# Chapter 1
# Historical Survey of Chronobiology with Reference to Studies in Insects

**Hideharu Numata**

**Abstract** Chronobiology is the study of the temporal characteristics of biological phenomena. Humans must have recognized before the establishment of civilization that the activity of organisms has periodicity. Studies in chronobiology have advanced from the folklore to the molecular level by way of natural history and classic experiment levels. During these processes, observations and experiments in insects have made significant contributions. The climax was the discovery of molecular mechanisms of the circadian clock in *Drosophila melanogaster* in the late twentieth century. Currently, chronobiology is expanding further to various aspects, such as circadian clocks in various organisms, molecular and neural mechanisms of photoperiodism, clocks of which the period is different from approximately 24 h, and the ecological aspect of biological clocks.

**Keywords** Biological clock · Circadian clock · Exogenous timing hypothesis · Photoperiodism · Solar compass · Time memory

## 1.1 What Is Chronobiology?

Chronobiology is a combination of *chronos*, which means time in Greek, and biology. This word was proposed by Franz Halberg in 1950 and became a common term after his review named "Chronobiology" (Halberg 1969). According to Halberg (1969), chronobiology is defined as the study of the temporal characteristics of biological phenomena. If we understand it as time-related biology, all developmental phenomena should be the objects of chronobiology. However, the discipline of chronobiology actually focuses on the periodic activity of living organisms that repeats over time, rather than phenomena such as development that progresses in one direction along the time axis.

H. Numata (✉)
Institute for the Future of Human Society, Kyoto University, Kyoto, Japan
e-mail: numata.hideharu.8r@kyoto-u.jp



H. Numata, K. Tomioka (eds.), *Insect Chronobiology*, Entomology Monographs,
https://doi.org/10.1007/978-981-99-0726-7_1

Almost all organisms on the Earth are subject to environmental changes. Whereas some environmental changes occur completely irregularly, others have a fixed period. There are at least five types of environmental changes with constant periods due to geophysical mechanisms. These cycles are the tidal cycle (12.4 h), daily cycle (24 h), semilunar cycle (spring tide and neap tide cycle, 14.8 days), lunar cycle (29.5 days), and annual cycle (365.2 days). All of them are brought by the positional relationship between the Earth, the moon, and the sun. Changes in the environment with such cycles may directly affect the activity of the organism and produce periodicity, but conversely, to respond to the periodic change in the environment, the organism autonomously becomes periodic. Organisms have acquired a physiological mechanism that indicates the above, the biological clock. The main object of chronobiology is the phenomenon related to the biological clock.

It is common knowledge today that “the clock exists in the body of organisms” and at least those who have learned biology do not doubt its existence. However, when we think about it without knowledge in modern biology, the biological clock seems to be a truly mysterious mechanism. The first clock invented by human beings was the ancient Egyptian sundial. However, the sundial did not keep track of time autonomously but used the movement of the sun in the sky. Later, water clocks and hourglasses were invented, but none of them autonomously showed periodicity. They were one-shot mechanisms that ended when water or sand fell down. Most likely the first clock rotating once a day was made by improving the water clock in China during the Tang dynasty. Eventually, mechanical watches using pendulums, springs, and gears developed, and wristwatches appeared approximately 1800. It has not been easy to believe that organisms have such a mechanism because small and accurate clocks were invented only in modern times in the long history of mankind. In fact, there was fierce controversy before the idea that the periodicity of organisms was produced by the biological clock was established (see Sect. 1.4). In this chapter, I summarize the history of chronobiology, focusing on insect clocks.

## 1.2 From Folklore to Natural History

Humans must have recognized before the establishment of civilization that the activity of organisms has periodicity. Humans are animals that grow and act by eating other organisms. To acquire food resources efficiently, therefore, it is essential to know when and where prey organisms exist. Especially for human ancestors who began to eat the meat of other animals instead of the fruit diet, it must have become even more important to know when and what activities the prey animals perform. Moreover, it is also important to know the activities of animals that are harmful to humans. Therefore, knowledge of chronobiology must have increased the survival value of humans since prehistoric times. That is, we are born chronobiologists.

Let me give you one famous example. The palolo worm *Palola viridis* (Annelida: Polychaeta) reaching 40 cm in length lives in a cave at a depth of 3–5 m on a coral reef of Fiji and Samoa in the southwest Pacific (Fig. 1.1). When a palolo worm

**Fig. 1.1** A sexually matured adult female of the Palolo worm *Palola viridis*. The green posterior region of the body (epitoke) contains mature eggs. Photo by Masa Ushioda, Blue Planet Archive LLC

sexually matures, the posterior region of the body swells with developed gonads (the epitoke). Then, twice at the end of October and the beginning of November, when the dawn overlaps with the high tide on neap tide days, the developed posterior region tears off from the head region and swims, reaching the sea surface, and spawns. This phenomenon is called rising. Thereafter, the head region remaining in the cave regenerates the posterior region. William Burrows, a resident commissioner of Fiji, reported that the developed gonads of palolo worms are very tasty, and people living on these islands board a small boat and scoop up a large number of gonads every year at the time of rising (Burrows 1945). In other words, the people of the islands accurately handed down the day and time when palolo worms swim. Schulze (2006) summarized the knowledge in the phylogeny of palolo worms and showed early references of their rising and its use as a food source by native people of Pacific islands.

In the eighteenth century, Jean-Jacques d'Ortous de Mairan observed that the movement of the leaves of the sensitive plant (probably *Mimosa pudica*) to open during the day and hang down at night continued even when the plant was transferred to dark places. In the current knowledge, this is proof of the existence of a biological clock and an excellent experimental result in chronobiology. However, he interpreted the result that the plant is sensitive to external stimuli showing day and night, even without sunlight (Anonymous 1729).

In the 1900s, observations that the honeybee *Apis mellifera* might learn and memorize the time were reported (see Renner 1960). Hugo von Buttel-Reepen noticed that bees came to the buckwheat field exactly between 10 and 11 am when the buckwheat flowers secreted nectar, as if the bees knew the time. He concluded that such behavior was only possible if the bees had a sense of time (Zeitsinn) (von Buttel-Reepen 1900, 1915). In 1906, when Auguste Forel had breakfast on the terrace facing the garden every day between 7:30 and 9:30 am, he always observed that bee workers came to the jam that he intended to spread to pieces of bread. Even on the day when Forel did not supply jam, the bees came to the terrace. This result means that the bees were not attracted to the color or smell of the jam but remembered the time and place in relation to each other (Forel 1910). Based on this observation, Forel (1910) proposed the term time memory (Zeitgedächtnis).

## 1.3 From Natural History to Experimental Science

It was the group of Karl von Frisch, one of the winners of the Nobel Prize in Physiology or Medicine 1983, who experimentally proved the time memory in honeybees suggested by Forel (1910). Ingeborg Beling placed sugar solution on a desk a few meters away from a honeybee nest and trained bee workers to come at a fixed time every day, marking each bee to identify the individual. Then, on the last day, she observed which bees came to the desk all day without sugar solution, and most of the bees came to the desk at the time of training. In other words, the bees actually learned the time. Next, she performed the same experiment in the laboratory where the light, temperature, and humidity were kept constant, but the behavior of the bees did not change, so the change in the position and brightness of the sun, temperature, and humidity was not used as a clue. However, the electrical conductivity of air changed during the day, and it was possible that the air was reacting to the bees as it freely moved in and out of the laboratory. Therefore, radium was used to increase the ions in the air to increase the electrical conductivity throughout the day, but the time that the bees remembered was still correct (Beling 1929). In addition, Oskar Wahl, another student of von Frisch, examined the effects of cosmic rays. Cosmic rays fluctuate daily, passing through the roofs and walls of buildings and reaching the inside of the laboratory. Therefore, he brought a honeybee nest into a salt mine that was too deep for cosmic rays to reach. The same experiment was performed, where the bees showed that they knew the time (Wahl 1932). In this way, even if the external cues were eliminated, the bees remembered the time, so it became accepted that there is an endogenous clock.

Before these experiments, Garner and Allard (1920) reported that the Maryland mammoth variety of the tobacco *Nicotiana tabacum* had flower buds when the light period of a day was artificially shortened. They first revealed that an organism reacts to the photoperiod and named the response photoperiodism. Three years later, Marcovitch (1923) showed the first example of photoperiodism in animals. Under natural conditions, the strawberry aphid, *Aphis forbesi*, switches from parthenogenesis to bisexual reproduction in November in Tennessee. When transferred to a short day in February, the aphid changed the reproductive mode in May, much earlier than under natural conditions. Furthermore, Kogure (1933) showed that the induction of egg diapause depends on the photoperiod and temperature of the maternal egg period in the silk moth *Bombyx mori*. Thereafter, it was shown in many insects that diapause is regulated by photoperiodism (see Chap. 12).

Erwin Bünning proposed the idea that time measurement in photoperiodism is determined by the relationship between the phase of an endogenous rhythm and light, based on the experimental results on the endogenous rhythm in the runner bean, *Phaseolus coccineus* (Bünning 1936; see Bünning 1960 also). He postulated the existence of distinct scotophil (dark-requiring) and photophil (light-requiring) sections of the rhythm, and a photoperiodic effect is triggered according as to whether light falls in the scotophil. In 1936, when Bünning first proposed the idea, the word circadian clock had not yet been coined for a biological clock with a period of approximately a day (see Sect. 1.4), but this idea in current terms that "the circadian clock is involved in the measurement of daylength in photoperiodism" is later called Bünning's hypothesis (Pittendrigh 1960). It is now known that the time measurement in photoperiodism is not as simple as the original Bünning's hypothesis, which cannot explain various responses in photoperiodism. However, it is now believed that the circadian clock is involved in photoperiodism (e.g., Numata et al. 2015; Saunders 2021). Because the involvement of the circadian clock was first presented by Bünning (1936), the monumental value of Bünning's hypothesis is great. Although Bünning was a plant physiologist, he also published some experimental results on the photoperiodic induction of pupal diapause in the large white butterfly, *Pieris brassicae*, which supported Bünning's hypothesis (e.g., Bünning and Joerrens 1959; Bünning 1960).

The first insect shown to have diapause controlled by photoperiod was *B. mori*, which can only live in an artificial environment (Kogure 1933). However, Danilevskii (1961) clarified the implications of photoperiodism in the life cycle of wild insects from the 1940s to the 1960s. He examined geographical variation in the critical daylength, the daylength at the boundary that distinguishes between long days and short days in photoperiodism, within a species and revealed that variation in the critical daylength shows the life cycle adaptation to local climates of the insect. In general, the higher the latitude is, the faster the arrival of winter and the larger the fluctuation of the daylength. Therefore, the higher the latitude is, the longer the critical daylength for inducing winter diapause. By comparing populations in vast areas of the Soviet Union, including current Russia, Ukraine, and Georgia, Danilevskii (1961) concluded that a 5-degree higher latitude would increase the critical daylength by approximately 1.5 h. It is notable that he showed that we can discuss seasonal adaptations of insects based on the experimental results obtained in the laboratory.

I mentioned above the studies by two disciples of von Frisch, but here I show a study by himself. In 1919, von Frisch found that when a honeybee worker returned to the nest after finding food in the field, she was dancing to inform nestmate workers that there was food. In 1948, von Frisch published that honeybees are telling the

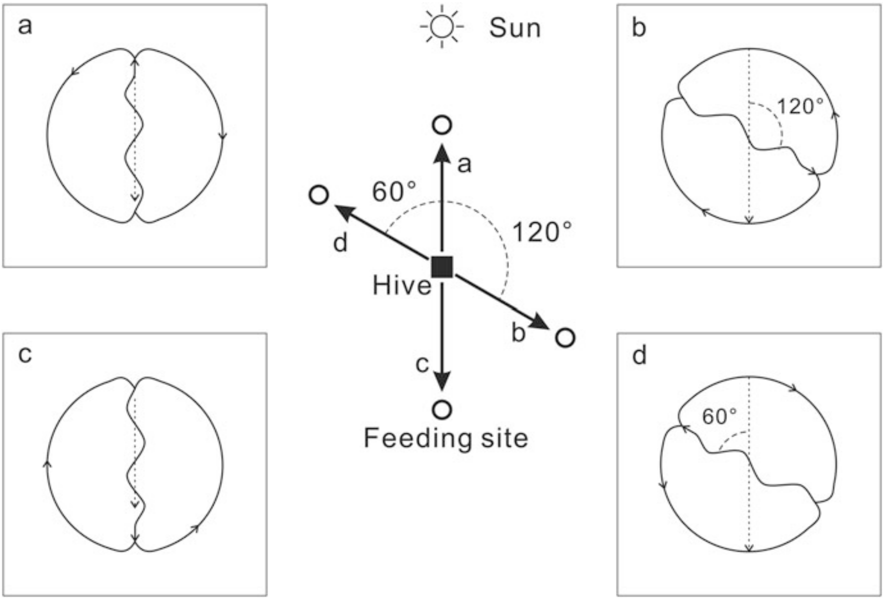


**Fig. 1.2** Solar compass of the honeybee *Apis mellifera*. Workers show the direction of the feeding site by waggle dance on the vertical honeycomb according to the position of the sun. Broken arrows show the direction of gravitational force. Based on von Frisch (1948)

direction and distance of the feeding site with this dance, later known as the waggle dance. The angle between the direction of the feeding site and the direction of the sun is expressed as the angle between the straight line in the middle of the waggle dance and the vertical line (Fig. 1.2; von Frisch 1948). This mechanism of orientation based on the position of the sun is called the solar compass. Even more surprisingly, honeybees can know the position of the sun even if they cannot see the sun itself. If honeybees can see the blue sky, they use its polarization pattern. Unlike the magnetic compass, where the north pole always points north and the South Pole points south, in the case of a solar compass, the direction indicated by the sun changes over time. Therefore, the sun compass is useless unless the direction indicated by the sun is corrected according to the time of day. In fact, honeybees know the change in the position of the sun and correct the direction indicated by the solar compass. Von Frisch (1950) observed that honeybees doing a waggle dance change the straight part of the dance counterclockwise over time. Moreover, when the nest was transferred elsewhere during the night when the bees were resting, honeybees searched for food in the same direction as yesterday in the next morning (even if the position of the sun was opposite). The results showed that the solar compass of the honeybee is time-compensated. Kramer (1950) also reported a time-compensated solar compass in the common starling, *Sturnus vulgaris*. It is called celestial navigation that an animal knows the direction based on the position of a celestial body to move, and its typical example is a solar compass. Thus, time-compensated celestial navigation was discovered almost at the same time by von Frisch and Kramer.

Approximately a quarter century after Beling (1929) and Wahl (1932), Max Renner, also a student of von Frisch, transported honeybees on a passenger plane over the Atlantic and examined what time they arrived for food. Renner (1955a) placed a honeybee nest in a large box of 7 m × 3 m × 3 m to allow humans to enter and feed the bees. Renner (1955b) prepared two boxes in Paris and in New York and first flew bees who learned when to feed in Paris to New York. Because a jet plane entered service on the transatlantic route in 1958, it took more than 16 h to be transported by a propeller plane at this time. The bees, trained to take sugar solution at 8 am in Paris, flew to the feeding place at 3 am on the next day in New York. Considering the time difference of 5 h between Paris and New York, it means that they flew to the feeding place 24 h after the time when they fed the day before. Next, Renner (1955b) conducted an experiment in which other bees were trained in New York and then carried to Paris, but again the bees visited the feeding place at the time of the city where they were first trained. In other words, it was clarified that the honeybee does not respond to any stimulus from the outside world after moving, but the time memory is based on the time indicated by the endogenous clock. Today, every time we travel abroad by jet, we suffer from jet lag as an unintentional experimental result, but the significance of conducting such an experiment in an animal for the first time is great.

## 1.4 Endogenous or Exogenous?

It came to be recognized that there is an endogenous clock in organisms because the endogenous clock was considered essential for the time memory and the correction of the solar compass of honeybees and the photoperiodic time measurement of many plants and animals. This concept is called the biological clock theory. As mentioned above, the role played by the experiments in insects was great in the establishment of the theory.

However, Frank Brown Jr. raised a strong doubt on the biological clock theory and argued against it (Brown 1960, 1970). The most obvious rationale for those who insist on the biological clock theory is that the activity of organisms is repeated at regular intervals when the environmental conditions are kept constant in the laboratory. In chronobiology, the rhythm observed under constant conditions is called the free-running rhythm, and the cycle length is called the free-running period, abbreviated as $\tau$ in the Greek letter.

Brown argued that the researchers kept the environmental conditions constant only by keeping some conditions constant within the range that the researchers could control. In many experiments that apparently have shown a free-running rhythm, light and temperature are kept constant, and food and water are continuously supplied. However, what about other factors? In fact, many factors, such as atmospheric pressure, gravity, magnetic field, electric field, electrical conductivity of air, and cosmic rays, should change periodically in these experiments. There are some cases where the effects of electrical conductivity and cosmic rays are individually denied (Beling 1929; Wahl 1932), but it is extremely difficult to keep all conditions constant. Brown argued that some factors from the outside world that researchers could not keep constant may affect the activity of organisms, resulting in the appearance of periodicity. In other words, what looks like the nature of an organism's clock is the manifestation of the organism's constant response to geophysical and astrophysical actions. This is called the exogenous timing hypothesis (Brown 1983). In many cases, the fact that the cycle of the free-running rhythm deviates from 24 h, which is the cycle of environmental fluctuations, and that there are slight differences among individuals is the argument of the biological clock theory. However, Brown argued that the combination of responses to various external stimuli could be explained without a biological clock. Then, to prove the exogenous timing hypothesis, various experiments were conducted, such as using cesium-137 to periodically apply weak gamma rays to organisms (Brown 1970, 1983).

Despite Brown's struggle, the biological clock theory is generally accepted today. However, the exogenous timing hypothesis was not denied by a single definitive experiment. In principle, the exogenous timing hypothesis is a hypothesis that cannot be logically denied. This is because even if we conduct an experiment with all possible environmental conditions constant and claim that there is an endogenous clock in the organism, there are many other factors that cannot be controlled by the experiment. However, no biologist currently supports the exogenous timing hypothesis. This is because those who believe in the existence of biological clocks have become more confident by accumulating experimental evidence one after another, and at the same time, Brown's explanation by the influence from the outside world was becoming increasingly complicated. Finally, no one accepts it.

There are numerous experiments conducted by those who support the biological clock theory, but here I show a large-scale experiment that clearly aims to counter Brown's theory. In 1960, Karl Hamner and his collaborators in the United States carried the following five organisms to the South Pole: the golden hamster, *Mesocricetus auratus*, the common bean *Phaseolus vulgaris*, the red bread mold *Neurospora crassa*, the fruit fly *Drosophila pseudoobscura*, and the American cockroach *Periplaneta americana*. It was already known that the locomotor activity of *M. auratus* and *P. americana*, the eclosion of *D. pseudoobscura*, the vertical movement of the leaves of *P. vulgaris*, and the mycelium growth of *N. crassa* show a free-running rhythm. Hamner et al. (1962) placed these organisms on an aluminum turntable that rotates counterclockwise once a day in a garage only approximately 800 m from the South Pole. The temperature was kept at 20–22 °C, and the activity of these organisms was recorded in darkness. As a result, the four species of organisms except *P. americana* showed a free-running rhythm, similar to that observed in the United States (Hamner et al. 1962). Under these conditions, at least the stimuli associated with the rotation of the Earth were denied as the cause of the rhythms because the four organisms showed free-running rhythms for different activities even though all geophysical changes of the day were removed. Curiously, *P. americana* did not show periodicity in its activity in Antarctica, but when the same strain was examined later in the United States, it did not show periodicity. It seems that Hamner et al. (1962) accidentally brought such a strain to Antarctica.

Halberg (1959) proposed the term circadian rhythm by combining the Latin "approximately" *circa* and "day" *dies* for the endogenous rhythm that controls the diurnal activity of organisms. The term quickly became established and is now widely used.

## 1.5 Localization of the Circadian Clock

Although it became recognized that the clock was in the body of organisms, it was not clear for a long time where the clock actually existed in the body. Janet Harker was the first to be interested in this question. She concluded that the circadian clock is in the subesophageal ganglion and the light received by the ocellus entrains the clock to light-dark cycles based on the results of a series of experiments conducted on the nocturnal locomotor activity rhythm in *P. americana* (Harker 1956).

Colin Pittendrigh had doubts about these experimental results and their interpretation by Harker (1956). Pittendrigh was studying the circadian eclosion rhythm of *D. pseudoobscura* and clarified the properties of the circadian clocks one after another since the 1950s: the temperature compensation of the free-running rhythm, the phase response curve to light stimuli, and the existence of a transient are all shown first by Pittendrigh and his coworkers (Pittendrigh 1954, Pittendrigh and Bruce 1957, Pittendrigh et al. 1958; see Pittendrigh 1993 also). Pittendrigh conducted a replication study of Harker's experiment with his graduate student Shephard Roberts but could not reproduce the results at all (Roberts 1965, 1966). Therefore, Pittendrigh welcomed Junko Nishiitsutsuji-Uwo (Fig. 1.3), who specializes in surgery of the insect nervous system, to his laboratory and examined the effects of painting and removal of photoreceptors, cutting of nerves and partial removal of the nervous system on the locomotor activity rhythm in the cockroach *Rhyparobia* (*Leucophaea*) *maderae*. The result was quite different from Harker's: the circadian clock that controls the activity rhythm exists in the optic lobe, and the light that entrains this clock to light-dark cycles is received by the compound eye (Nishiitsutuji-Uwo and Pittendrigh 1968a, 1968b). The optic lobe is located between the compound eye and the central brain and processes the optical information that enters the compound eye. It was pointed out that Harker's experiments and analyses had some deficiencies, and the results were completely denied. Nishiitsutuji-Uwo and Pittendrigh (1968a, 1968b) is the first localization of the biological clock before the discovery of the mammalian circadian clock in the suprachiasmatic nucleus (Moore and Eichler 1972; Stephan and Zucker 1972).

Thereafter, in *R. maderae* and the cricket *Gryllus bimaculatus*, it was shown that even if the optic lobe is completely excised from the body and cultured, the electrical activity maintains a periodicity of approximately one day (Collwell and Page 1990; Tomioka and Chiba 1992). Therefore, it was undoubtedly proven that a circadian

**Fig. 1.3** Colin Pittendrigh (left) and Junko Nishiitsutsuji-Uwo (right). Pittendrigh visited Kyoto, Japan, for attending the 16th International Congress of Entomology in August 1980. Photo by Hideharu Numata

clock exists in the optic lobe. In addition, from the expression of clock genes and clock proteins, some cell groups in the brain are shown to be the main body of the circadian clock in *D. melanogaster* (Ewer et al. 1992).

## 1.6 Molecular Mechanism of the Circadian Clock

Because the biological clock is innate, it is naturally expected that genes control it. However, showing the expectation by experiments seemed very difficult even approximately 1970, when the biological clock theory was almost accepted. Konopka and Benzer (1971) obtained three mutants of a single locus on the X chromosome in *D. melanogaster* by treatment with a chemical mutagen. These mutants had abnormal circadian rhythms in eclosion and adult activity, and the gene was named *period*. This is the first study to demonstrate that a gene constitutes a biological clock (Konopka and Benzer 1971).

Beginning with the sequence of *period* of *D. melanogaster*, clock gene structures have been determined one after another in various insects (Bargiello et al. 1984; Reddy et al. 1984; see Tomioka and Matsumoto 2015). Studies on the molecular mechanism of the circadian clock in vertebrates were started to find a homolog of *period* of *D. melanogaster* (Tei et al. 1997; Sun et al. 1997). The Nobel Prize in Physiology or Medicine 2017 was awarded jointly to Jeffrey Hall, Michael Rosbash, and Michael Young for their discoveries of molecular mechanisms controlling the circadian rhythm (https://www.nobelprize.org/prizes/medicine/2017/summary/).

The most important knowledge for this award is that the negative feedback loop between clock genes and their product proteins produces oscillation of the circadian clock. This was also reported first in *D. melanogaster* (Hardin et al. 1990).

## 1.7 Future Forecast

Insects show various phenomena related to clocks, and many interesting studies have been conducted. I counted the number of research papers on insect clocks indexed in Web of Science™ over the past 73 years (Fig. 1.4). The number of papers in this field has increased drastically since 1990, and more than 200 papers have been published every year since 2007. This increase started just after the discovery of the negative feedback loop (Hardin et al. 1990), and the proportion of *Drosophila* papers also increased in this period (gray bars, Fig. 1.4). Therefore, the increase is apparently due to the discovery of the molecular mechanism controlling the circadian rhythm, for which the Nobel Prize in Physiology or Medicine 2017 was awarded later.

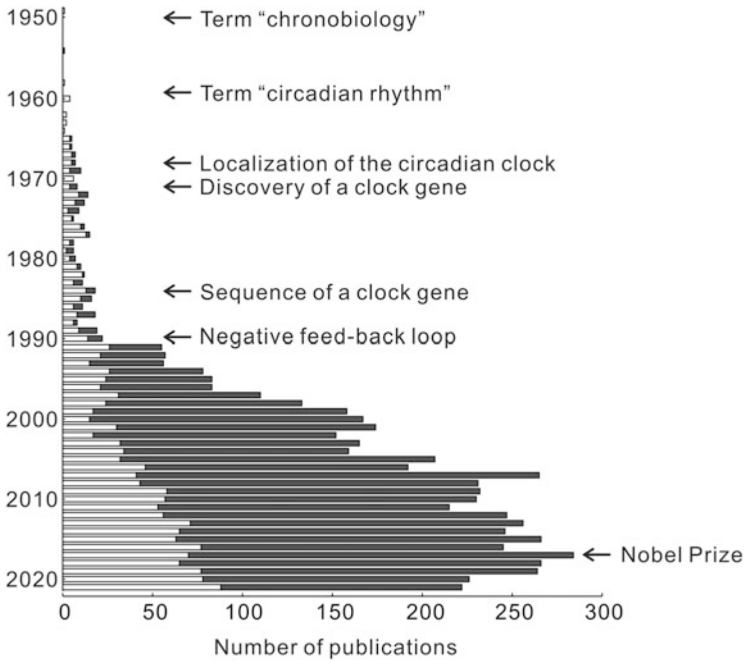


**Fig. 1.4** The number of research papers on insect clocks indexed in Web of Science™ over the past 73 years. Historically important events in chronobiology are also shown. Gray and white sections of horizontal bars represent the number of papers in *Drosophila* and that in the other insects, respectively

As shown in this chapter, chronobiology has gone deeper into the elucidation of the molecular mechanism of the circadian clock in *Drosophila*. However, insect chronobiology should not be restricted to the molecular mechanism of the circadian clock nor in *Drosophila*. In the next era, I expect that chronobiology will expand more widely: for example, circadian clocks in various organisms; the molecular and neural mechanisms of photoperiodism, the period of which is different from approximately 24 h; and the ecological aspect of biological clocks will be in the limelight. The fact that the number of chronobiology papers out of *Drosophila* has steadily increased since 2000 is a sign of such expansion (white bars, Fig. 1.4).

## References

Anonymous (1729) Observation botanique. In: Histoire de l'Académie Royale des Sciences. Année 1729, pp 35–36. https://www.biodiversitylibrary.org/item/88101#page/49/mode/1up

Bargiello TA, Jackson FR, Young MW (1984) Restoration of circadian behavioural rhythms by gene transfer in *Drosophila*. Nature 312:752–754. https://doi.org/10.1038/312752a0

Beling I (1929) Über das Zeitgedähtnis der Bienen. Z Vgl Physiol 9:259–338. https://doi.org/10.1007/BF00340159

Brown FA Jr (1960) Response to pervasive geophysical factors and the biological clock problem. Cold Spring Harb Symp Quant Biol 25:57–71. https://doi.org/10.1101/SQB.1960.025.01.007

Brown FA Jr (1970) Hypothesis of environmental timing of the clock. In: Brown FA Jr, Hastings JW, Palmer JD (eds) The biological clock two views. Academic Press, New York

Brown FA Jr (1983) The biological clock phenomenon: exogenous timing hypothesis. J Interdiscipl Cycle Res 14:137–162. https://doi.org/10.1080/09291018309359807

Bünning E (1936) Die endogene Tagesrhythmik als Grundlage der Photoperiodischen Reaktion. Ber Dtsch Bot Ges 54:590–607. (cited in Bünning, 1960)

Bünning E (1960) Circadian rhythms and the time measurement in photoperiodism. Cold Spring Harb Symp Quant Biol 25:249–256. https://doi.org/10.1101/SQB.1960.025.01.026

Bünning E, Joerrens G (1959) Versuche zur photoperiodischen Diapause-Induktion bei *Pieris brassicae* L. Naturwissenschaften 46:518–519. https://doi.org/10.1007/BF00703549

Burrows W (1945) Periodic spawning of 'Palolo' worms in Pacific waters. Nature 155:47. https://doi.org/10.1038/155047a0

Collwell CS, Page TL (1990) A circadian rhythm in neural activity can be recorded from the central nervous system of the cockroach. J Comp Physiol A 166:643–649. https://doi.org/10.1007/BF00240014

Danilevskii AS (1961) Photoperiodism and seasonal development of insects. Leningrad University Press, Leningrad (in Russian). English translation by Johnston J. Oliver & Boyd, Edinburgh (1965)

Ewer J, Frisch B, Hamblen-Coyle MJ, Rosbash M, Hall JC (1992) Expression of the period clock gene within different cell types in the brain of *Drosophila* adults and mosaic analysis of these cells' influence on circadian behavioral rhythms. J Neurosci 12:3321–3349. https://doi.org/10.1523/JNEUROSCI.12-09-03321

Forel A (1910) Das Sinnesleben der Insekten. Reinhardt, München

Garner WW, Allard HA (1920) Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. J Agricultural Res 58:553–606

Halberg F (1959) Physiologic 24-hour periodicity; general and procedural considerations with reference to the adrenal cycle. Z Vitamin Hormon Fermentforsch 10:225–296. (cited in Halberg, 1969)

Halberg F (1969) Chronobiology. Annu Rev Physiol 31:675–726. https://doi.org/10.1146/annurev.ph.31.030169.003331

Hamner KC, Flinn JC, Sirohi GS, Hoshizaki T, Carpenter BH (1962) The biological clock at the south pole. Nature 195:476–480. https://doi.org/10.1038/195476a0

Hardin PE, Hall JC, Rosbash M (1990) Feedback of the *Drosophila period* gene product on circadian cycling of its messenger RNA levels. Nature 343:536–540. https://doi.org/10.1038/343536a0

Harker JE (1956) Factors controlling the diurnal rhythm of activity of *Periplaneta americana* L. J Exp Biol 33:224–234. https://doi.org/10.1242/jeb.33.1.224

Kogure M (1933) The influence of light and temperature on certain characters of the silkworm, *Bombyx mori*. J Dept Agric Kyushu Imp Univ 4:1–93. https://doi.org/10.5109/22568

Kramer G (1950) Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. Naturwissenschaften 37:377–378. https://doi.org/10.1007/BF00626007

Konopka RJ, Benzer S (1971) Clock mutants of *Drosophila melanogaster*. Proc Natl Acad Sci U S A 68:2112–2116. https://doi.org/10.1073/pnas.68.9.2112

Marcovitch S (1923) Plant lice and light exposure. Science 58:537–538. https://doi.org/10.1126/science.58.1513.537-a

Moore RY, Eichler VB (1972) Loss of circadian adrenal corticosterone rhythm following suprachiasmatic nucleus lesion in the rat. Brain Res 42:201–206. https://doi.org/10.1016/0006-8993(72)90054-6

Nishiitsutuji-Uwo J, Pittendrigh CS (1968a) Central nervous system control of circadian rhythmicity in the cockroach. II. The pathway of light signals that entrain the rhythm. Z Vergl Physiol 58: 1–13. https://doi.org/10.1007/BF00302433

Nishiitsutuji-Uwo J, Pittendrigh CS (1968b) Central nervous system control of circadian rhythmicity in the cockroach. III. The optic lobes, locus of the driving oscillation? Z Vergl Physiol 58:4–46. https://doi.org/10.1007/BF00302434

Numata H, Miyazaki Y, Ikeno T (2015) Common features in diverse insect clocks. Zool Lett 1:10. https://doi.org/10.1186/s40851-014-0003-y

Pittendrigh CS (1954) On temperature independence in the clock system controlling emergence time in *Drosophila*. Proc Natl Acad Sci U S A 40:1018–1029. https://doi.org/10.1073/pnas.40.10.1018

Pittendrigh CS (1960) Circadian rhythms and the circadian organization of living systems. Cold Spring Harb Symp Quant Biol 25:59–184. https://doi.org/10.1101/SQB.1960.025.01.015

Pittendrigh CS (1993) Temporal organization: reflections of a Darwinian clock-watcher. Annu Rev Physiol 55:17–54. https://doi.org/10.1146/annurev.ph.55.030193.000313

Pittendrigh CS, Bruce VG (1957) An oscillator model for biological clocks. In: Rudnick D (ed) Rhythmic and synthetic processes in growth. Princeton University Press, Princeton, pp 75–109

Pittendrigh CS, Bruce VG, Kaus P (1958) On the significance of transients in daily rhythms. Proc Natl Acad Sci U S A 44:965–973. https://doi.org/10.1073/pnas.44.9.965

Reddy P, Zehling WA, Wheeler DA, Pirrotta V, Hadfield C, Hall JC, Rosbash M (1984) Molecular analysis of the *period* locus in *Drosophila melanogaster* and identification of a transcript involved in biological rhythms. Cell 38:701–710. https://doi.org/10.1016/0092-8674(84)90265-4

Renner M (1955a) Über die Haltung von Bienen in geschlossenen, künstich beleuchteten Räumen. Naturwissenschaften 42:539–540. https://doi.org/10.1007/BF00630155

Renner M (1955b) Ein Transozeanversuch zum Zeitsinn der Honigbiene. Naturwissenschaften 42: 540–541. https://doi.org/10.1007/BF00630156

Renner M (1960) The contribution of the honey bee to the study of time-sense and astronomical orientation. Cold Spring Harb Symp Quant Biol 25:361–367. https://doi.org/10.1101/SQB.1960.025.01.037

Roberts SK (1965) Photoreception and entrainment of cockroach activity rhythms. Science 148: 958–959. https://doi.org/10.1126/science.148.3672.958

Roberts SK (1966) Circadian activity rhythms in cockroaches. III. The role of endocrine and neural factors. J Cell Physiol 67:473–486. https://doi.org/10.1002/jcp.1040670312

Saunders D (2021) Insect photoperiodism: Bünning's hypothesis, the history and development of an idea. Eur J Entomol 118:1–13. https://doi.org/10.14411/eje.2021.001

Schulze A (2006) Phylogeny and genetic diversity of palolo worms (*Palola,* Eunicidae) from the tropical North Pacific and the Caribbean. Biol Bull 210:25–37

Stephan FK, Zucker I (1972) Circadian rhythms in drinking behavior and locomotor activity are eliminated by suprachiasmatic lesions. Proc Natl Acad Sci U S A 54:1521–1527. https://doi.org/10.1073/pnas.69.6.1583

Sun ZS, Albrecht U, Zhuchenko O, Bailey J, Eichele G, Lee CC (1997) RIGUI, a putative mammalian ortholog of the *Drosophila period* gene. Cell 90:1003–1011. https://doi.org/10.1016/S0092-8674(00)80366-9

Tei H, Okamura H, Shigeyoshi Y, Fukuhara C, Ozawa R, Hirose M, Sakaki Y (1997) Circadian oscillation of a mammalian homologue of the *Drosophila period* gene. Nature 389:512–516. https://doi.org/10.1038/39086

Tomioka K, Chiba Y (1992) Characterization of an optic lobe circadian pacemaker by in situ and in vitro recording of neural activity in the cricket, *Gryllus bimaculatus*. J Comp Physiol A 171:1–7. https://doi.org/10.1007/BF00195955

Tomioka K, Matsumoto A (2015) Circadian molecular clockworks in non-model insects. Curr Opin Insect Sci 7:58–64. https://doi.org/10.1016/j.cois.2014.12.006

von Buttel-Reepen H (1900) Sind die Bienen Refllex-maschinen? Experimental Beiträge zur Biologie der Honigbiene. Biol Zentralbl 20:97–108. (cited in Renner, 1960)

von Buttel-Reepen H (1915) Leben und Wesen der Bienen. Vieweg und Sohn, Braunschweig. (cited in Renner, 1960)

von Frisch K (1948) Gelöste und ungelöste Rätsel der Bienensprache. Naturwissenschaften 35:12–23. https://doi.org/10.1007/BF00626624

von Frisch K (1950) Die Sonne als Kompaß im Leben der Bienen. Experientia 6:210–221. https://doi.org/10.1007/BF02173654

Wahl O (1932) Neue Untersuchungen über das Zeitgedächtnis der Bienen. Z Vergl Physiol 16:529–589. https://doi.org/10.1007/BF00338333