensated navigation. Early work by von Frisch in honeybees has shown that bees learn to visit a food source at a particular time of day and convey that information to the hive via its famous dance. Using this information, bees navigate to the food source by interpolating the position of the sun's azimuth with the bees' internal sense of time. The fact that an internal sense of time (Zeitgedachnis) was required for this navigation was demonstrated by shifting the light: dark cycles of the hive by 6hrs (or 90° of the 24hrs day) and showing that the bees consistently make a 90° error in orientation. This capacity has also been demonstrated in several species of birds, including European starlings and domestic pigeons. One question that has arisen from these studies was whether the internal sense of time was one and the same as the biological circadian clock. In an elegant series of studies, Hoffmann (1960) showed that starlings maintained in constant dim light exhibited gradual shifting in the birds' orientation with a period equivalent to the period of their free-running rhythms in locomotion. These data suggested that the orientation clock and the circadian clock shared clock properties, but the studies were conducted before any neuroscientific or molecular components of the clock had been identified.

Present Scenario of Research and Future Prospects

Research on bird migration by both professional scientists and the many citizen scientists has revealed considerable insights into the patterns of migration and the behaviour of migrants during recent decades. Numerous observational data exist that describe the spatial and temporal distribution of migratory bird species in considerable detail (Glutz von Blotzheim & Bauer 1966–98, Moreau 1972, Cramp et al. 1977–94, Keast & Morton 1980, Curry-Lindahl1981, Brown et al. 1982–2000, Hagan & Johnston 1992, Poole et al. 1992–2002, Rappole et al. 1995). In addition, exciting behavioural and physiological work give insights into the general principles of bird migration (Alerstam 1990, Gwinner 1990, Berthold 1996, Berthold 2001, Berthold et al. 2003). There is still much to be explored with respect to migration routes and the distribution of migrants, migration systems, winter ecology of migrants, the integration of migration in the annual cycle of a migratory species. New techniques have become available that allow detailed tracking of migrants to identify key areas for stopover and wintering and to reveal connectivity between breeding and non-breeding areas. Moreover, it requires much more comparative research and a more integrative approach at various spatial and temporal scales.

Conclusion

Endogenous circannual clocks determine the onset and the end of migrations as well as changes in migratory direction. Temporal variations in migratory speed also seem to be partly programmed in a circannual clock. Some evidence suggests that even the migratory distance covered during the autumn migratory season is to some extent a consequence of endogenous circannual programming. Circannual clocks control seasonal variations in migratory behaviour, circadian clocks provide the basis for adjustments of daily patterns, as is particularly obvious in species that are normally day-active, but migrate at night. The role played by circannual and circannual rhythms has so far almost exclusively been studied on a formal level and little attention has been paid to investigations of the underlying physiological mechanisms. Research on the possible physiological basis of circannual rhythms has not yet even suggested where the main mechanisms might be localized. Indeed, it is not even clear whether there are distinct localizable circannual clocks or whether the oscillation results from the interaction of a variety of neuronal, neuroendocrine and endocrine functions. In this review we discuss about the significance of the circadian system in the control of avian migrations – not only in determining the time of day of migration but also in sun compass orientation.

References

1.ASCHOFF, J., HOFFMANN, K., POHL, H. AND WEVER, R. (1975).Re entrainment of circadian rhythms after phase shift of the zeitgeber. *Chronobiol.* **2**, 23–78.

2.BAILEY MJ, BEREMAND PD, HAMMER R, BELL-PEDERSEN D, THOMAS TL, CASSONE VM. Transcriptional profiling of the chick pineal gland, a photoreceptive circadian oscillator and pacemaker. Mol Endocrinol. 2003 Oct;17(10):2084–95.

3.BAILEY MJ, BEREMAND PD, HAMMER R, REIDEL E, THOMAS TL, CASSONE VM. Transcriptional profiling of circadian patterns of mRNA expression in the chick retina. J Biol Chem. 2004 Dec 10;279(50):52247–54.

4.BAIRLEIN, F. (1985). Efficiency of food utilization during fat deposition in the long-distance migratory garden warbler, *Sylvia borin. Oecologia* **68**, 118–125.

5.BAIRLEIN, F. (1986). Spontaneous, approximately semimonthly rhythmic variations of body weight in the migratory garden warbler (*Sylvia borin* Boddaert). *J. comp. Physiol.* B **156**, 859–865.

6.BAIRLEIN, F. (1987). The migratory strategy of the garden warbler: a survey of field and laboratory data. *Ringing and Migration* **8**, 59–72.

7.BECK, W. AND WILTSCHKO, W. (1988). Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca* Pallas). In *Proceedings of the 19th International Ornithological Congress,Ottawa* (ed. H. Quellet), pp. 1955–1962. Ottawa: University of

8.Ottawa Press.

9.BERTHOLD, P. (1988). The control of migration in European warblers. In *Proceedings of the International Ornithological Congress, Ottawa* (ed. H. Quellet), pp. 215–249. Ottawa: University of Ottawa Press.

10.BERTHOLD, P. (1993). *Bird Migration. A General Survey*. Oxford, New York, Tokyo: Oxford University Press.

11.BERTHOLD, P. AND QUERNER, U. (1982). Genetic basis of moult, wing length and body weight in a migratory bird species, *Sylvia atricapilla*. *Experientia* **38**, 801–802.

12.BIEBACH, H. (1985). Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia* **41**, 695–697.

13.BIEBACH, H., FRIEDRICH, W. AND HEINE, G. (1986). Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* **69**, 370–379.

14.BINKLEY, S. (1988). *The Pineal: Endocrine and Neuroendocrine Function*. Englewood Cliffs, NJ: Prentice Hall.

15.CASSONE, V. M. (1990). Effects of melatonin on vertebrate circadian systems. *Trends Neurosci.* **13**, 457–464.

16.GWINNER, E. (1974). Endogenous temporal control of migratory restlessness in warblers. *Naturwissenschaften* **61**, 405.

17.GWINNER, E. (1975). Circadian and circannual rhythms in birds. In *Avian Biology*, vol. 5 (ed. D. S. Farner and J. R. King), pp. 221–285. New York: Academic Press.

18.GWINNER, E. (1986). Circannual rhythms in the control of avian migrations. *Adv. Stud. Behav.* **16**, 191–228.

19.GWINNER, E. (1987). Annual rhythms of gonadal size, migratory disposition and molt in garden warblers *Sylvia borin* exposed in winter to an equatorial or a southern hemisphere photoperiod. *Ornis scand.* **18**, 251–256.

20.GWINNER, E. (1988). Refractoriness in equatorial migrants. In *Proceedings of the 19th International Ornithological Congress, Ottawa* (ed. H. Quellet), pp. 626–633. Ottawa: University of Ottawa Press.

21.GWINNER, E. (1989*a*). Photoperiod as a modifying and limiting factor in the expression of avian circannual rhythms. *J. biol. Rhythms* **4**, 237–250.

22.GWINNER, E. (1989*b*). Einfluß der Photoperiode auf das circannuale System des Halsbandschnäppers (*Ficedula albicollis*) und des Trauerschnäppers (*F. hypoleuca*). *J. Orn.* **130**, 1–13.

23.GWINNER, E. (1990*a*). Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. In *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner), pp. 257–268. Berlin, Heidelberg: Springer Verlag.

24.GWINNER, E. (1990*b*). *Bird Migration: Physiology and Ecophysiology.* Berlin, Heidelberg: Springer Verlag.

25.GWINNER, E. (1996). Circannual clocks in avian reproduction and migration. *Ibis* **138** (in press).

26.GWINNER, E., BIEBACH, H. AND VON KRIES, I. (1985). Food availability affects migratory restlessness in caged garden warblers (*Sylvia borin*). *Naturwissenschaften* **72**, 51–52.

27.GWINNER, E., DITTAMI, J. P. AND BELDHUIS, J. A. (1988*a*). The seasonal development of photoperiodic responsiveness in an

28.equatorial migrant, the garden warbler *Sylvia borin*. *J. comp.Physiol.* A **162**, 389–396.

29.GWINNER, E., HAU, M. AND HEIGL, S. (1994). Phasic and tonic effects of melatonin on avian circadian systems. In *Evolution of Circadian Clock* (ed. T. Hiroshige and K. Honma), pp. 127–137. Sapporo: Hokkaido University Press.

30.GWINNER, E., SCHWABL, H. AND SCHWABL-BENZINGER, I. (1988*b*). Effects of food-deprivation on migratory restlessness and diurnal activity in the garden warbler *Sylvia borin*. *Oecologia* **77**, 321–326.

31.GWINNER, E., SCHWABL, H. AND SCHWABL-BENZINGER, I. (1992). The migratory time program of the garden warbler: is there compensation for interruptions? *Ornis scand*. **23**, 264–270.

32.GWINNER, E., SCHWABL-BENZINGER, I., SCHWABL, H. AND DITTAMI, J.(1993). Twenty four hour melatonin profiles in a nocturnally migrating bird during and between migratory seasons. *Gen. comp. Endocr.* **90**, 119–124.

33.GWINNER, E. AND WILTSCHKO, W. (1978). Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. *J. comp. Physiol.* **125**, 267–273.

34.GWINNER, E. AND WILTSCHKO, W. (1980). Circannual changes in migratory orientation of the garden warbler, *Sylvia borin*. *Behav. Ecol. Sociobiol.* **7**, 73–78.

35.HAU, M. AND GWINNER, E. (1994). Melatonin facilitates synchronization of sparrow circadian rhythms to light. *J. comp. Physiol.* A **175**, 343–347.

36.HAU, M. AND GWINNER, E. (1995). Melatonin administration accelerates resynchronization following phase shifts of a light–dark cycle. *Physiol. Behav.* **58**, 89–95.

37.HELBIG, A. J., BERTHOLD, P. AND WILTSCHKO, W. (1989). Migratory orientation of blackcaps (*Sylvia atricapilla*): population-specific shifts of direction during the autumn. *Ethology* **82**, 307–315.

38.HOFFMANN K. Experimental manipulation of the orientational clock in birds. Cold Spring Harb Symp Quant Biol. 1960;25: 379–387.

39.JANDER, R. (1963). Insect orientation. *A. Rev. Ent.* **8**, 95–114.

40.MCMILLAN, J. P. (1972). Pinealectomy abolishes the circadian rhythm of migratory restlessness. *J. comp. Physiol.* **79**, 105–112.

41.ROWAN, W.: Relation of Light to Bird Migration and Developmental Changes. Nature,

42.vol. 115, 1925, pp. 494-495.

43.ROWAN, W.: On Photoperiodism, Reproductive Periodicity and the Annual Migrations of Birds and Certain Fishes. Proc. Boston SOC. Nat. Hist., vol. 38, 1926, pp. 147-189.