Review Article

Biological Rhythms in *Drosophila melanogaster*: Genetic Regulation, Adaptation, and Ecological Significance

Mubashar Hussain*, Sheeza Sakhawat and Aniza Iftikhar

Department of Zoology, University of Gujrat, Gujrat- 50700, Punjab, Pakistan.

Abstract | *Drosophila melanogaster* (Drosophilidae: Diptera) has been a preferred model organism for studying biological rhythms, owing to its short life cycle, genetic simplicity, and fully sequenced genome. Biorhythms in *D. melanogaster* include circadian (~24 hours), ultradian (< 24 hours), and infradian (> 24 hours), which orchestrate various physiological processes such as homeostasis, feeding, reproduction, and movement. These rhythms are controlled by a core set of clock genes like clock (*clk*), period (*per*), timeless (*tim*), and cycle (*cyc*) that interact in transcription-translation feedback loops to keep internal time in synchronize with environmental light and temperature cycles. This genetic machinery enables fruit flies to align behaviour and physiology with external cues, optimizing foraging strategies and energy expenditure. Circadian rhythms regulate daily cycles such as sleep-wake patterns, feeding, and hormone release. Ultradian rhythms (<24 h) play significant roles in feeding and grooming, ensuring metabolic balance and predator avoidance. Infradian rhythms (> 24 hours but less than a year) are influenced by photoperiod and hormonal changes. Owing to biorhythms, precisely timed mating and egg-laying behaviours ensure that offspring develop under favourable environmental conditions. Understanding physiology and genetic mechanisms of rhythms in other fruit flies, especially pest species, could provide valuable insights into the ecological and evolutionary strategies of organisms. In periods of environmental stress, such as extreme temperatures or food scarcity, flies can enter diapause, which enhances the survival of fruit flies. By applying the knowledge of biorhythms, we can accurately identify the periods when they are most active or reproductively viable. This insight can significantly enhance the timing and effectiveness of pest management strategies. Understanding biological rhythms is not only essential for ecological and evolutionary perspectives but also offers practical applications in agriculture and environmental management.

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***Correspondence** | Mubashar Hussain, Department of Zoology, University of Gujrat, Gujrat- 50700, Punjab, Pakistan; **Email:** dr.mubashar@uog.edu.pk
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Introduction

Biorhythms are recurring physiological or behavioural events recognised in animals by the duration of time. In insects, ultradian (<20 h), circadian (20–28 h) and infradian (>28 h) rhythms have been studied. Ultradian rhythms show variations in periods (from milliseconds to hours), occur multiple times

per day (thermoregulation, micturition, appetite, etc.) and also differ in functions and mechanisms (Lamont and Amir, 2017). Circadian rhythms are inevitable behavioural oscillations that a living organism evolves in its bid to synchronize with the temporal environment. Such oscillations (rhythmic patterns) as those that can take place with periods ranging across the different temporal scales are rather essential for survival (Forger, 2024). Infradian rhythms (> 24 h but less than a year) are influenced by photoperiod and hormonal changes. These rhythms fine-tune reproductive and metabolic functions over longer time scales. Biorhythms help fruit flies to optimize foraging, ensuring maximal energy intake while minimizing risks and energy expenditure (Koyama *et al.*, 2020).

Circadian rhythms

Circadian rhythms, which oscillate nearly 24 h, include the endocrine, sleep-wake, and feeding cycles. Circadian rhythms are regulated from inside the organism through homeostatic and exogenous components; zeitgeber (refers to environmental variables that are capable of acting as circadian time cues), for instance, light, temperature, and feeding, which help to synchronise the activities of organisms to match the change in the environment (Sharma and Chandrashekaran, 2005). The biological rhythms, if disrupted, impact negatively; these disruptions include genetic alterations, and environmental manipulations, disturbing survival, reproduction, and fitness of the organism (Amaral *et al.*, 2014).

These rhythms run at various levels from biochemical and cellular to individual or population levels, with hierarchical subordinate oscillators that control vital processes including feeding, mating, migration, and predator evasion. For instance, diurnal insects plan their foraging at daytime since there are more openings during the day than nocturnal insects that target to forage at night, so that the chances of them being attacked by a predator are minimal by adjusting activity (Miyatake, 2011; Khyati *et al.*, 2017). Weather cycles help insects and their pests to avert stress by entering a state of diapause. Moreover, biological rhythms regulate social activities within the colony in eusocial insects, including honeybees (Bashir *et al.*, 2023). Additionally, these rhythms provide many opportunities to understand insect biology, given their applications in pest management and conservation (Khyati *et al.*, 2017).

The reproductive success in an enhanced survival scenario in fruit flies, such as *Drosophila,* is accomplished by regulating energy expenditure and establishing metabolic controls in internally channelized oscillations of around 24 h called circadian rhythms. These rhythms regulate major tasks in daily life, such as motor control, eating and drinking, sex, and sleep. Biorhythms are controlled by a molecular clock located in brain cells and feedback-loop circuits working in a coordinating way with other clock genes (Beauchamp *et al.*, 2018; Horn *et al.*, 2019). These genes are involved in the regulation of proteins that fluctuate in concentration throughout the day, creating a cycle known as circadian rhythm (Helfrich-Förster, 2020; De and Chatterjee, 2021). Light is a zeitgeber in this case and sets forward or backwards the clock to the prevailing external environment at any one point in time (Beauchamp *et al.*, 2018). Cytochrome (CRY) is a protein (Subramanian *et al.*, 2016) that is necessary for perceiving the change in light and the changes within the body to match the circadian rhythm. Disruptions of these rhythms can undoubtedly lead to behavioural change and diminished viability of fruit flies and other animals exhibiting circadian rhythms (Wong *et al.*, 2023; Córdoba *et al.*, 2024).

Ultradian rhythms

Ultradian rhythm is an intracellular oscillator (cellular mechanism) that generates rhythmic activity within a cell. In contrast to circadian rhythms, which have a shorter period, this type of oscillator regulates the periodicity of energy intake and utilization by fruit flies (Horn *et al.*, 2019). Ultradian rhythms are characterised by less than 24 hours of recurring activity that exists multiple times in the day, shaping some behaviours in *D. melanogaster* (De and Chatterjee, 2021). For example, feeding, grooming, and episodes of locomotor activity in *D. melanogaster* last for less than 24 hours (Seki and Tanimura, 2014). The efficiency of maintaining the behaviour of fruit flies is thus determined by environmental signals and needs (Pyża and Cymborowski, 2001; De *et al.*, 2012). For example, shorter cycles of feeding patterns make the animal feed often, but it does not endanger itself through predation (Rhoades *et al.*, 2018; Goh *et al.*, 2019; Tang *et al.*, 2022). Although ultradian oscillators are not explored as much as circadian rhythms (Goh *et al.*, 2019). In *D. melanogaster*, ultradian rhythms are expressed as an oscillation of feeding and activity cycles during the day (Yee, 2014). These ultradian

rhythms also have the further function of maintaining energy balance, or homeostasis (Yusuf *et al.*, 2024). However, these are not involved in storing foodstuffs for longer periods, where they can avoid predators or bad environmental conditions (Schlichting and Helfrich-Foerster, 2015). Moreover, the grooming activity in fruit flies does not just occur with a circadian level, but an ultradian level, so the body senses and its cleanliness are always right on time (Thakurdas *et al.*, 2010). Thus, such activities are governed by neural circuits and metabolic homeostatic feedbacks (Kühnlein, 2010; Kadow, 2019) which may act at least for the local and real physiological requirements (Frank, 2014; Gardner *et al.*, 2016; Münch *et al.*, 2020).

Genetic basis of biological rhythms

Drosophila melanogaster has long been recognized as an ideal model for studying biological rhythms due to its short life cycle, genetic tractability, and fully sequenced genome. Like many other animals, its behaviours, such as movement, feeding, and reproduction, are regulated by internal biological clocks. Foundational genes involved in these rhythms include clock (clk), cycle (cyc), period (per), and timeless (tim) (Tataroglu and Emery, 2014; De and Chatterjee, 2021). The experimental evidence from studies on biological rhythms, such as circadian and ultradian rhythms, can be used to relate other animal groups, including vertebrates. These genes work together in interconnected feedback loops to maintain rhythmic activity (Zordan and Sandrelli, 2015). Variations in the photoperiod and temperature influence these rhythms both positively and negatively, which ultimately regulate energy expenditure. Metabolic controls in fruit flies help them to become well established in their ecological niches. *per* and *tim* genes are transcribed at night, both to degrade proteins (PER and TIM). Whereas at daytime, PER and TIM proteins are transcribed (De and Chatterjee, 2021). At a higher concentration of PER and TIM proteins, they can form complexes as they are retained in the cytoplasm, but can cycle back to the nucleus. The direct down-regulation of transcription by binding to CLK and CYC proteins occurs (Tataroglu and Emery, 2015). These loops of negative feedback result in cyclic changes in PER and TIM that enable the temporal organization of behaviour and physiologic processes to recur daily (Meyer *et al.*, 2006; Tataroglu and Emery, 2015). Light is processed through the Cryptochrome (CRY), which is light responsive and through this influences the degradation of TIM to reset the clock (Meyer *et al.*, 2006). This molecular mechanism ensures feeding and movement activity of fruit flies is governed by the circadian rhythm (Goto and Denlinger, 2002). Temperature and light cycles, known as zeitgebers, help align internal rhythms with the external world, ensuring energy-efficient behaviour. This coordination allows fruit flies to optimize survival and reproduction in their ecological niches. The role of epigenetic regulation, such as DNA methylation and histone modifications, in fine-tuning the expression of clock genes is also crucial in biorhythms. These changes, which can be triggered by environmental factors, may influence the strength or timing of rhythmic behaviours and can sometimes even be inherited across generations (Gibert and Peronnet, 2021).

Feedback loops are core regulatory circuits that fine-tune gene activity. Positive loops amplify transcription, whereas negative loops dampen it, together safeguarding cellular homeostasis. In Drosophila, PER and TIM proteins first accumulate in the cytoplasm; once they reach a threshold, they form complexes that relocate to the nucleus (Saez and Young, 1996). There, the complexes bind to and silence the CLK/CYC transcription factors, blocking the phosphorylation events required to restart per and tim transcription (Taylor and Hardin, 2008). As daylight promotes PER and TIM degradation, the inhibition lifts and the cycle recommences, producing a ~24 h rhythm that can synchronize with light and temperature cues (Sidote *et al.*, 1998; Patke *et al.*, 2020).

Beyond these protein feedback loops, epigenetic layers add another level of time control (Hardin, 2011). DNA methylation and histone modifications can modulate core-clock gene expression and adjust circadian amplitude (Libbrecht *et al.*, 2020). Such epigenetic marks may be inherited or triggered by external factors, occasionally pushing the clock out of synchronisation. Environmental signals like light, temperature, and food availability act as zeitgebers that align internal rhythms with the outside world (Stevenson, 2018; Wu *et al.*, 2024). Together, protein feedback and epigenetic tuning ensure the circadian system stays flexible under changing conditions (Qureshi and Mehler, 2014; Jarabo and Martin, 2017; Faragó, 2021).

Environmental cues (zeitgebers)

Zeitgebers refer to environmental cues that are required to entrain or synchronise biological rhythms (Beer *et al.*, 2019; Quante *et al.*, 2019). These environmental cues (such as light, temperature, etc.) provide input to the circadian clock (Quante *et al.*, 2019), which are significant in time keeping in fruit flies (De and Chatterjee, 2021). Such cues help the flies maintain coordination between the internal biological clock and the environmental conditions in order to enhance their living and physiological standards (Horn *et al.*, 2019). Light is an external stimulus or zeitgeber because, in addition to other roles that it plays, it also controls the number of clock genes and synchronizes the circadian cycle with photoperiod. Cryptochrome (CRY), a photoprotein, detects light and directs the ubiquitination of the TIM protein to govern the daily entrainment (Helfrich-Förster, 2020; Cong *et al.*, 2023). Temperature is another factor that triggers the circadian cycle when coordinated with light cycles (Cavieres *et al.*, 2018; Fiaboe *et al.*, 2021). The oscillatory activity and clock genes are sensitive to temperature fluctuations (Fiaboe *et al.*, 2021). In particular, the whole biological rhythm oscillates at a higher frequency in fruit flies at higher temperatures and at a slower rate at lower temperatures. Thus, providing them with a mechanism of adaptation to different temperature regimes (Amin *et al.*, 2019; Choudhary *et al.*, 2019; Huang *et al.*, 2020). The availability of resources determines the feeding and overall activity (Cavieres *et al.*, 2018; Fiaboe *et al.*, 2021; Yu *et al.*, 2022). For example, the fruit flies adjust the hours of activity or food intake, taking into consideration the foods, so that the ones consuming energy are high when the predators are least around. Together, these stimuli enable fruit flies to regulate activity and metabolic rates in response to cyclical changes in the environment to optimize chances of survival and propagation (Amin *et al.*, 2019; Huang *et al.*, 2020).

Fluctuations in photoperiod and temperature play a critical role in modulating biological rhythms in *D. melanogaster*, ultimately influencing energy expenditure and metabolic efficiency (Dubowy and Sehgal, 2017). These rhythms enable fruit flies to fine-tune their physiological processes to match environmental conditions, ensuring better adaptation and survival within their ecological niches. Circannual rhythms, for instance, allow fruit flies to perceive and respond to seasonal changes in photoperiod and temperature, factors essential for synchronising key biological processes like reproduction and diapause. Light is detected through the photoreceptor CRY protein, which influences the degradation of TIM protein and thereby resets the circadian clock (Meyer *et al.*, 2006). This molecular feedback mechanism ensures that feeding and locomotor activity are tightly regulated in alignment with the day–night cycle (Goto and Denlinger, 2002).

External cues known as zeitgebers (such as light, temperature, and food availability) play a central role in entraining or synchronising internal biorhythms to environmental cycles (Mistlberger and Rusak, 2021). Light, for example, entrains the circadian rhythm by modulating gene expression through CRY-mediated degradation of TIM, affecting behaviours such as sleep, foraging, and metabolism (Schlichting *et al.*, 2019). Temperature, when acting in concert with photoperiod, also serves as a potent entrainment cue. Clock genes exhibit sensitivity to thermal fluctuations, with circadian rhythms typically accelerating at higher temperatures and decelerating in cooler conditions. Moreover, the availability of food resources functions as a behavioural cue that influences both feeding and activity patterns (Krittika and Yadav, 2020). Fruit flies often adjust their foraging schedules based on resource abundance and predator avoidance strategies (Drew and Yuval, 1999). These combined environmental signals help to optimize metabolic rate and behavioural activity, ultimately enhancing survival and reproductive success across changing conditions.

Disruption of rhythms and survival challenges

The oscillations in the metabolic rate also impact population dynamics since the fruit flies can go through low temperatures or scarcity of food during times of unsuitable climate (Dos Santos and Cochemé, 2024; Fangninou *et al.*, 2024). Thus, fruit flies can overcome definite population minima and are capable of maintaining constant population density within the seasons (Hui, 2024; Thoré *et al.*, 2024; Vivekanandhan *et al.*, 2024). Disturbance of rhythms in fruit flies (such as *Drosophila melanogaster*) poses several challenges and survival risks (Fangninou *et al.*, 2024). This is because behaviour and physiology, both oscillators, are decoupled from the environment, as measures and programs are out of alignment (Pham *et al.*, 2024; Vivekanandhan *et al.*, 2024). Disruptions of the circadian rhythm create problems in feeding

and reproductive activity.

Conclusion

Biorhythms, through precise synchronisation with environmental cues, are crucial in maintaining physiological balance, enhancing survival, and ensuring reproductive success. The genetic regulation of these rhythms, particularly circadian, ultradian, and infradian, demonstrates how molecular feedback loops allow fruit flies to adapt to daily, short-term, and seasonal changes. The study of these biological rhythms not only offers insights into fundamental chronobiological processes but also holds practical value in pest management by identifying optimal timings for control strategies. Ultimately, understanding the rhythmic behaviour of *Drosophila* enhances our knowledge of ecological adaptation, evolutionary fitness, and the broader implications of biological timing in insects.

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Novelty Statement

This review uniquely synthesizes the molecular and epigenetic regulation of circadian rhythms in Drosophila melanogaster. It highlights how classical feedback loops involving PER, TIM, CLK, and CYC are genetically conserved. The biorhythms are also dynamically modulated by epigenetic mechanisms such as DNA methylation and histone modifications.

Author's Contribution

SK and MH conceived the idea and prepared the original draft.
AI and MH critically reviewed and revised the manuscript.

Conflict of interest
The authors have declared no conflict of interest.

References

Amaral, F.G.D., A. Castrucci, J. Cipolla-Neto, M.O. Poletini, N. Mendez, H.G. Richter and M.T. Sellix. 2014. Environmental control of biological rhythms: Effects on development, fertility and metabolism. J. Neuroendocrinol., 26(9): 603-612. https://doi.org/10.1111/jne.12144

Amin, M.R., N.P. Nancy, M.R.U. Miah, M.G. Miah, O. Kwon and S.J. Suh. 2019. Fluctuations in fruit fly abundance and infestation in sweet gourd fields in relation to varied meteorological factors. Entomol. Res., 49(5): 223-228. https://doi.org/10.1111/1748-5967.12351

Bashir, S., M.F. Malik and M. Hussain. 2023. Spatiotemporal occurrence of beehives of genus Apis in Northern Punjab and Azad Jammu and Kashmir, Pakistan. Kuwait J. Sci., 50(2): 40-46. https://doi.org/10.1016/j.kjs.2023.02.007

Beauchamp, M., E. Bertolini, P. Deppisch, J. Steubing, P. Menegazzi and C. Helfrich-Förster. 2018. Closely related fruit fly species living at different latitudes diverge in their circadian clock anatomy and rhythmic behavior. J. Biol. Rhyth., 33(6): 602-613. https://doi.org/10.1177/0748730418798096

Beer, K., M. Schenk, C. Helfrich-Förster and A. Holzschuh. 2019. The circadian clock uses different environmental time cues to synchronize emergence and locomotion of the solitary bee *Osmia bicornis*. Sci. Rep., 9(1): 17748. https://doi.org/10.1038/s41598-019-54111-3

Cavieres, G., J.M. Bogdanovich, P. Toledo and F. Bozinovic. 2018. Fluctuating thermal environments and time-dependent effects on fruit fly egg-hatching performance. Ecol. Evol., 8(14): 7014-7021. https://doi.org/10.1002/ece3.4220

Choudhary, J.S., S.S. Mali, D. Mukherjee, A. Kumari, L. Moanaro, M.S. Rao, B. Das, A. Singh and B. Bhatt. 2019. Spatio-temporal temperature variations in MarkSim multimodel data and their impact on voltinism of fruit fly, Bactrocera species on mango. Sci. Rep., 9(1): 9708. https://doi.org/10.1038/s41598-019-45801-z

Cong, R., J. Zhang, J.X. Yuan, W. Yun-qi-qi-ge, S.C. Yan, L. Wei and G.R. Wang. 2023. Light intensity regulates the sexual behaviors of oriental fruit fly Bactrocera dorsalis under laboratory conditions. J. Integr. Agric., 22(9): 2772-2782. https://doi.org/10.1016/j.jia.2023.04.025

Córdoba, L., A.P. de Rosas, B. García, M.d.C.

Serradell, C. Remón, G. Mougabure-Cueto and M. Stroppa. 2024. RNA interference of the clock gene period disrupts circadian rhythms in the expression of genes related to insecticide resistance in the chagas disease vector Triatoma infestans (Hemiptera: Reduviidae). Acta Trop., 257: 107329. https://doi.org/10.1016/j.actatropica.2024.107329

De, J. and A. Chatterjee. 2021. Perception of daily time: Insights from the fruit flies. Insects, 13(1): 3. https://doi.org/10.3390/insects13010003

De, J., V. Varma and V.K. Sharma. 2012. Adult emergence rhythm of fruit flies Drosophila melanogaster under seminatural conditions. J. Biol. Rhyth., 27(4): 280-286. https://doi.org/10.1177/0748730412448360

Dos Santos, E. and H.M. Cochemé. 2024. How does a fly die? Insights into ageing from the pathophysiology of Drosophila mortality. Gero Sci., pp. 1-13. https://doi.org/10.1007/s11357-024-01158-4

Drew, R.A. and B. Yuval. 1999. The evolution of fruit fly feeding behavior. In: Fruit flies (Tephritidae). CRC press; pp. 749-768. https://doi.org/10.1201/9781420074468-38

Dubowy, C. and A. Sehgal. 2017. Circadian rhythms and sleep in *Drosophila melanogaster*. Genetics. 205(4):1373-1397. https://doi.org/10.1534/genetics.115.185157

Fangninou, F.F., Z. Yu, W. Li, L. Xue and D. Yin. 2024. Metastatic effects of perfluorooctanoic acid (PFOA) on Drosophila melanogaster with metabolic reprogramming and dysrhythmia in a multigenerational exposure scenario. Sci. Total Environ., 912: 169305. https://doi.org/10.1016/j.scitotenv.2023.169305

Faragó, A., 2021. Investigation into the effects of epigenetic modifications and circadian rhythm defects in a Drosophila model of Huntington's disease, University of Szeged.

Fiaboe, K.K., S. Kekeunou, S.N. Nanga, A.F. Kuate, H.E. Tonnang, D. Gnanvossou and R. Hanna. 2021. Temperature-based phenology model to predict the development, survival, and reproduction of the oriental fruit fly Bactrocera dorsalis. J. Therm. Biol., 97: 102877. https://doi.org/10.1016/j.jtherbio.2021.102877

Forger, D.B., 2024. Biological clocks, rhythms, and oscillations: the theory of biological timekeeping.

Frank, C.A., 2014. Homeostatic plasticity at the Drosophila neuromuscular junction. Neuropharmacology, 78: 63-74. https://doi.org/10.1016/j.neuropharm.2013.06.015

Gardner, B., E. Strus, Q.C. Meng, T. Coradetti, N.N. Naidoo, M.B. Kelz and J.A. Williams. 2016. Sleep homeostasis and general anesthesia: are fruit flies well rested after emergence from propofol? Anesthesiology, 124(2): 404-416. https://doi.org/10.1097/ALN.0000000000000939

Gibert, J.-M. and F. Peronnet. 2021. The paramount role of *Drosophila melanogaster* in the study of epigenetics: from simple phenotypes to molecular dissection and higher-order genome organization. Insects, 12(10): 884. https://doi.org/10.3390/insects12100884

Goh, G.H., S.K. Maloney, P.J. Mark and D. Blache. 2019. Episodic ultradian events ultradian rhythms. Biology, 8(1): 15. https://doi.org/10.3390/biology8010015

Goto, S.G. and D.L. Denlinger. 2002. Short-day and long-day expression patterns of genes involved in the flesh fly clock mechanism: period, timeless, cycle and cryptochrome. J. Insect Physiol., 48(8): 803-816. https://doi.org/10.1016/S0022-1910(02)00108-7

Hardin, P.E., 2011. Molecular genetic analysis of circadian timekeeping in Drosophila. Adv. Genet., 74: 141-173. https://doi.org/10.1016/B978-0-12-387690-4.00005-2

Helfrich-Förster, C., 2020. Light input pathways to the circadian clock of insects with an emphasis on the fruit fly Drosophila melanogaster. J. Comp. Physiol. A., 206(2): 259-272. https://doi.org/10.1007/s00359-019-01379-5

Horn, M., O. Mitesser, T. Hovestadt, T. Yoshii, D. Rieger and C. Helfrich-Förster. 2019. The circadian clock improves fitness in the fruit fly, *Drosophila melanogaster*. Front. Physiol., 10: 1374. https://doi.org/10.3389/fphys.2019.01374

Huang, Y., X. Gu, X. Peng, M. Tao, G. Chen and X. Zhang. 2020. Effect of short-term high-temperatures on the growth, development and reproduction in the fruit fly, Bactrocera tau (Diptera: Tephritidae). Sci. Rep., 10(1): 6418. https://doi.org/10.1038/s41598-020-63502-w

Hui, C., 2024. Circadian disruption in genes, brain, and behavior.

Jarabo, P. and F.A. Martin. 2017. Neurogenetics of Drosophila circadian clock: Expect the unexpected. J. Neurogenet., 31(4): 250-265. ttps://doi.org/10.1080/01677063.2017.13704

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Kadow, I.C.G., 2019. State-dependent plasticity of innate behavior in fruit flies. Curr. Opin. Neurobiol., 54: 60-65. https://doi.org/10.1016/j.conb.2018.08.014

Khyati, I. Malik and R.K. Seth. 2017. Insect clocks: implication in an effective pest management. Biol. Rhyth. Res., 48(5): 777-788. https://doi.org/10.1080/09291016.2017.1345460

Koyama, T., M.J. Texada, K.A. Halberg and K. Rewitz. 2020. Metabolism and growth adaptation to environmental conditions in Drosophila. Cell. Mol. Life Sci., 77(22): 4523-4551. https://doi.org/10.1007/s00018-020-03547-2

Krittika, S. and P. Yadav. 2020. Circadian clocks: An overview on its adaptive significance. Biol. Rhyth. Res., 51(7): 1109-1132. https://doi.org/10.1080/09291016.2019.1581480

Kühnlein, R.P., 2010. Energy homeostasis regulation in Drosophila: A lipocentric perspective. Sensory and metabolic control of energy balance. pp. 159-173. https://doi.org/10.1007/978-3-642-14426-4_13

Lamont, E. and S. Amir. 2017. Circadian and ultradian clocks/rhythms. https://doi.org/10.1016/B978-0-12-809324-5.00283-2

Libbrecht, R., D. Nadrau and S. Foitzik. 2020. A role of histone acetylation in the regulation of circadian rhythm in ants. Iscience, 23(2). https://doi.org/10.1016/j.isci.2020.100846

Meyer, P., L. Saez and M.W. Young. 2006. PER-TIM interactions in living *Drosophila* cells: An interval timer for the circadian clock. Science, 311(5758): 226-229. https://doi.org/10.1126/science.1118126

Mistlberger, R.E. and B. Rusak. 2021. Biological rhythms and behavior. The Behavior of Animals, 2nd Edition: Mechanisms, Function and Evolution. pp. 78-110. https://doi.org/10.1002/9781119109556.ch4

Miyatake, T., 2011. Insect quality control: Synchronized sex, mating system, and biological rhythm. Appl. Entomol. Zool., 46: 3-14. https://doi.org/10.1007/s13355-010-0017-7

Münch, D., G. Ezra-Nevo, A.P. Francisco, I. Tastekin and C. Ribeiro. 2020. Nutrient homeostasis translating internal states to behavior. Curr. Opin. Neurobiol., 60: 67-75. https://doi.org/10.1016/j.conb.2019.10.004

Patke, A., M.W. Young and S. Axelrod. 2020. Molecular mechanisms and physiological importance of circadian rhythms. Nature reviews Mol. Cell Biol., 21(2): 67-84. https://doi.org/10.1038/s41580-019-0179-2

Pham, K., M. Choi, K. Yamada and H. Wada. 2024. Zebra finches (*Taeniopygia castanotis*) display varying degrees of stress resilience and recovery in response to constant light. Gen. Compar. Endocrinol., pp. 114644. https://doi.org/10.1016/j.ygcen.2024.114644

Pyża, E. and B. Cymborowski. 2001. Circadian rhythms in behaviour and in the visual system of the blow fly, *Calliphora vicina*. J. Insect Physiol., 47(8): 897-904. https://doi.org/10.1016/S0022-1910(01)00062-2

Quante, M., S. Mariani, J. Weng, C.R. Marinac, E.R. Kaplan, M. Rueschman, J.A. Mitchell, P. James, J.A. Hipp and E.M.C. Feliciano. 2019. Zeitgebers and their association with rest-activity patterns. Chronobiol. Int., 36(2): 203-213. https://doi.org/10.1080/07420528.2018.1527347

Qureshi, I.A. and M.F. Mehler. 2014. Epigenetics of sleep and chronobiology. Curr. Neurol. Neurosci. Rep., 14: 1-11. https://doi.org/10.1007/s11910-013-0432-6

Rhoades, S.D., K. Nayak, S.L. Zhang, A. Sehgal and A.M. Weljie. 2018. Circadian-and light-driven metabolic rhythms in Drosophila melanogaster. J. Biol. Rhyth., 33(2): 126-136. https://doi.org/10.1177/0748730417753003

Saez, L. and M.W. Young. 1996. Regulation of nuclear entry of the Drosophila clock proteins period and timeless. Neuron, 17(5): 911-920. https://doi.org/10.1016/S0896-6273(00)80222-6

Schlichting, M. and C. Helfrich-Foerster. 2015. Photic entrainment in Drosophila assessed by locomotor activity recordings. Methods Enzymol., 552: 105-123. https://doi.org/10.1016/bs.mie.2014.10.017

Schlichting, M., P. Weidner, M. Diaz, P. Menegazzi, E. Dalla Benetta, C. Helfrich-Foerster and M. Rosbash. 2019. Light-mediated circuit switching in the Drosophila neuronal clock network. Curr. Biol., 29(19): 3266-3276. e3263 https://doi.org/10.1016/j.cub.2019.08.033.

Seki, Y. and T. Tanimura. 2014. Ultradian rhythm unmasked in the Pdf clock mutant of Drosophila. J. Biosci., 39: 585-594. https://doi.org/10.1007/s12038-014-9450-z

Sharma, V.K. and M. Chandrashekaran. 2005. Zeitgebers (time cues) for biological clocks.

Curr. Sci., pp. 1136-1146.

Sidote, D., J. Majercak, V. Parikh and I. Edery. 1998. Differential effects of light and heat on the Drosophila circadian clock proteins PER and TIM. Mol. Cell. Biol., 18(4): 2004-2013. https://doi.org/10.1128/MCB.18.4.2004

Stevenson, T.J., 2018. Epigenetic regulation of biological rhythms: an evolutionary ancient molecular timer. Trends Genet., 34(2): 90-100. https://doi.org/10.1016/j.tig.2017.11.003

Subramanian, P., J.J. Jayapalan, P.S. Abdul-Rahman, M. Arumugam and O.H. Hashim. 2016. Temporal regulation of proteome profile in the fruit fly, Drosophila melanogaster. PeerJ., 4: e2080. https://doi.org/10.7717/peerj.2080

Tang, M., L.H. Cao, T. Yang, S.X. Ma, B.Y. Jing, N. Xiao, S. Xu, K.R. Leng, D. Yang and M.T. Li. 2022. An extra-clock ultradian brain oscillator sustains circadian timekeeping. Sci. Adv., 8(35): eabo5506. https://doi.org/10.1126/sciadv.abo5506

Tataroglu, O. and P. Emery. 2014. Studying circadian rhythms in Drosophila melanogaster. Methods, 68(1): 140-150. https://doi.org/10.1016/j.ymeth.2014.01.001

Tataroglu, O. and P. Emery. 2015. The molecular ticks of the *Drosophila* circadian clock. Curr. Opin. Insect Sci., 7: 51-57. https://doi.org/10.1016/j.cois.2015.01.002

Taylor, P. and P.E. Hardin. 2008. Rhythmic E-box binding by CLK-CYC controls daily cycles in per and tim transcription and chromatin modifications. Mol. Cell. Biol., 28(14): 4642-4652. https://doi.org/10.1128/MCB.01612-07

Thakurdas, P., S. Sharma, B. Sinam, M. Chib and D. Joshi. 2010. Nocturnal illumination dimmer than starlight altered the circadian rhythm of adult locomotor activity of a fruit fly. Chronobiol. Int., 27(1): 83-94. https://doi.org/10.3109/07420520903398567

Thoré, E.S., A.E. Aulsebrook, J.A. Brand, R.A. Almeida, T. Brodin and M.G. Bertram. 2024. Time is of the essence: The importance of considering biological rhythms in an increasingly polluted world. PLoS Biol., 22(1): e3002478. https://doi.org/10.1371/journal.pbio.3002478

Vivekanandhan, P., K. Swathy, P. Sarayut and K. Patcharin. 2024. Classification, biology and entomopathogenic fungi-based management and their mode of action against Drosophila species (Diptera: Drosophilidae): A review. Front. Microbiol., 15: 1443651. https://doi.org/10.3389/fmicb.2024.1443651

Wong, K.C., J.J. Jayapalan, P. Subramanian, M.N. Ismail and P.S. Abdul-Rahman. 2023. Label-free quantitative mass spectrometry analysis of the circadian proteome of Drosophila melanogaster lethal giant larvae mutants reveals potential therapeutic effects of melatonin. Arch. Insect Biochem. Physiol., 113(2): e22008. https://doi.org/10.1002/arch.22008

Wu, C., J. Wang, X. Luo, B. Wang, X. Zhang, Y. Song, K. Zhang, X. Zhang and M. Sun. 2024. Lead exposure induced transgenerational developmental neurotoxicity by altering genome methylation in Drosophila melanogaster. Ecotoxicol. Environ. Saf., 271: 115991. https://doi.org/10.1016/j.ecoenv.2024.115991

Yee, W.L., 2014. Feeding substrates and behaviors of western cherry fruit fly (Diptera: Tephritidae). Environ. Entomol., 37(1): 172-180. https://doi.org/10.1603/0046-225X(2008)37[172:FSABOW]2.0.CO;2

Yu, C., R. Zhao, W. Zhou, Y. Pan, H. Tian, Z. Yin and W. Chen. 2022. Fruit fly in a challenging environment: Impact of short-term temperature stress on the survival, development, reproduction, and trehalose metabolism of *Bactrocera dorsalis* (Diptera: Tephritidae). Insects, 13(8): 753. https://doi.org/10.3390/insects13080753

Yusuf, A.O., B. Danborno, Z.M. Bauchi, D. Sani and I.S. Ndams. 2024. Aging impaired locomotor and biochemical activities in Drosophila melanogaster Oregon R (fruit fly) model. Exp. Gerontol., 197: 112593. https://doi.org/10.1016/j.exger.2024.112593

Zordan, M.A. and F. Sandrelli. 2015. Circadian clock dysfunction and psychiatric disease: Could fruit flies have a say? Front. Neurol., 6: 80. https://doi.org/10.3389/fneur.2015.00080