Journal of Entomology and Zoology Studies

Available online at www.entomoljournal.com

E-ISSN: 2320-7078
P-ISSN: 2349-6800
JEZS 2018; 6(4): 1861-1866
© 2018 JEZS
Received: 24-05-2018
Accepted: 25-06-2018

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Circadian rhythm and their significance in relation to physiological functions of animals: A review

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Abstract

Circadian rhythm regulates the physiological processes of animals. The ambient conditions viz. wavelength, intensity of light, timing and duration of the light stimulus, temperature etc deregulates the circadian rhythm. Circadian rhythms are generated at the cellular level in living organisms. Sleep–wake cycle, fattening, hibernation, reproductive behavior and migration pattern/ behavior in birds are controlled by biological rhythms in animals. Biological rhythms are controlled endogenously by self-contained circadian clocks. The timing of sleep and wakefulness under natural conditions is in synchrony with the circadian control of the sleep cycle and all other circadian-controlled rhythms. Generally, the circadian rhythm is regulated by the light/dark cycle of the solar day, but it also persists during constant conditions. Change in the photoperiod (daylength) is the most important environmental factor for the deviation in physiology and behavior, timing of migration, hibernation, reproduction etc. Arctic animals (ptarmigan, reindeer) show circadian rhythms only in the parts of the year that have daily sunrises and sunsets. Circadian clocks have been reported in each and every mammalian cell including cardiovascular system, such as cardiomyocytes and vascular smooth muscle cells. Circadian rhythmicity of physiological systems can have several purposes in reproduction. The important functions are viz. coordination of ovulation, receptivity and wakefulness in the female with activity/wakefulness in the male. The advantages to a species of restricting onset of fertility and the resulting pregnancy and offspring care to favorable times of the year are obvious.

Keywords: Circadian rhythm, reproduction, puberty, behavior and physiology

Introduction

Pittendrigh [1] and Aschoff [2] are considered as founder of chronobiology and they reported the circadian rhythmicity in fruit flies and humans, respectively. The area of sleep research, which is also subsumed under the field of chronobiology, began to develop independently, with the identification of various sleep stages by Nathaniel Kleitman around the same time [3]. The periodic variation with shorter periods (higher frequencies) than circadian is called ultradian rhythms. The circadian rhythms are super imposed upon rhythms with longer periods (lower frequencies), the so called infradian rhythms, which include, among others, rhythms with a period of about 1 week (circaseptan rhythms), rhythms with a period of about 30 days (circatrigintan rhythms) and rhythms with a period of about 1 year (circannual rhythms and/or seasonal variations) [4].

Table 1: Frequency range in biological rhythm

Domain	Range
Ultradian	t<20 h
Circadian	20h≤ t≤ 28h
Infradian	t>28h
Circaseptam	t=7± 3days
Circadiseptan	t=14± 3days
Circaviginatan	t=21± 3days
Circatriginatan	t=30± 3days
Circannual	t=1year±3months

(**Source:** Piccione and Caola, [5])

2. Circadian Rhythms

A circadian rhythm is a roughly 24-hour cycle in the biochemical, physiological, or behavioral processes of living entities, The term "circadian" comes from the Latin *circa*, "around", and *diem* or *dies*, "day", meaning literally "approximately one day. The nature of the rhythms is thus endogenous and innate and driven by an endogenous clock. Such self-sustained oscillations with a period of about one day are called "circadian rhythms"**.** One of the most dramatic features of the world in which we live is the cycle of day and night. Correspondingly, almost all the species exhibit daily changes in their behavior/ physiology. Circadian rhythm exerts a profound influence on various physiological responses and ultimately the productivity of animals. Exposure to extremes hot/ cold affects the animals at cellular level and which is reflected in production and accumulation of the damaging molecules *i.e.* free radicals.

2.1 Basic characteristic of circadian rhythms

The circadian rhythm is self-sustained in nature [6]. Therefore, all diurnal rhythms that occur under natural conditions continue to cycle under laboratory conditions devoid of any external time giving cues from the physical environment. Circadian rhythms that are expressed in the absence of any 24-hour signals from the external environment are called free running. This indicates that the rhythm is not synchronized by any cyclic change in the physical environment. A diurnal rhythm should not be called circadian until it has been shown to persist under constant environmental conditions and thereby can be distinguished from those rhythms that are simply a response to 24-hour environmental changes. However, almost all diurnal rhythms are found to be circadian. Uncontrolled geomagnetic cues play a role in the persistence of rhythmicity can be refuted by a second characteristic feature of circadian rhythms. These cycles persist with a period of close to 24 hours. If the rhythms were exogenously driven, they should persist with a period of exactly 24 hours. The deviation from a 24-hour cycle actually provides means for the internal time keeping system to be continuously aligned by and aligned to the light-dark environment [7]. This continuous adjustment results in greater precision in controlling the timing, or phase, of the expressed rhythms, because little drift is allowed to occur before the rhythm is "reset" to the correct phase. In the absence of a dark-light cycle or other exogenous time signal (i.e., a Zeitgeber) the persistence of rhythms clearly seems to indicate the existence of some kind of internal timekeeping mechanism, or biological clock. The persistence of rhythmicity does not necessarily exclude the possibility that other, uncontrolled cycles generated by the Earth's revolution on its axis might be driving the rhythm [2].

2.2 Molecular basis of circadian rhythms

Mutagenesis approach led to the discovery of the first circadian clock mutants, which were called period (per) and frequency (frq, pronounced "freak"). The genes that carried the mutations in these organisms were cloned in the 1980s [8]. However, researchers sought to isolate the equivalent genes in mammals (i.e., mammalian homologs'). Finally, in 1994, researchers began a similar mutagenesis screening approach in the mouse and described the first mouse circadian mutation, called Clock [9]. In 1997 the gene affected by this mutation became the first mammalian circadian clock gene to be cloned [9]. Recent advances in molecular biology and genetics led to the cloning of many mammalian ''clock'' genes and to the discovery of new, extracerebral sites containing circadian oscillators [10]. Wang *et al.* [11] reported that circadian gene (PER2) not only plays a prominent role in the development of the milk duct, the maintenance of polarity and morphology of mammary epithelial cells, but also relates to the synthetic metabolism of milk protein and milk fat in the mammary gland.

To be called circadian, a biological rhythm must meet these four general criteria:

1. **The rhythms repeat once a day (they have a 24-hour period):** In order to keep track of the time of day, a clock must be at the same point at the same time each day, i.e. repeat every 24 hours.
2. **The rhythms persist in the absence of external cues (endogenous):** The rhythm persists in constant conditions with a period of about 24 hours. The rationale for this criterion is to distinguish circadian rhythms from simple responses to daily external cues. A rhythm cannot be said to be endogenous unless it has been tested in conditions without external periodic input.
3. **The rhythms can be adjusted to match the local time (entrainable):** The rhythm can be reset by exposure to external stimuli (such as light and heat), a process called entrainment. The rationale for this criterion is to distinguish circadian rhythms from other imaginable endogenous 24-hour rhythms that are immune to resetting by external cues and, hence, do not serve the purpose of estimating the local time. Travel across time zones illustrates the ability of the human biological clock to adjust to the local time; a person will usually experience jet lag before entrainment of their circadian clock has brought it into sync with local time.
4. **The rhythms maintain circadian periodicity over a range of physiological temperatures (exhibit temperature compensation):** Some organisms live at a broad range of temperatures, and the thermal energy will affect the kinetics of all molecular processes in their cell(s). In order to keep track of time, the organism's circadian clock must maintain a roughly 24-hour periodicity despite the changing kinetics, a property known as temperature compensation.

3. Circadian rhythm and animal behavior

The physiological processes of an organism are regulated by a circadian rhythm, the length of which is approximately 24 hours. This rhythm was first described in the movement of plant leaves by the French scientist Jean Jacques d'Ortous de marian [12]. Circadian rhythms affects animals sleeping and feeding pattern, brain wave activity, hormone production and other biological activities related to the daily cycle [13]. In the retina of eye light is transformed into nerve impulses that are conveyed to the hypothalamic nuclei of the central nervous system. Hypothalamic suprachiasmatic nuclei (SCNs) are the principal generators of circadian rhythms and the part of entrainment system that synchronizes the animal with its environment, especially with lighting conditions. The circadian system is regulated by the wavelength, intensity, timing and duration of the lighting stimulus [14]. These endogenous biological rhythms allow us to anticipate periodic changes in the environment and are thus important for adaptive behavior. Vander Veen *et al.* [15] stated that in most mammals, daily rhythms in physiology are driven by a circadian timing system composed of a master pacemaker in the suprachiasmatic nucleus (SCN).

4. Circadian rhythm and physiological responses

Domestic animals exhibited a diurnal rhythm in body temperature, which depends mainly on the climatic conditions. There are small circadian or nychthermal (24Hrs) fluctuations in core body temperature of cattle in both the natural environment and in steady temperature environments [16]. It has been widely reported that seasonal changes in ambient temperature can affect the body temperature in cows, for example, the mean body temperature and the amplitude of the body temperature rhythm are higher in the summer than in spring or winter [17]. Animals exposed to a natural and fluctuating environment will show diurnal variations of less than 1ºc [18]. The diurnal variation of rectal temperature was significantly higher during open environment as compared to under shade, irrespective of seasons. Knowledge of the relationship between the circadian change in body temperature and environmental thermal conditions is needed to increase our understanding of maintenance requirements and limitations to productivity performance [19]. Likewise, such information is essential for the evaluation of the benefits of any environmental modifications [20]. Zhang *et al*. [21] also demonstrated a circadian rhythm in beef calves exposed to hot and cold stress conditions, core body temperature, exposed to cold (1^0C), Thermoneutral (21^0C) and hot (32^0C) conditions in controlled environmental chambers (relative humidity 50%.Lights remained on from 0800 to 2100 h and animals were fed at 0800 to 2000 h. a daily fluctuations in temperature of 1^0C was noted for each environmental condition. Furthermore, the time at which the highest and lowest core temperature occurs differed between environmental conditions. Animals under cold conditions reached a maximum core temperature between 1600 and 2100 h compared to thermoneutral 0300 to 0500 h and hot 1800 to 1900 h. The threshold for onset of sweating and forearm blood flow has been reported to be higher at 16:00 and 20:00 compared to 24:00 and 04:00 [22]. These observations are consistent with the conclusion that it is the control of body temperature rather than the loss or gain of heat that varies in a circadian cycle [23]. Banerjee and Ludri [24] reported that physiological responses were lower in the morning and showed an increasing trend and reached the highest value in the afternoon. Whereas, blood Na+ and K+ concentrations decreased from 11.00 hours to 19.00 hours due to heat exposure. The increase in physiological responses and decreases in blood electrolyte levels were greater in Karan Fries than Tharparkar heifers indicating higher sensitivity of Karan Fries (crossbred) than indigenous cattle.

Table 2: Physiological functions under the control of biological clock

Circadian Process	Physiological functions
Activity/rest	Glomerular filtration
Some clock gene RNAs/protein	Feeding behaviour
Body temperature	Renal plasma flow
Heart rate	Urine production
Respiratory rate	Acid secretion into gastrointestinal tract
Blood pressure	Gastric emptying time
Liver metabolism	Locomotor activity
Liver blood flow	Physical performance

(**Source:** Piccione *et al*., [25])

5. Metabolic heat production, heat loss and the circadian rhythm of body temperature

Refinetti [26] reported that metabolic heat production (calculated from oxygen consumption), dry heat loss (measured in a calorimeter) and body temperature (measured by telemetry) were recorded simultaneously at 6 min intervals over five consecutive days in rats maintained in constant darkness. Robust circadian rhythmicity was observed in all three variables. The rhythm of heat production was phase advanced by about half an hour in relation to the body temperature rhythm, whereas the rhythm of heat loss was phase-delayed by about half an hour. The balance of heat production and heat loss exhibited a daily oscillation 180 deg out of phase with the oscillation in body temperature. Computations indicated that the amount of heat associated with the generation of the body temperature rhythm (1.6 kJ) corresponds to less than 1% of the total daily energy budget (172 kJ) in this species. Because of the small magnitude of the fraction of heat balance associated with the body temperature rhythm, it is likely that the daily oscillation in heat balance has a very slow effect on body temperature, thus accounting for the 180 deg phase difference between the rhythms of heat balance and body temperature.

6. Importance of the circadian clock

Nearly all physiological and behavioral functions in animals occur on a rhythmic basis, which in turn leads to dramatic diurnal rhythms in animal performance capabilities. A disturbed circadian rhythmicity in animals has been associated with a variety of mental and physical disorders and may negatively impact safety, performance, and productivity. Adverse effects of disrupted circadian rhythmicity may be linked to disturbances in the sleep-wake cycle. Some rhythmic processes are more affected by the circadian clock than by the sleep-wake state, whereas other rhythms are more dependent on the sleep-wake state. The timing of sleep and wakefulness under natural conditions is in synchrony with the circadian control of the sleep cycle and all other circadian-controlled rhythms. Adverse effects may ensue when the sleep-wake cycle is out of phase with the rhythms that are controlled by the circadian clock.

Circadian rhythm abnormalities also are often associated with various disease states, but the importance of these rhythm abnormalities in the development of the disease remains unknown. If scientists knew more about the mechanisms responsible for the rhythmicity of these disorders, they might be able to identify more rational therapeutic strategies to influence these events. Dramatic changes occur in the circadian clock system with advanced age; these changes may underlie, or at least exacerbate, the age-related deterioration in the physical and mental capabilities of aged ones. Vadiya *et al*. [27] also reviewed the importance of circadian rhythm for health and reproduction management in large domestic animals.

6.1 Importance in animals

Circadian rhythmicity is present in the sleeping and feeding patterns of animals, including human beings. There are also clear patterns of core body temperature, brain wave activity, hormone production, cell regeneration and other biological activities. In addition, photoperiodism, the physiological reaction of organisms to the length of day or night, is vital to both plants and animals, and the circadian system plays a role in the measurement and interpretation of day length. Timely prediction of seasonal periods of weather conditions, food availability or predator activity is crucial for survival of many species. Although not the only parameter, the changing length of the photoperiod ('daylength') is the most predictive environmental cue for the seasonal timing of physiology and behavior, most notably for timing of migration, hibernation and reproduction. Body temperature in cattle exhibits a profound circadian rhythm with a minimum in the morning and maximum in the afternoon. The rhythm is linked to the light-dark cycle. Animals kept in total darkness for extended periods eventually function with a "free-running" rhythm, meaning that their sleep-wake cycle persists even though environmental cues are absent. Each "day," their sleep cycle is pushed back or forward depending whether they are nocturnal (sleeps during day and is active at night) or diurnal (active during the day) animals by approximately one hour. Free-running rhythms of diurnal animals are close to 25 hours. The human free-running circadian rhythm is just over 24 hours, not 25 hours, as many textbooks assert [28]. Antle *et al.* [29] suggested that understanding of the intracellular and intercellular responses to light, as well as the spatial arrangements of such responses may help identify important pharmacological targets for therapeutic interventions to treat sleep and circadian disorders.

6.2 Arctic animals

Norwegian researchers at the University of Troms have shown that some Arctic animals (ptarmigan, reindeer) show circadian rhythms only in the parts of the year that have daily sunrises and sunsets. In one study of reindeer, animals at 70 degrees North showed circadian rhythms in the autumn, winter, and spring, but not in the summer. Reindeer at 78 degrees North showed such rhythms only autumn and spring. The researchers suspect that other Arctic animals as well may not show circadian rhythms in the constant light of summer and the constant dark of winter.

However, another study in northern Alaska found that ground squirrels and porcupines strictly maintained their circadian rhythms through 82 days and nights of sunshine. The researchers speculate that these two small mammals see that the apparent distance between the sun and the horizon is shortest once a day, and, thus, a sufficient signal to adjust by.

6.3 Butterfly migration

The navigation of the fall migration of the Eastern North American monarch butterfly (*Danaus plexippus*) to their overwintering grounds in central Mexico uses a time-compensated sun compass that depends upon a circadian clock in their antennae.

7. Circadian rhythms within the cardiovascular system

Circadian clocks have been identified in every mammalian cell investigated to date, including key components of the cardiovascular system, such as cardiomyocytes and vascular smooth muscle cells [30, 31]. Circadian rhythms are regulated by three components: (1) the circadian pacemaker or ‘‘clock’’, (2) an ‘‘input’’ mechanism, which allows the clock to be reset by environmental stimuli, and (3) an ‘‘output’’ mechanism, which regulates physiological and behavioral processes. For many years, it has been accepted that neurons in the suprachiasmatic nucleus were responsible for the control of circadian rhythms in peripheral tissues, acting via neural and humoral signals (eg. melatonin). It is currently believed that cells in other systems, including the cardiovascular system (i.e. cardiomyocytes and vascular smooth muscle cells), are under the influence of circadian clocks similar to that in the suprachiasmatic nucleus. The intrinsic properties of the heart and the vascular tree exhibit marked oscillations over 24 h. The intracellular circadian clock comprises a series of transcriptional modulators that together allow the cell to ‘‘perceive’’ the time of day, thus enabling suitable responses to expected stimuli. These molecular timepieces have been identified and characterized within both vascular smooth muscle cells and cardiomyocytes, giving rise to a multitude of hypotheses regarding the potential role of the circadian clock as a modulator of physiological and pathophysiological cardiovascular events. This article summarizes the evidence available at present linking circadian rhythm disruption and cardiovascular disease.

7.1 Circadian rhythms and reproduction

Circadian rhythmicity of physiological systems can have several purposes in reproduction. The most obvious is to provide an organism with the sense of time of day to ensure that physiological and behavioral events coincide. An example would be the coordination of ovulation, receptivity and wakefulness in the female with activity/wakefulness in the male. In many species, especially those with short life cycles or duration of gestation and time to weaning of, 1 year, circadian rhythms can provide a sense of time of year. Thus the changes in the time of the re-entraining stimulus of light may be associated with tightly controlled seasonal onset of puberty and adult infertility/fertility cycles. Shehab-El-Deen *et al.* [32] reported that heat stress metabolic changes are reflected in the follicular fluid. The circadian changes observed in the present study associated with heat stress may imply that also the microenvironment of the oocyte is affected. Hastings *et al.* [33] reported that animals restrict the time of birth of offspring to the most advantageous time of year, usually spring or summer. This is achieved by controlling the preceding period of fertility and, in some cases, by delaying implantation of the zygote.

7.2 Circadian rhythms and puberty

Since puberty reflects the maturation of all systems required for optimal reproductive performance it may be expected that circadian rhythmicity will have a role in puberty. In rodents, puberty onset is altered by day length such that long durations of darkness inhibit sexual maturation (Reiter, [34]. The impact of short day length is obvious in animals such as hamsters, which, outside the laboratory setting, live in higher latitudes and/or environments where food availability is highly seasonal. In longer-lived species such as sheep, the time of puberty of animals born late in the season may even be delayed until the following year [35]. The advantages to a species of restricting onset of fertility and the resulting pregnancy and offspring care to favorable times of the year are obvious. In the case of laboratory rats and mice maintained for hundreds of generations in constant environmental conditions and selected for high fertility and fecundity, circadian or photoperiodic effects on puberty are far less common [36]. Nevertheless some strains, e.g. Fisher 344 rats, do retain photo-responsiveness, although the basis for this is not known [37]. Extending the photoperiod by artificial light for 4 h during winter season resulted in better growth rate and early onset of puberty in Murrah buffalo heifers [38]. Hagenauer and Lee [39] also suggested that the changes in sleep timing that occur during adolescence may represent the influence of pubertal hormones on the circadian system, potentially providing an evolutionary benefit of allowing young animals to occupy a distinct temporal niche from that of older.

8. Conclusions

Circadian rhythm is a fundamental homeostatic system influencing behavior and physiology of animals. After birth there is progressive maturation of the circadian system with day-night rhythms. Suprachiasmatic nucleus is responsible for the control of circadian rhythms in peripheral tissues, acting through neural and humoral signals like melatonin. Biological rhythms are controlled endogenously by self-contained circadian clocks. The timing of sleep and wakefulness are under natural conditions in synchrony with the circadian control of the sleep cycle. Circadian rhythm is regulated by the light/dark cycle, but it also persists during constant conditions of the day. Change in the photoperiod (daylength) is the most important environmental factor affecting physiology and behavior, timing of migration, hibernation, production and reproduction etc of animals. With the continued elucidation of circadian system development and influences on human and animal physiology and illness, it is anticipated that consideration of circadian biology will become an important component of neonatal care and livestock production system.

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