Photoperiodic time measurement, photoreception, and circadian clocks in insect photoperiodism

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REVIEW

Photoperiodic time measurement, photoreception, and circadian clocks in insect photoperiodism

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Abstract

Photoperiodism is an adaptive response used by organisms to assess day length and anticipate upcoming seasons and to coordinate their (or their offspring's) development and physiology with the environmental changes. These physiological mechanisms have long been studied to understand insect life cycles, combat pests, conserve endangered species, and rear beneficial insects. Recent genetic manipulations have greatly expanded our knowledge of the molecular mechanisms underlying photoperiodism. Here, I review our current knowledge of the physiological and molecular mechanisms underlying photoperiodic time measurement, photoreception, and circadian clocks, which constitute insect photoperiodism modules, with a special emphasis on photoperiodic time measurement models.

Keywords Diapause · Opsin · Cryptochrome · Circadian clock genes · RNA interference

Introduction

Most temperate insects and mites have evolved a seasonal timing system that enables them to use day length (photoperiod) as a cue to coordinate their development and physiology (or that of their offspring) with the annual changes in the environment (Denlinger 2022). This biological ability is termed photoperiodism and the organismal response to photoperiod is referred to as a photoperiodic response. The most prevalent photoperiodic event is diapause, characterized by the suppression or arrest of development or reproduction in conjunction with an extensive shutdown of metabolic activity (Košťál 2006). Diapause is an adaptive, plastic phenotype and a form of dormancy that allows insects and mites to persist in seasonally variable environments. Diapause at egg (embryonic), larval (or nymphal), and pupal stages are characterized by developmental arrest or retardation, while that at the adult stage manifests as a cessation of reproduction. For example, the flesh fly, *Sarcophaga similis* develops into an adult without any interruption during long summer days, whereas it overwinters at the pupal stage by entering diapause characterized by developmental arrest (Goto 2009) (Fig. 1). Adult female jewel wasp, *Nasonia vitripennis* that is a parasitoid of the flesh fly, lays eggs that develop into adulthood without developmental interruption under long days, but enters diapause at the final (4th) instar larval stage under short days, due to maternal induction of photoperiodic diapause (Mukai and Goto 2016) (Fig. 1). Most insects destined to enter diapause accumulate additional energy reserves before the onset of diapause. Sufficient energy reserves and low metabolic activity ensure a high probability of survival during and after adverse seasons (Hahn and Denlinger 2011).

Photoperiodism was first demonstrated in plants a century ago (Garner and Allard 1920). Shortly thereafter, it was described in the strawberry root aphid *Aphis forbesi* (Marcovitch 1923). Being a crucial mechanism regulating insect life history, photoperiodism has been the focus of numerous studies in various biological fields spanning from molecular biology to ecology. Photoperiodic regulation of diapause is important not only from a basic biology perspective, but also from that of applied entomology. To combat various pests or to conserve endangered species, it is crucial to understand their life cycles and environmental adaptations, which are mainly regulated by photoperiodism. Particularly, predictive models to accurately determine the seasonal activity of insects require knowledge of environmental cues that regulate developmental speed, initiate diapause, and terminate

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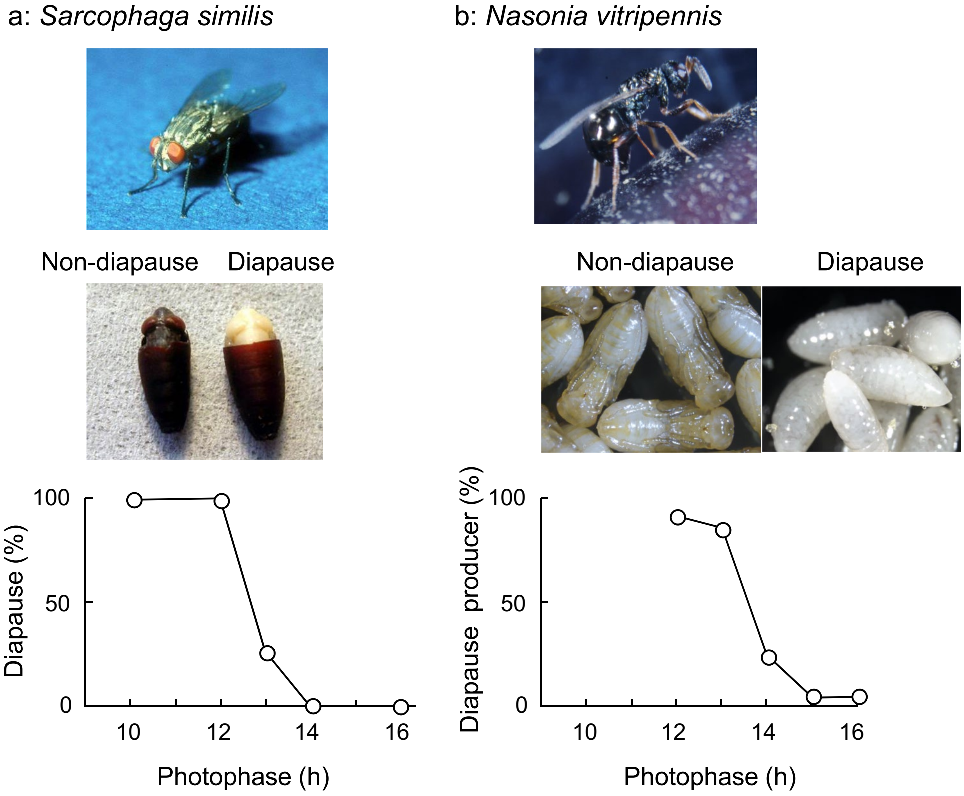


Fig. 1 Photoperiodic responses of *Sarcophaga similis* (**a**) and *Nasonia vitripennis* (**b**). **a** Upper panel, an adult female. Middle panel, developing pupa (non-diapause) and diapausing pupa. Lower panel, the photoperiodic response curve for diapause induction (Goto 2009). This species enters pupal diapause in response to short days. **b** Upper panel, an adult female. Middle panel, developing pupae (non-diapause) and larvae in diapause. Lower panel, the photoperiodic response curve for the production of diapause producers (Mukai and Goto 2016). Females of this species lay eggs destined to enter diapause in short days. Photos of *N. vitripennis* are courtesy of A. Mukai at Setsunan University. From Goto (2009) and Mukai and Goto (2016)

diapause (Grevstad et al. 2022; Grevstad and Coop 2015; Kumar et al. 2015; Lindestad et al. 2019; Nielsen et al. 2016; Peffers et al. 2021; Pollard et al. 2020).

One of the greatest challenges for the industry of biological control agents and beneficial species is to store the agents without incurring a significant loss of vitality (Colinet and Boivin 2011). Diapause is suitable for increasing their shelf lives and reducing the costs of continuously maintaining a colony. However, to successfully manage diapause in the program, knowledge of the environmental cues regulating diapause entry and termination is a necessity (Ichikawa et al. 2020; Li et al. 2018). Artificial light at night (ALAN) is a serious issue in urbanization that causes disruption of physiological function and behavior in birds and mammals, including humans (Stevenson et al. 2015). ALAN disrupts insect photoperiodic responses and interferes with local adaptations (Fyie et al. 2021; Mukai et al. 2021; van Geffen et al. 2014; Westby and Medley 2020). In contrast, prevention of photoperiodic diapause by extending day length or by administering light pulse at selected times during the night using supplemental artificial light can promote “ecological suicide” of pest species (Ankersmit 1968; Beach and Craig 1979; Berlinger and Ankersmit 1976; Hayes et al. 1970, 1974; Schechter et al. 1971). Such photoperiodic manipulations are very attractive due to their non-reliance on chemicals. Although extensive field trials were conducted in the late 1960s and 1970s, only a few recent attempts have tested the viability of this approach possibly due to the economic feasibility of the installation of light sources and energy. Such attempts would benefit from more energy-efficient light sources such as light-emitting diodes (LEDs) (Shimoda and Honda 2013).

Insect photoperiodism is constituted by several physiological modules (see below). In this review, I present our current knowledge of the physiological and molecular mechanisms of some of the modules, including the photoperiodic time measurement system, photoreceptors, and circadian clocks, with a special emphasis on photoperiodic time measurement models.

Physiological mechanisms underlying photoperiodism

Figure 2 describes the physiological modules that constitute insect photoperiodism (Goto and Numata 2014). Photoreceptors extract photic information from environments. This is subsequently transferred to a circadian clock, which is a biological time-keeping system that controls the biological rhythms within a period of approximately 24 h; it sets its own phase and conveys the temporal information to a photoperiodic time measurement system. The photoperiodic time measurement system assesses the length of day or night by referring to the photic information from photoreceptors and/

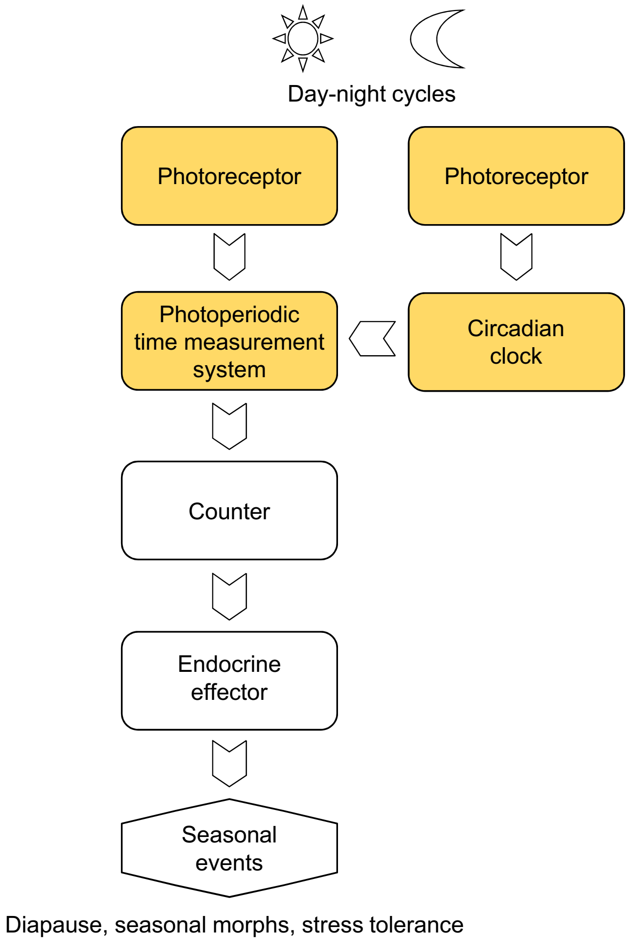


Fig. 2 Physiological mechanisms underlying insect photoperiodism. The modules discussed in this review are shaded

or to the temporal information from the circadian clock. A counter system accumulates the number of long days and/or short days. When the number of photoperiodic cycles exceeds an internal threshold in the counter system, endocrine effectors activate or inactivate target organs to induce or avert diapause.

The model insect, *Drosophila melanogaster,* may also show photoperiodic responses in female ovarian development, male spermatogenesis and accessory gland development, energy resource accumulation, and gene expression (Kubrak et al. 2016; Saunders et al. 1989). However, this photoperiodic response is weak and variable. Further, the response is observed only at a low temperature, which is very close to the lower limit of their development (developmental zero). Furthermore, temperature plays a major role in the induction of dormancy while photoperiod has little or no effect in this species (Anduaga et al. 2018; Emerson et al. 2009b; Erickson et al. 2020). Despite several studies on *D. melanogaster* (Abrieux et al. 2020; Nagy et al. 2019; Sandrelli et al. 2007; Tauber et al. 2007), only the molecular elements that are possibly involved in photoperiodic response are described in this review.

Photoperiodic time measurement

Photoperiodic time measurement is the core module in insect photoperiodism. Erwin Bünning first proposed that photoperiodic time measurement is one of the functions of the circadian clock (Bünning 1936). Later Bünning's hypothesis was further cultivated into the external coincidence model (Pittendrigh and Minis 1964). In this model, time measurement is based on a single circadian clock that is entrainable to light and positions the photoinducible phase (φ_i) at the late scotophase (Fig. 3). The φ_i is critical for photoperiodic assessment. During autumn, φ_i falls in the dark phase, which induces a short-day response. During summer, a longer light phase delays the phase of the clock and φ_i, thus, falls in the light period, which elicits a long-day response. Thus, light plays two roles in this model, i.e., entraining the oscillator and inducing an event determined by the φ_i. For the sake of simplicity, this mechanism of time measurement is usually discussed as a qualitative or all-or-none mechanism in most studies (i.e., the system distinguishes long from short days, or short from long nights). However, insects measure photoperiod quantitatively (Goto 2009; Goto and Numata 2009b). Thus, insects measure how long the φ_i is exposed to light. The photoperiodic response of flesh fly species (*Sarcophaga argyrostoma*, *Sarcophaga crassipalpis*, and *S. similis*) is a perfect example of the external coincidence model (Goto and Numata 2009a; Gnagey and Denlinger 1984; Saunders 1979).

Another influential clock-based model is the internal coincidence model, which proposes the involvement of two circadian clocks; one clock is entrained to dawn (dawn oscillator) and the other to dusk (dusk oscillator) (Tyshchenko 1966) (Fig. 3). The phase relationships between these oscillators produce long-day or short-day effects; certain phases of these oscillators are active, and long-day responses are induced when these active phases overlap (Danilevsky et al. 1970). In this model, light plays the single role of entraining these two oscillators. The photoperiodic response of *N. vitripennis* best fits this model (Saunders 1974).

Another influential model is the hourglass model, which does not propose the involvement of an oscillator but involves an hourglass or non-repetitive timer. The photoperiodic response of the vetch aphid, *Megoura viciae,* strongly supports this model (Lees 1973). However, the role of a circadian oscillator in photoperiodic timing has also been revealed in this species (Vaz Nunes and Hardie 1993). The hourglass model is considered to be a variation of the external coincidence model, which involves an oscillator dampening below the threshold in extended periods of

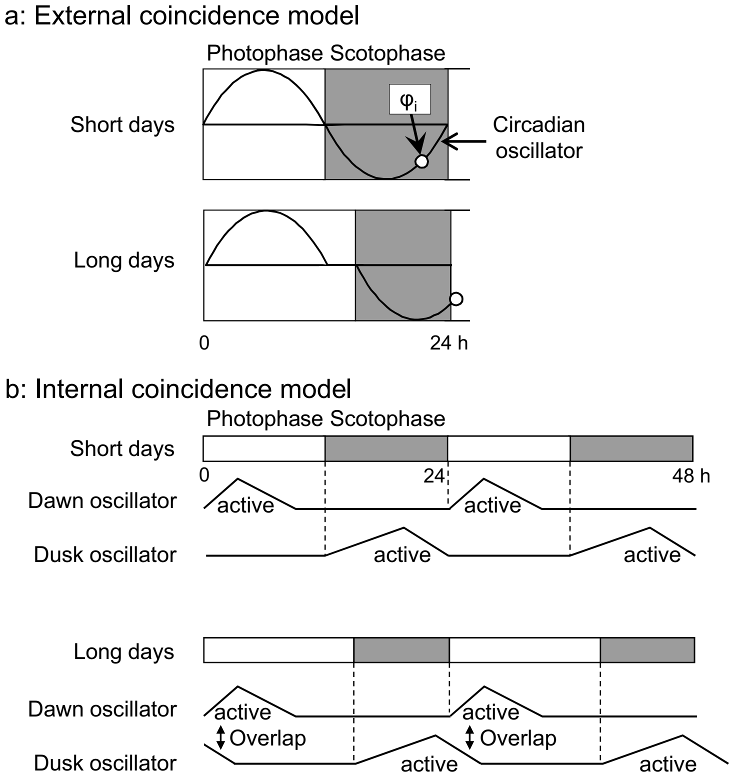


Fig. 3 Schematic concepts of external coincidence and internal coincidence models. **a** The external coincidence model is based on a circadian clock, which sets its phase at dusk and positions the photoinducible phase (φ_i) in the latter circadian phase. Under short days, φ_i is in darkness, eliciting a short-day response; whereas under long days, φ_i is exposed to light and a long-day response is induced. **b** The internal coincidence model proposes two oscillators entrained by dawn and dusk, whose internal phase relationship changes with photophase and scotophase lengths. Specific phases for each oscillator are active, and long-day responses occur when these overlap

darkness (Saunders 2010). Another aphid, *Acyrthosiphon pisum*, also displays a circadian clock that is dampened easily under constant darkness, which operates the rhythmicity of metabolism and locomotor activity (Barberà et al. 2017, 2022; Beer et al. 2017).

Although several models have been proposed to explain various photoperiodic responses under different experimental conditions (Vaz Nunes and Saunders 1999), the molecular mechanisms underlying these models remain unknown.

Photoreceptors and photopigments

Several methods, such as surgical ablation, covering with paints that prevent light penetration, supplemental illumination, and transplantation of the cultured organ, have been used to identify the photoreceptive organ responsible for photoperiodism (Goto et al. 2010). Extraretinal photoreception has long been believed to be significant in photoperiodism. For example, the blow fly *Calliphora vicina* continues to be sensitive to photoperiod even after surgical removal of the optic lobes that connect the compound eyes to the central brain, suggesting possible photoreception in the cerebral lobe (Saunders and Cymborowski 1996). Supplemental illumination at the central region of the dorsal area of the head disrupted the photoperiodic response in *M. viciae*, suggesting possible photoreception in the brain (Lees 1964). Furthermore, transplantation experiments demonstrated that cultured brain successfully distinguished photoperiods in vitro in tobacco hornworm *Manduca sexta* and silkmoth *Bombyx mori* (Bowen et al. 1984; Hasegawa and Shimizu 1987). The significance of the retinal photoreceptors has also been demonstrated. For example, the anterior and posterior eyes (simple eyes) were removed in the two-spotted spider mite *Tetranychus urticae,* either bilaterally or unilaterally using a laser ablation system, to investigate their role in its photoperiodic termination of diapause. Intact females terminate diapause in response to long-day conditions, whereas they remain in diapause when exposed to short-day conditions or constant darkness (Fig. 4). Bilateral and unilateral removal of the anterior eyes did not affect photoperiodic discrimination. Similarly, bilateral and unilateral removal of the posterior eyes did not affect photoperiodic discrimination. Contrarily, mites with no eyes, via the bilateral removal of both anterior and posterior eyes, failed to discriminate photoperiods and remained in diapause, irrespective of the photoperiod (Fig. 4). Thus, in *T. urticae*, both anterior and posterior eyes function as photoreceptors and mediate photoperiodic regulation of diapause (Hori et al. 2014). In the carabid beetle *Leptocarabus kumagaii*, stemmata (larval eyes) are indispensable for the photoperiodic regulation of larval diapause. However, the stemmata-derived organs are not necessary for photoperiodic regulation of adult diapause. The adults use compound eyes for photoreception (Shintani et al. 2009). Surgical removal of the compound

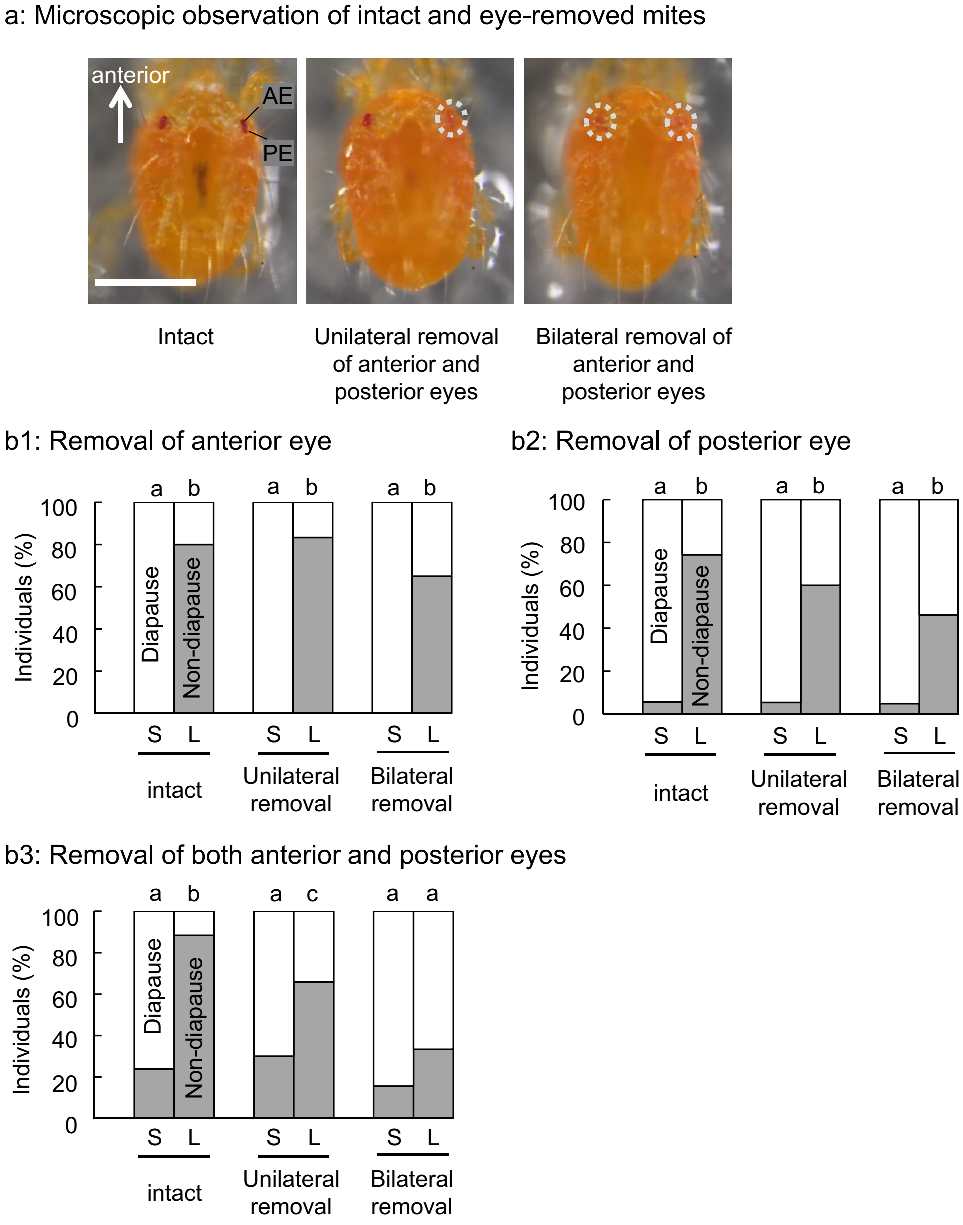


Fig. 4 External observation of eyes and effects of eye removal on the photoperiodic termination of diapause in the two-spotted spider mite *Tetranychus urticae* (Hori et al. 2014). **a** External observation (dorsal view) of intact and eye-removed mites on the day of assessment of diapause status. An intact mite (left), a mite of which anterior eye (AE) and posterior eye (PE) were unilaterally removed (middle), and a mite of which AEs and PEs were bilaterally removed (right). Dotted circles indicate the positions of the eyes treated. Scale bar 200 µm. **b** Effects of eye removal on photoperiodic termination of diapause. Diapause mites that had their eyes removed were maintained at 5 °C for 20 days and then transferred to short-day (S) or long-day (L) conditions at 17 °C. (b1) Removal of anterior eyes only; (b2) removal of posterior eyes only; (b3) removal of both anterior and posterior eyes. No significant difference was observed among treatments with the same letter (Tukey-type multiple comparisons for proportions, $P > 0.05$). From Hori et al. (2014)

eyes, in the cricket *Modicogryllus siamensis,* eliminated the photoperiodic response, indicating the compound eyes to be the photoreceptors (Sakamoto and Tomioka 2007). In the brown-winged green bug *Plautia stali*, retinal and extraretinal photoreceptors were proposed to be involved in the photoperiodic induction of diapause (Morita and Numata 1999). Thus, either retinal or extraretinal photoreceptors or both are responsible for photoreception in photoperiodism.

Arthropods use opsins as photoreceptive molecules to receive light (Van Der Kooi et al. 2021). Opsins generally exhibit a narrow range of spectral sensitivity, however, each species possesses multiple opsins with distinct spectral classes that enable them to receive the light of a broad range of wavelengths. Opsins are commonly observed in the retinal photoreceptor where they contribute to color vision (Van Der Kooi et al. 2021), but also act as circadian photoreceptors (Senthilan et al. 2019). Opsins are also reported in extraretinal photoreception (Shimizu et al. 2001; Velarde et al. 2005). Although their roles are still unknown, photoentrainment of the clock by the extraretinal photoreceptor is demonstrated in *D. melanogaster* and is proposed in the honeybee *Apis mellifera* (Beer and Helfrich-Förster 2020; Helfrich-Förster 2020). Classic dietary-deficiency experiments suggest that a vitamin A-based pigment, opsins, plays a role in photoreception in insect photoperiodism (Goto et al. 2010). Furthermore, the involvement of the retinal photoreceptor in photoperiodism also indicates the significance of opsin.

The role of opsins in photoperiodic response was directly examined using RNA interference (RNAi) in *M. siamensis,* whose photoperiodic photoreceptor is the compound eyes (Sakamoto and Tomioka 2007). This species shows photoperiod-dependent changes in the nymphal period. RNAi of three opsins (UV-, blue-, and long wavelength-sensitive opsins), which are expressed in the compound eyes, resulted in partial disruption of the long-day response. Interestingly, though RNAi of UV-sensitive opsins also disrupted the short-day response, RNAi of other opsins did not (Tamaki et al. 2013). These results indicate that opsins are the photoreceptive molecules involved in the photoperiodic response, but their specific roles are different. The monarch butterfly, *Danaus plexippus,* relies on photoreception by the brain, not by the compound eyes, for photoperiodic regulation of ovarian development. The loss-of-function mutant of *neither inactivation nor after potential B* (*ninaB1*), which encodes the rate-limiting enzyme that converts carotenoids into retinaldehyde, displayed a loss of the ability to respond to short days to suppress ovarian development in this species, suggesting the involvement of opsin in the brain in photoperiodic discrimination (Iiams et al. 2019).

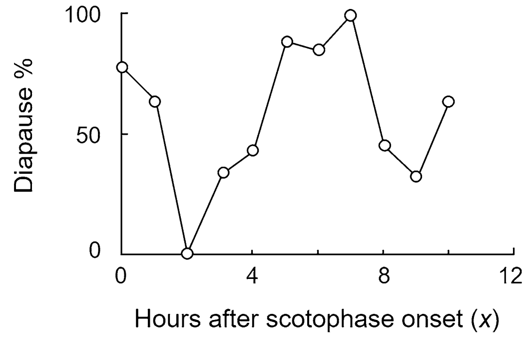
Insects and mites possess another photoreceptor called cryptochrome. Notably, the two forms of cryptochrome are encoded by the genes *Drosophila*-type cryptochrome (CRY-d, dCRY or CRY1) and mammalian-type cryptochrome (CRY-m, mCRY or CRY2). CRY-d absorbs light of a short wavelength, from UV to blue and functions as the main photopigment that resets the circadian clock (phase delays and advances) (Berndt et al. 2007; Stanewsky et al. 1998). In contrast, CRY-m has lost the ability of photoreception and acts as a transcriptional repressor in the circadian clock system (Merlin et al. 2013; Yuan et al. 2007). Many insects possess both cryptochromes. However, during the course of insect evolution, a lineage including the higher Diptera such as *D. melanogaster* lost *cry-m*, while some lineages in Hymenoptera and Coleoptera independently lost *cry-d* (Kotwica-Rolinska et al. 2022a). Insects that lost *cry-d* possibly use opsins as the photopigments responsible for photoentrainment of the circadian clock (Beer and Helfrich-Förster 2020).

The role of CRY-d in photoperiodism was also examined in *M. siamensis* via RNAi (Ueda et al. 2018). RNAi of *cry-d* partially prevented long-day response. Interestingly, RNAi enhanced the short-day response with a further delay of adult emergence and further increment of the moulting number in comparison with that in the control short-day insects. However, CRY-d is not the major photoreceptor for the entrainment of the circadian clock in a cricket (Kutaragi et al. 2018; Tokuoka et al. 2017). No other studies have demonstrated the role of *cry-d* in the photoperiodism of insects, where *cry-d* plays a central role in the photoentrainment of the circadian clock. Thus, the significance of *cry-d* in insect photoperiodism is still unknown.

Photoreception and photoperiodic time measurement

In *S. similis*, which measures photoperiod via external coincidence, a systematic interruption of scotophase by a short light pulse revealed that light pulses at the early and late phases of scotophase effectively prevented diapause entry (Goto and Numata 2009a) (Fig. 5). The early scotophase is sensitive to light at wavelengths ≤ 470 nm, but not at wavelengths ≥ 583 nm. In contrast, the late scotophase is sensitive to light of a broad range of wavelengths, ranging from 395 to 660 nm (Goto and Numata 2009a). The sensitivity at the early scotophase is higher than that at the late scotophase. These results indicate that distinct photoreceptors mediate the photoperiodic response. The spectral sensitivity and the role of light in external coincidence (photoentrainment) suggest a possibility that CRY-d is responsible for photoreception at the early scotophase. In contrast, the broad spectral sensitivity suggests that several types of opsins operate light perception during the late scotophase, i.e., φ_i. Photoentrainment of the circadian clock through CRY-d in the brain is demonstrated in *D. melanogaster* larvae (Klarsfeld et al. 2004). Fly larvae also possess a photoreceptive organ, Bolwig's organ, which is located on the mouth hook and expresses Rhodopsin 5 and 6 (Sprecher et al. 2011). *S. similis* may use CRY-d in the brain and opsins in the Bolwig's organ to display a photoperiodic response. This hypothesis has to be further verified.

Similarly, distinct spectral sensitivity was reported in *M. viciae*, which may also measure photoperiod via external coincidence using the dampening oscillator. The early scotophase exhibits maximal sensitivity at 450–470 nm with a rapid fall at shorter and longer wavelengths. Maximum action is still in the 450–470 nm region during the late phase; however, the most striking feature is the considerable extension of sensitivity at longer wavelengths (Lees 1981). The results indicate that this species also used distinct photoreceptors for photoperiodism, which was verified to be in the brain (Lees 1964). Immunostaining with 20 antibodies directed against invertebrate and vertebrate opsins and phototransduction proteins revealed positive signals in an anterior ventral neuropile region of the protocerebrum (Gao et al. 1999). The expression of several opsins and *cry-d* in the brain was also reported in another aphid *A. pisum* (Barberà et al. 2022; Colizzi et al. 2021; Collantes-Alegre et al. 2018). The large cabbage butterfly *Pieris brassicae* also measures photoperiod via external coincidence. A systematic interruption of scotophase by a short light pulse revealed a: Night interruption (LDLD = 12:*x*:2:[10-*x*] h)



b: Monochromatic night interruption

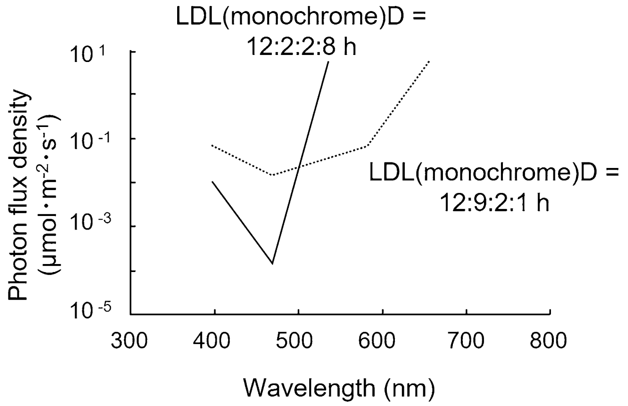


Fig. 5 Effects of a pulse of white light (**a**) and monochromatic light (**b**) on diapause incidence in *Sarcophaga similis* (Goto and Numata 2009a). **a** Diapause incidence under night interruption photoperiod with a 2-h light pulse with a fluorescent lamp. Diapause-destined larvae, reared under short-day conditions (LD 12:12 h) until the onset of the wandering larval stage, were placed on wet wood chips (water treatment) and exposed to night-interruption photoperiods (LDLD = 12:*x*:2; [10-*x*] h, where *x* ranged from 0 to 10) with a fluorescent lump for 4 days. Thereafter, larvae were transferred onto dry wood chips under short-day conditions. Note that phases 2 h and 9 h after scotophase onset are more sensitive to the light pulse for diapause aversion than other phases. **b** Spectral sensitivity during night interruption photoperiods with various photon flux densities of monochromatic light. Diapause-destined larvae that had been reared under short-day conditions were exposed to night-interruption photoperiods of LDL (monochromatic light) D = 12:2:2:8 h (solid line) or 12:9:2:1 (broken line). Lines in the graph indicate estimated values of the photon flux density at which half of the individuals entered diapause. From Goto and Numata (2009a)

that light pulses at the early and late phases of scotophase effectively prevented diapause entry. The larvae that were fed a vitamin A-deficient diet lost the photosensitivity at the late scotophase but not at the early scotophase (Claret and Volkoff 1992). These results suggest the involvement of a non-opsin photoreceptor, possibly CRY-d, in photoreception at the early scotophase and the involvement of opsins at the late scotophase.

Tomioka and his colleagues discussed the results of RNAi directed to opsins in the photoperiodic response in *M. siamensis*, based on the external coincidence model (Tamaki et al. 2013). Partial disruption of the long-day effect in RNAi of UV-, blue- and long wavelength-sensitive opsins possibly indicates prevention of photoperiodic time measurement by disturbing light detection at φ_i. On the contrary, disruption of the short-day response through RNAi of UV-sensitive opsin suggests the involvement of UV-sensitive opsin in the photic entrainment of a circadian clock responsible for photoperiodic time measurement. This is a fascinating hypothesis, but it is unclear whether the external coincidence model is indeed applicable to the photoperiodic time measurement of this species.

Photoreceptors responsible for photoperiodism that measure photoperiod via internal coincidence have not been extensively studied. In *N. vitripennis*, the action spectra at the early scotophase and late scotophase are very similar with maximum sensitivity between 554 and 586 nm and considerable sensitivity extending up to 617 nm (Saunders 1975). This indicates that a single photoreceptor system regulates the entrainment of the dawn and dusk oscillator. This species does not possess *cry-d* gene in its genome and, thus, opsins are hypothesized to play a role in the photoentrainment of the oscillators (Saunders 2012). This species possesses at least 3 opsin genes (UV-, blue-, and long wavelength-sensitive opsins), but their functions have not been examined yet.

Previous studies investigated the relationship between the photoreceptor involved in photoperiodism and that involved in the circadian locomotor activity rhythm (Goto et al. 2010). Some studies have revealed that photoperiodism and circadian rhythm share the same photoreceptors, while others revealed discrepancies. For example, in cricket, *Dianemobius nigrofasciatus,* and blow fly, *Protophormia terraenovae*, surgical removal of the compound eyes prevented the adults from responding to the photoperiod to control embryonic and adult diapause (Shiga and Numata 1996, 1997). However, the same operation did not interfere with the photic entrainment of the circadian locomotor rhythms in both species (Hamasaka et al. 2001, Shiga et al. 1999). These results indicate the involvement of the brain CRY-d in photic entrainment of the circadian clock and that of opsins expressed in the retinal photoreceptor in photoperiodic time measurement. By contrast, removal of the optic lobes did not interfere with photoperiodic control of larval diapause and with the entrainment of circadian activity rhythms in *C. vicina* (Cymborowski et al. 1994; Saunders and Cymborowski 1996). This indicates that both responses used extraretinal receptors in a part of the brain other than the optic lobe. It is of interest to investigate how this species measured photoperiods. It is also interesting to investigate the spectral sensitivity at the early and late scotophases and the possible involvement of opsins and/or CRY-d in photoperiodism.

The molecular machinery of the circadian clock

The molecular mechanism of the circadian clock regulating circadian behavior has been investigated mainly in *D. melanogaster* (Patke et al. 2020). The basic mechanisms of the clock are transcriptional-translational negative feedback loops, consisting of the circadian clock genes (hereafter, clock genes) that produce rhythmic gene expression in a period of approximately 24 h (Fig. 6). In brief, the protein products of *Clock* (*Clk*) and *cycle* (*cyc*) (i.e., CLK and CYC) form a heterodimer, which activates the transcription of *period* (*per*) and *timeless* (*tim*) genes from late day to early night. Subsequently, the protein products of *per* and *tim* (i.e., PER and TIM) are accumulated during the night. They form a heterodimer at late night, enter the nucleus, and repress the transcriptional activity of the CLK/CYC complex. The repression reduces the mRNA levels of *per* and *tim*, which results in a reduction of their proteins, and finally releases the CLK/CYC complex from repression. Then the next round begins. Based on their roles, PER and TIM are regarded as negative regulators, while CLK and CYC as positive regulators. The transcriptional targets of CLK–CYC include downstream "clock-controlled genes", whose cyclic expression confers circadian rhythmicity to cell and tissue function. The rhythmic expression of *Clk* is regulated by a negative element *vrille* (*vri*) and a positive element *Par domain protein 1* (*Pdp1*) in the second loop. CLK–CYC activity is negatively regulated by *clockwork orange* (*cwo*) in the third loop (Tomioka and Matsumoto 2019).

Although the basic machinery is nearly identical to *D. melanogaster*, few significant variations exist among insects (Fig. 6). One of the striking variations of the clock machinery is the presence or absence of *cry-d*, *cry-m*, and/or *tim*. Ancestral insects possessed these, but during the course of insect evolution, a lineage in Blattodea lost *cry-d*, and one of its descendant lineages further lost *tim*. Independent loss of *cry-d* is assumed to have occurred in lineages of Heteroptera, Psocodea, and Coleoptera and the ancestor of Hymenoptera. Loss of *tim* and *cry-m* occurred in Hymenoptera and a lineage in the suborder Brachycera, respectively (Kotwica-Rolinska et al. 2022a). Causal involvement of CRY-m as a transcriptional repressor in the circadian feedback loop is demonstrated in butterflies, as well as a mosquito, a beetle, a honeybee, and a cricket (Tokuoka et al. 2017; Yuan et al. 2007; Zhu et al. 2006, 2008) (Fig. 6). In addition, *cry-m* has several splicing variants and some of the protein products are speculated to form a complex with other CRY-m or CRY-d proteins and repress their transcription by inhibiting CLK/CYC transcriptional activity in a cricket (Tokuoka et al. 2017). Moreover, both CRY-d and CRY-m are also involved in the photic entrainment pathway of the circadian clock (Kutaragi et al. 2018). Since *tim* has also been lost in several insect lineages of Hymenoptera and Termitidae in addition to the absence of *cry-d*, their clockwork appears to be simplified (Beer and Helfrich-Förster 2020; Kotwica-Rolinska et al. 2022a) (Fig. 6). *tim* plays an important role in the circadian clockwork of *D. melanogaster* (Sehgal et al. 1994), but not in Orthoptera and Hemiptera (Danbara et al. 2010; Kotwica-Rolinska et al. 2022a). The amino acid sequence of PER in *D. melanogaster* possesses the threonine–glycine (TG) repeat region that is proposed to provide temperature compensation for the circadian clock (Sawyer et al. 1997). However, such a long thread of TG was not found even in other dipterans (Goto and Denlinger 2002). CLK of *D. melanogaster* has the polyglutamine (Q) region, which forms a coiled coil and is involved in transcription activation (Allada et al. 1998), but the region is not found in other insect species (Sandrelli et al. 2008). CLK is the main transcriptional activator in *Drosophila*, but its role substitutes for CYC in other insects (Sandrelli et al. 2008). Oscillatory patterns of the core elements are also diversified among insect species (Tomioka and Matsumoto 2019). Therefore, the clockwork diversity must be considered while interpreting the results of genetic manipulations.

Involvement of clock genes in insect photoperiodism

Two approaches have been adopted to assess the role of clock genes in insect photoperiodism. One is the photoperiodic regulation of clock gene expression under distinct photoperiods (Saunders 2020). For example, the peak in *per* expression shifts with the timing of scotophase onset in *S. crassipalpis*. A shift in *tim* is less pronounced but the amplitude of the *tim* peak is severely dampened under long days (Goto and Denlinger 2002). Photosensitive larvae of *S. crassipalpis* show peak expression of both mRNAs during the light phase under long days and during the dark phase under short days (Koštál et al. 2009). In the head of *N. vitripennis*, the peaks of *per* and *cry-m* mRNA oscillations occurred in late photophase under long-day and in the middle of the scotophase under short-day conditions (Bertossa et al. 2014), although such photoperiodic difference was less pronounced in another strain (Mukai and Goto 2016). In a holocyclic strain of *A. pisum*, the *per* mRNA amounts peaked at late photophase and late scotophase under long and short days, respectively. In addition, the expression of core clock genes was higher at any time in aphids reared

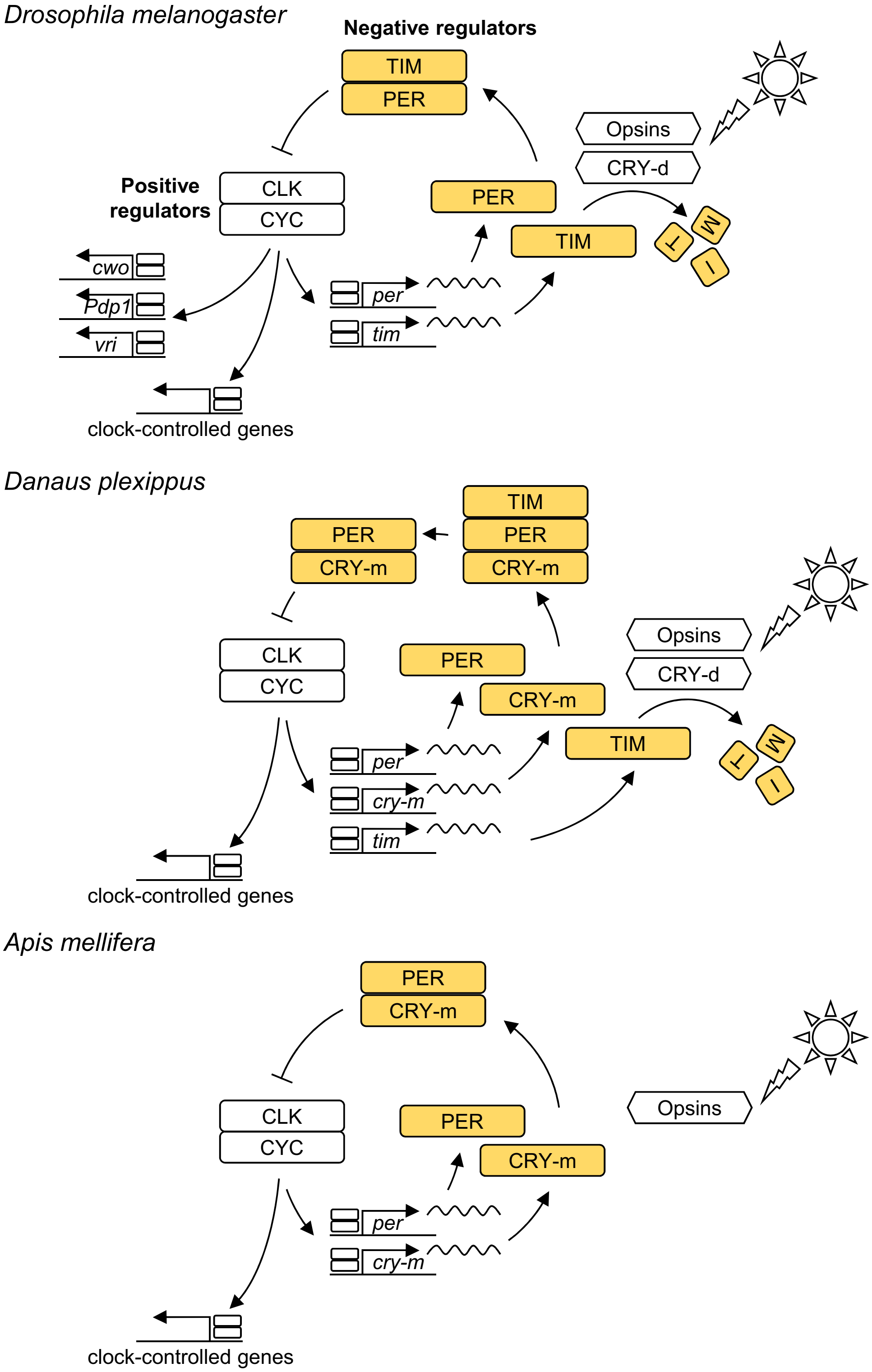


Fig. 6 Molecular machinery of the circadian clock in the fruit fly *Drosophila melanogaster*, the monarch butterfly *Danaus plexippus*, and the honeybee *Apis mellifera*. In *Drosophila*, CLOCK (CLK) and CYCLE (CYC) act as positive regulators to induce transcription of *period* (*per*), *timeless* (*tim*), and other circadian clock genes participating in the interlocked feedback loops of the clock such as *clockwork orange* (*cwo*), *Par-domain protein 1* (*Pdp1*), and *vrille* (*vri*), as well as many clock-controlled genes that mediate downstream signaling cascades. PER and TIM act as negative regulators that inhibit the transcriptional activity of the CYC–CLK heterodimer. *Drosophila* CRYPTOCHROME (CRY-d) induces the degradation of TIM in a light-dependent manner. *Danaus* has a nearly identical clock, except that mammalian-type CRY (CRY-m), of which gene is not found in the *Drosophila* genome, also acts as a negative regulator by forming a complex with PER and TIM to inhibit the transcriptional activity of CYC–CLK. *Apis* lost *tim* and *cry-d* from its genome and thereby possesses rather simplified clockwork. Negative regulators are shaded

under short days than in those reared under long days. By contrast, such differences were not detected in the anholocyclic (no photoperiodic) strain of the same species (Barberà et al. 2017). These distinct patterns of expression under long and short days suggest that photoperiodic information could be transformed into oscillation patterns to determine photoperiodic responses such as diapause. However, such photoperiodic difference is simply one aspect of circadian rhythmicity, rather than the photoperiodic regulation of diapause. Thus, their utility is limited.

Recently, more instructive studies involving genetic manipulation have been conducted to clarify the involvement of clock genes in the photoperiodic response of a diverse range of insect species in the orders Orthoptera (Goto and Nagata 2022; Sakamoto et al. 2009), Heteroptera (Ikeno et al. 2010; Kotwica-Rolinska et al. 2017; Tamai et al. 2019), Coleoptera (Zhu et al. 2019), Hymenoptera (Mukai and Goto 2016), Lepidoptera (Iiams et al. 2019; Ikeda et al. 2021; Mohamed et al. 2014), and Diptera (Meuti et al. 2015; Pavelka et al. 2003). These studies used species with all the diapause stages (embryonic, nymphal, larval, pupal, and adult diapauses) regulated by distinct endocrine cascades. Furthermore, these studies were conducted in long-day species (reproduce or develop under long days) and in a short-day species (reproduce or develop under short days) (Table S1).

Loss of function of *per,* mediated by genome editing technology, resulted not only in the disruption of the circadian rhythms during adult emergence and egg hatching but also in the disruption of the photoperiodic response in *B. mori*. The knockout adults failed to respond to short days and produced non-diapause eggs (Ikeda et al. 2019, 2021). Females of the *cry-m* knockout strains in the linden bug *Pyrrhocoris apterus* failed to enter diapause under any photoperiods, although a small portion of individuals entered diapause under much shorter day lengths (Kotwica-Rolinska et al. 2022b). The cabbage beetle, *Colaphellus bowringi,* enters diapause in response to long days and accumulates more lipid as an overwintering energy reserve. Knockdown of *per* and *tim* resulted in a reduction of the lipid content in diapause-destined individuals, which is a typical phenotype in non-diapause-destined individuals (Zhu et al. 2019). In *P. apterus*, *Clk* RNAi does not affect reproduction in males under long days. However, it destroys the ability of diapause males to switch to reproductive mode after the transfer to long days (Urbanová et al. 2016). These results strongly support the involvement of *Clk* in photoperiodic time measurement.

More instructive approaches have been adopted in some species. In the bean bug, *Riptortus pedestris*, the effects of RNAi targeted to *per*, *cry-m*, *cyc*, and *Clk* on the photoperiodic regulation of reproductive organ development were examined. Simultaneously, cuticle deposition rhythm was also observed as an output of the clock function (Ikeno et al. 2010, 2011a, b, c, 2013). The insect cuticle is thickened by the alternation of the deposition of chitin microfibrils in two different orientations (lamellate and non-lamellate layers), which is regulated by the circadian clock (Ikeno et al. 2010; Ito et al. 2008). RNAi targeted to *per*, *cry-m*, *cyc* and *Clk* arrested the clock and, thereby, produced a single layer, but the layers deposited were depending on which clock genes were downregulated. RNAi targeted to *per* and *cry-m* resulted in the deposition of a single non-lamellate layer, whereas that of *cyc* and *Clk* resulted in a single lamellate layer (Ikeno et al. 2010, 2011a, 2013) (Fig. 7). These results suggest that RNAi of *per* and *cry-m* and that of *cyc* and *Clk* arrested the clock at different phases. This agrees with the roles of these genes in the circadian clock; the former and the latter genes act as negative and positive regulators, respectively (Fig. 6). RNAi directed to *per* and *cry-m* and that directed to *cyc* and *Clk* also result in different responses in reproductive organ development. The former resulted in reproductive organ development (female ovary and male accessory gland) even under diapause-inducing short days, whereas the latter resulted in suppression of the development even under diapause-averting long days (Ikeno et al. 2010, 2011b, c, 2013) (Fig. 7). Distinct phenotypes induced by silencing negative and positive regulators are also observed in the photoperiodic regulation of lipid accumulation in *R. pedestris* and the photoperiodic ovarian development in *D. plexippus* (Iiams et al. 2019; Omura et al. 2016). These results suggest that the photoperiodic time measurement is a function of the circadian clock, which comprises the clock genes. They further imply the causal significance of light input and the circadian clock, i.e., the external coincidence model. In intact insects, the circadian clock regulates the oscillatory expression of a key gene (gene *x*) that governs the position of φ_i. Only under long-day conditions, φ_i is exposed to light and the light-activation of an unknown factor occurs, thereby eliciting a long-day response (Fig. 8). In RNAi of the negative elements, constitutive activation of the positive elements leads to a high level of *x* throughout the day and thereby, light activation of the factor occurs even under short days. By contrast, in RNAi of the positive elements, transcription of the gene *x* does not occur. Therefore, light activation of the factor never occurs irrespective of the photoperiodic conditions (Fig. 8) (Ikeno 2012). The model proposed here needs to be verified in future studies.

In *N. vitripennis*, *per* RNAi females failed to discriminate photoperiods and remained non-diapause producers even under short days (Mukai and Goto 2016) (Fig. 9). Interestingly, *per* RNAi females laid diapause-destined eggs in response to the low-temperature treatment (Mukai and Goto 2016) (Fig. 9). This indicates that *per* RNAi did not disrupt the maternal physiology that is directly involved in the production of diapause-destined eggs, however, it possibly affected photoperiodic time measurement. The photoperiodic time measurement of this species is satisfactorily assumed to be an internal coincidence (Saunders 1974). The RNAi results indicate that either dawn or dusk oscillators or both are comprised of *per*. *D. melanogaster* shows a distinct bimodal rhythm in its locomotor activity. These morning and evening peaks are regulated by morning (M) and evening (E) oscillators, respectively. Since the M and E oscillators track dawn and dusk, respectively, the phase angle between the two oscillators under different day lengths differs (Yoshii

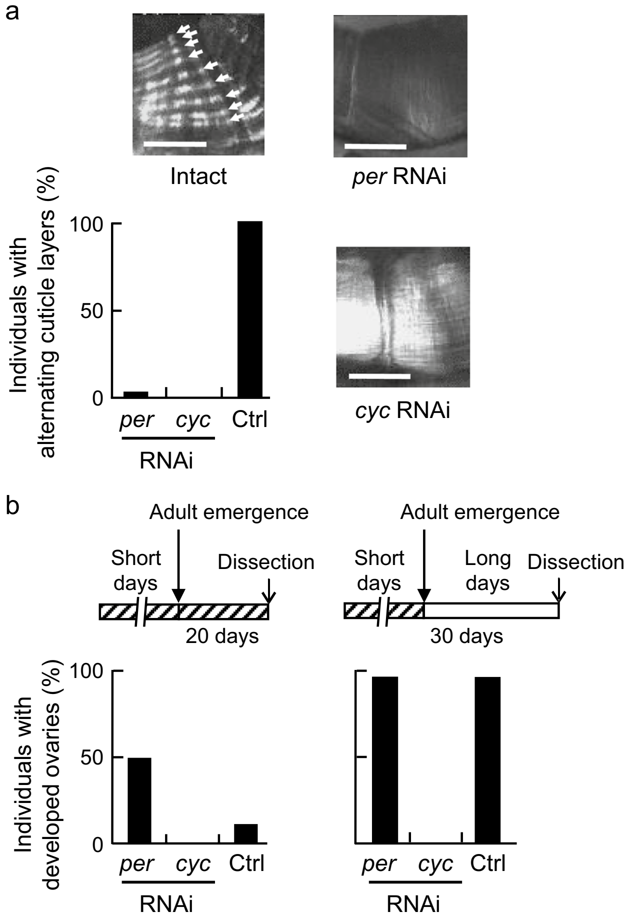


Fig. 7 Endocuticle and ovarian development in the bean bug *Riptortus pedestris*. RNA interference (RNAi) was performed by injecting double-stranded RNA on the day of adult emergence (Ikeno et al. 2010). **a** Cross-sections of the tibia in the hind leg of intact, *per* RNAi, and *cyc* RNAi insects 20 days after emergence. Alternating lamellate (arrows) and non-lamellate layers of the endocuticle are observed in intact insects. However, knockdown of *per* and *cyc* disrupted the production of alternating layers and produced single, thickened non-lamellate and lamellate layers, respectively. Scale bar, 25 μm. **b** Effects of *per* and *cyc* RNAi on ovarian development. The experimental schedules are shown as horizontal hatched and open bars (short- and long-day conditions, respectively). *per* RNAi females induced ovarian development, whereas *cyc* RNAi females suppressed it, irrespective of photoperiod. From Ikeno et al. (2010)

et al. 2012). M oscillators are considered to reside in the four small lateral ventral neurons (s-LNvs) expressing a neuropeptide, pigment-dispersing factor (PDF), and E oscillators in the 5th s-LNv and the 3–4 dorsal lateral neurons (LNds) (Grima et al. 2004; Stoleru et al. 2004). These cells are the primary candidates for the dawn and dusk oscillators in the internal coincidence model in *N. vitripennis*. In *D. melanogaster*, CRY-d in the E oscillators limits their ability to track dusk during long days, whereas light signaling from the visual system increases this ability. CRY-d signaling dampens PDP1 oscillation, whereas signaling from the visual system increases these amplitudes. Thus, light inputs from CRY-d and the visual system have different effects on photoperiodic locomotor activity (Kistenpfennig et al. 2018). However, *N. vitripennis* does not possess *cry-d* in its genome and opsins are its only photopigments. The photic input pathway, the location of PER-expressing clock neurons in the brain, their networks, and their role as the M and E oscillators in *N. vitripennis* must be investigated in future studies.

Discrepancies of the roles of clock genes in photoperiodism

Although clock genes play a crucial role in photoperiodic time measurement, striking discrepancies in the photoperiodic phenotypes after gene silencing are also observed, as shown in Table S1. For example, knockdown of *per* resulted in a long-day response in *R. pedestris*, *A. pernyi*, *C. pipiens*, *N. vitripennis*, and *B. mori*, whereas it resulted in an intermediate response between long and short days in *M. siamensis* (Ikeda et al. 2021; Ikeno et al. 2010, 2011b; Meuti et al. 2015; Mohamed et al. 2014; Mukai and Goto 2016; Omura et al. 2016; Sakamoto et al. 2009). RNAi targeted to *cry-m* induced a long-day response in *R. pedestris* and *C. pipiens*, whereas it induced a short-day response in *M. siamensis* (Ikeno et al. 2011c; Meuti et al. 2015; Ueda et al. 2018). In *P. apterus*, RNAi targeted to *cry-m* induced a weak short-day response in males, but null mutants of the gene induced a strong long-day response in females (Kotwica-Rolinska et al. 2022b; Urbanová et al. 2016). The short-day response was also induced by loss of function of *cry-m* in *D. plexippus* (Iiams et al. 2019). RNAi targeted to *Clk* induced a long-day response in *D. nigrofasciatus*, whereas it induced a short-day response in *R. pedestris* and *P. apterus* (Goto and Nagata 2022; Ikeno et al. 2013; Kotwica-Rolinska et al. 2017; Urbanová et al. 2016). In addition, distinct phenotypes induced by silencing negative and positive regulators were observed in *R. pedestris* and *D. plexippus*, but not in *P. apterus*, in which RNAi targeted to *cry-m*, *Clk*, and *cyc* produced the short-day response (Iiams et al. 2019; Ikeno et al. 2010, 2011b, c, 2013; Kotwica-Rolinska et al. 2017; Omura et al. 2016; Urbanová et al. 2016).

Although the reasons behind these discrepancies are largely unknown, several possibilities can be proposed. It could be based on the difference in photoperiodic time measurement among insects. Photoperiodic time measurement has been extensively studied in a limited number of species such as *T. urticae*, *M. viciae, Pectinophora gossypiella*, *Ostrinia nubilalis*, *Pieris* spp., *Mamestra brassicae*, *N. vitripennis, Sarcophaga* spp., and *Calliphora vicina* (Saunders 2002). On the contrary, the recent advance in our knowledge is based on species including *M. siamensis*, *R.*

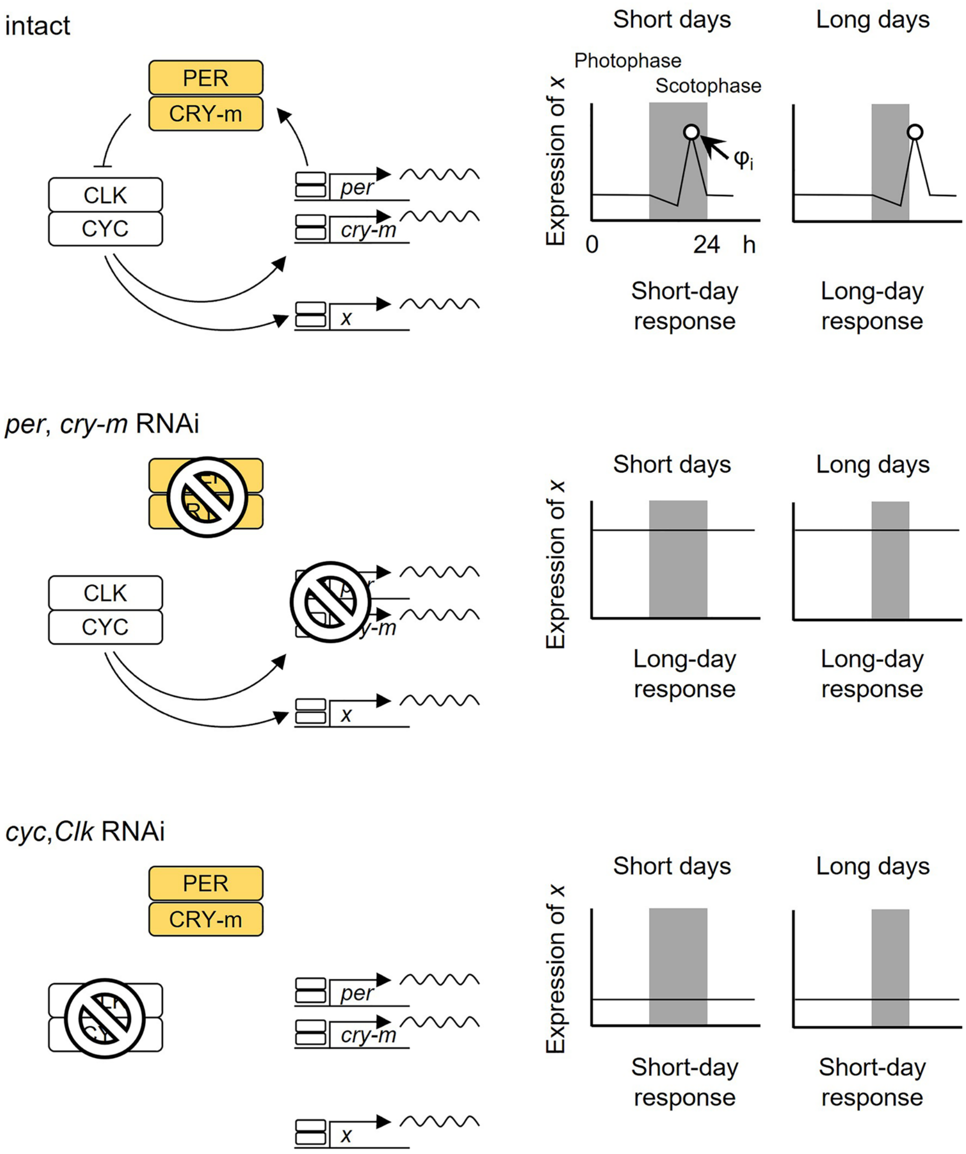


Fig. 8 Assumed processes in photoperiodic time measurement in intact and RNAi insects (Ikeno 2012). In intact insects, the negative feedback loop produces the oscillatory expression of thousands of clock-controlled genes. Gene *x* controlling the position of the photoinducible phase (φ_i), also shows oscillatory expression as one of the clock-controlled genes. Under short days, φ_i is in the dark phase, eliciting a short-day response; under long days, φ_i is in the light phase, eliciting a long-day response. In *per* and *cry-m* RNAi insects, the circadian clock remains at the phase in which transcription of the clock-controlled genes, including gene *x*, is activated. Constitutive upregulation of gene *x* expression may elicit a long-day response irrespective of photoperiods. By contrast, in *cyc* and *Clk* RNAi insects, the circadian clock remains at the phase in which transcription of the clock-controlled genes is inactivated. Constitutive downregulation of gene *x* may elicit a short-day response irrespective of photoperiods. Adapted from Ikeno (2012)

pedestris, *P. apterus*, and *C. pipiens* (Table S1), in which photoperiodic time measurement has rarely been investigated. Among these species, the circadian clock may be involved in photoperiodic time measurement differently. Divergence of the circadian clock machinery and their functions among insects may also cause discrepancies, at least partly (Kotwica-Rolinska et al. 2022a; Tomioka and Matsumoto 2019). Furthermore, the discrepancies may be caused by the malfunction of the peripheral circadian clock that is also involved in a downstream diapause program, or by the pleiotropic effect of the clock gene in the diapause programme (Emerson et al. 2009a). In the gut of *P. apterus*, transcript of *cry-m* and an isoform transcript of *Pdp1* (*Pdp-1*$_{iso1}$) are inversely regulated under diapause and reproductive conditions; the former remains high in diapausing but low in reproductive females, while the latter remains high in reproductive but low in diapausing females, with no daily oscillation. Their expression is indispensable for diapause-/non-diapause-specific gene expression in the gut. Notably, the expression of *cry-m* and *Pdp1*$_{iso}$ is controlled by *Clk* and *cyc,* as well as juvenile hormone, which directly determines the diapause/non-diapause phenotype. These results suggest a noncircadian function downstream of photoperiodic time measurement (Bajgar et al. 2013a, b). In *D. nigrofasciatus*, *Clk* is thought to be involved not only in photoperiodic time measurement but also in the production of diapause eggs (Goto and Nagata 2022). Females of this species deposit non-diapause eggs under long days, whereas they deposit diapause eggs under short days. When female crickets were reared under short days and transferred to long days, they gradually increased the number of non-diapause eggs while reducing that of diapause eggs. *Clk* RNAi induces

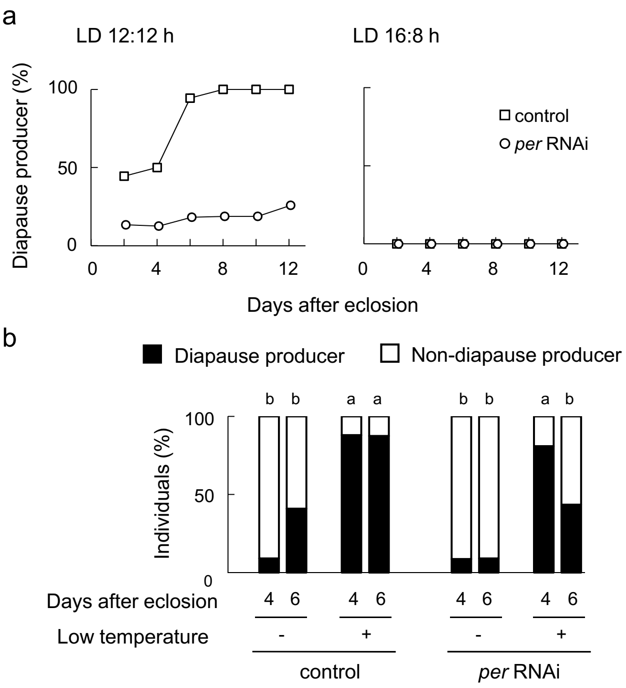


Fig. 9 Effects of *per* RNAi on the proportion of diapause producers under short and long days (**a**) and after low-temperature treatment (**b**) in *Nasonia vitripennis* (Mukai and Goto 2016). **a** Temporal changes in the proportion of diapause producers. The pupae that had been reared under long-day conditions (LD 16:8 h) were injected with double-stranded RNA (dsRNA) of *period* (*per*) or that of the control gene (*β-lactamase*). They were maintained under the same conditions or transferred to short-day conditions (LD 12:12 h). Newly emerged adults were mass-cultured for 2 days to allow them to mate, and females were reared individually. Flesh fly pupae were supplied as a host to each female and the diapause status of the wasp offspring was determined. Note that *per* RNAi females failed to be diapause producers in response to short days. **b** Low-temperature induction of diapause producers. The pupae were similarly treated with the dsRNA. Thereafter, they were kept under short-day conditions. One day after adult emergence, some wasps were exposed to 10 °C for 3 days. After treatment, wasps were returned to their original conditions. Flesh fly pupae were supplied on days 4 and 6 to assess their status as the diapause or non-diapause producers. Note that control insects transformed into diapause producers in response to low-temperature exposure on days 4 and 6. *per* RNAi females also responded to the low temperature and transformed into diapause producers on day 4. However, the proportion decreased on day 6, due to *per* silencing. From Mukai and Goto (2016)

long-day response even under short days (a gradual increment of the proportion of non-diapause eggs), suggesting the involvement of *Clk* in photoperiodic time measurement (Goto and Nagata 2022). Interestingly, *Clk* RNAi enabled females to deposit non-diapause eggs immediately irrespective of the photoperiod. This immediate effect cannot be adequately explained in terms of the dysfunction of a circadian clock involved in photoperiodic time measurement. This immediate response indicates the involvement of *Clk* in the production of diapause-type eggs (Goto and Nagata 2022). However, the processes that are regulated by *Clk* and whether *Clk* itself or a peripheral circadian clock including *Clk* is involved in the process have not been elucidated. In *Drosophila triauraria*, crossing between a northern population with a clear photoperiodic response and southern strains with no photoperiodic ability revealed that the additive association of *tim* and *cry-d* alleles affected diapause incidence (Yamada and Yamamoto 2011). No interaction between these alleles but their additive association suggests that these genes are independently involved in the diapause programme, i.e., noncircadian function.

Circadian outputs

Circadian output elements on insect photoperiodism are still largely unknown, but some clues are evident. Because this topic is beyond the scope of this review, I have described it very briefly. PDF is one of the crucial circadian output neuropeptides regulating circadian locomotor behavior in *D. melanogaster* and other insect species (Shafer and Yao 2014). Its significance in the photoperiodic response is proposed in *D. melanogaster*, *C. pipiens*, and *P. stali*, but was denied in *R. pedestris* (Hasebe et al. 2022; Ikeno et al. 2014; Meuti et al. 2015; Nagy et al. 2019). In *R. pedestris*, a significance of glutamate was proposed (Des Marteaux et al. 2022). Interestingly, in *P. apterus*, the loss-of-function mutants of *pdf* failed to enter diapause under a short-day condition, but they were able to enter diapause under much shorter day lengths; i.e., a 3-h shortening of the critical day length (CDL) (Kotwica-Rolinska et al. 2022b). The CDL is the length of the light fraction of the light-dark cycle that separates a strong long-day response from a strong short-day response in the photoperiodic response curve. These results indicate that PDF is involved in the photoperiod-dependent diapause induction but additional clock-regulated factors are also involved in the response. In *D. melanogaster*, the short neuropeptide F (sNPF) similarly regulates its dormancy as PDF (Nagy et al. 2019).

In the Chinese oak moth, *Antheraea pernyi* and the cabbage army moth, *Mamestra brassicae*, the involvement of melatonin, dopamine, and serotonin was evident (Mohamed et al. 2014; Noguchi and Hayakawa 1997; Wang et al. 2013, 2015a, 2015b). Further extensive studies on output molecules are awaited.

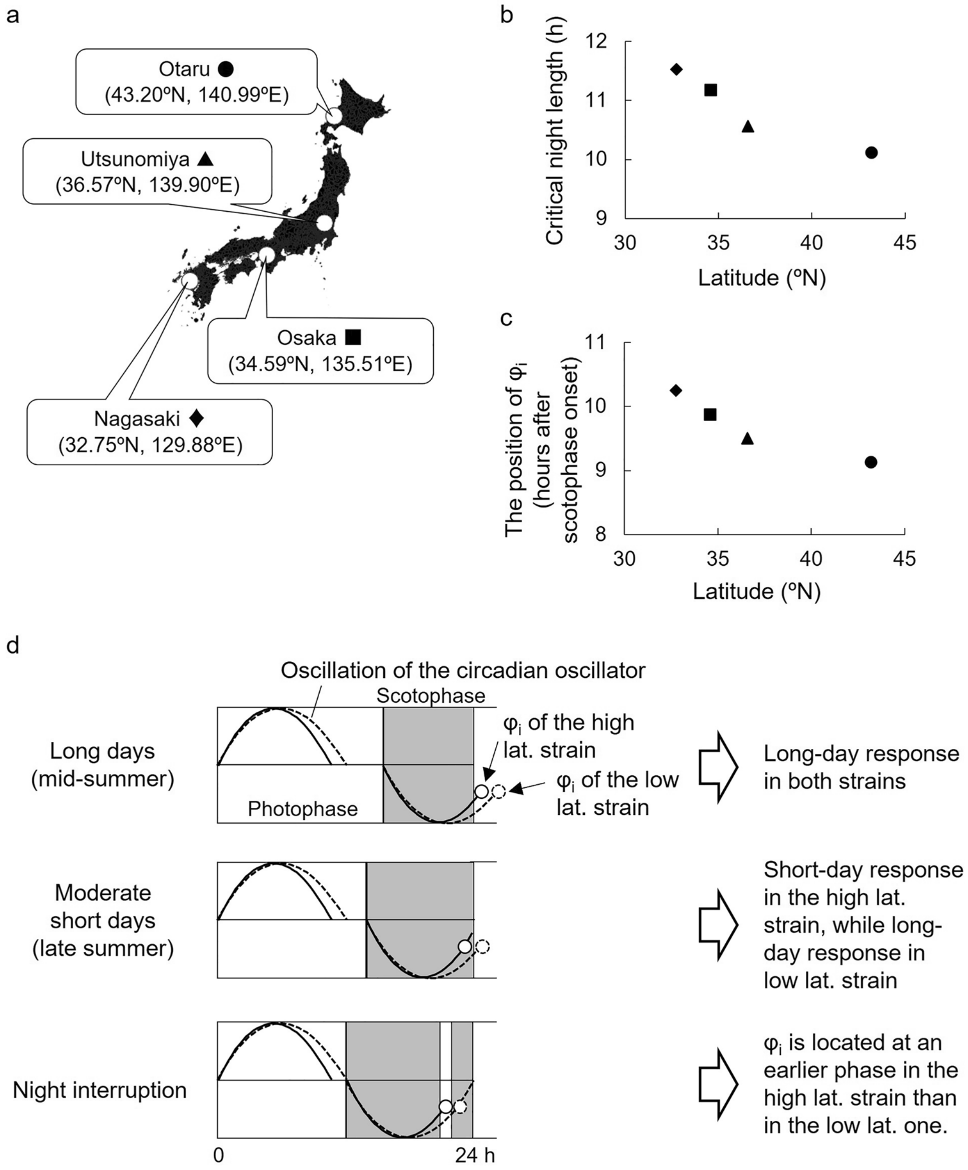


Fig. 10 Latitudinal cline of the critical night length and the positions of the photoinducible phase (φ_i) in *Sarcophaga similis* (Yamaguchi and Goto 2019). **a** Latitudes and longitudes of the sites where the geographic strains originated. **b** The relationship between the latitudes where the strains originated and their critical night lengths for diapause induction. Flies were reared under various photoperiodic conditions and the critical night lengths were calculated from diapause incidences. **c** The relationship between the latitudes where strains originated and the positions of φ_i. Mature larvae that had been reared under LD = 11.5:12.5 h were placed on wet wood chips (water treatment) and exposed to LDLD 10:*x*:2:(12-*x*) h, where *x* ranged from 8.5 to 11. The position of φ_i was defined as the position where a light pulse averted diapause most effectively. **d** Schemes of the relationship between the critical night lengths and the positions of φ_i under the assumption of the external coincidence model. The difference in the critical night lengths can be explained by the difference in the positions of φ_i. From Yamaguchi and Goto (2019)

Clock genes and local adaptations

The time of diapause entry is determined by the CDL. Although the term CDL is widely used in the literature, most insects measure the "night length", not the "day length", and therefore, the term "critical night length (CNL)" is more appropriate (Saunders 2013). The CNL is the difference between 24 h and the CDL. Latitudinal cline provides an expansive view of the adaptation of insects to spatial environmental heterogeneity. The latitudinal cline with shorter CNL in strains from higher latitudes is widely observed in various species (Hut et al. 2013). Moreover, the rapid evolution in changing CNL has been measured or inferred in the field after the colonization of several invasive species (Bean et al. 2012; Gomi 2007; Tanaka et al. 2015; Urbanski et al. 2012). The significance of the latitudinal cline in CNL can be explained in terms of ecological aspects. Nights are shorter at higher latitudes between the spring and autumn equinoxes, but the climate is colder and the summer ends earlier than in areas at lower latitudes. Therefore, insects at higher latitudes likely enter diapause earlier by responding to the shorter night length (Hut et al. 2013).

S. similis, in which time measurement occurs via external coincidence, also shows a clear latitudinal cline in CNL in the photoperiodic induction of diapause; a strain from higher latitudes has a shorter CNL than a strain from lower latitudes (Fig. 10). The phase positions of the φ_i, which can be verified by night interruption photoperiods, also showed a clear latitudinal cline; a strain from a higher latitude possesses a φ_i at an earlier phase in the scotophase than a strain from a lower latitude (Fig. 10).

These results indicate that the qualitatively different photoperiodic time measurement systems among geographic strains causally induce the latitudinal difference in the CNLs (Fig. 10) (Yamaguchi and Goto 2019). The difference in the φ_i position might be from the difference in the circadian clock and needs to be further verified.

N. vitripennis, in which time measurement is an internal coincidence, also shows a clear latitudinal cline in the CNL (Paolucci et al. 2013). Interestingly, the free-running period of the circadian clock-regulated locomotor activity rhythm is longer in strains from higher latitudes than in those from lower latitudes; i.e., the former has a slower clock than the latter (Paolucci et al. 2019). In addition, the quantitative trait locus (QTL) analysis using two geographic strains revealed that two genomic regions, which contain *per*, *cyc* and *cry-m*, are associated with photoperiodic diapause induction. Moreover, a clinal distribution of two main haplotypes of *per* correlates with the latitudinal cline for diapause induction (Paolucci et al. 2016), and oscillation patterns of *per*, *cry-m*, *cyc*, and *Clk* are distinct between geographic strains (Dalla Benetta et al. 2019). A latitudinal cline of the circadian clock elements or their regulatory elements may causally produce the circadian behavioral phenotype and the photoperiodic response in *N. vitripennis*. A causal relationship between the latitudinal clines of *tim* alleles and the photoperiodic response is also reported in *D. melanogaster* (Sandrelli et al. 2007; Tauber et al. 2007).

Recent genomic studies have also detected an association between the clock genes and the photoperiodic induction of diapause. A genome-wide scan between two populations of the butterfly *Pararge aegeria* that differ strongly in their diapause induction thresholds identified four genes present in two chromosomal regions, one with the gene *per*, and the other with genes *kinesin*, *carnitine O-acetyltransferase*, and *tim*. The frequency of the loci also showed a clear latitudinal cline among the five geographic strains (Pruisscher et al. 2018). A further population genomic approach identified candidate genes showing signs of divergent selection potentially associated with population differences (diapause thresholds and voltinism) among nine Scandinavian populations of *P. aegeria*. The candidate genes include some components of the circadian clock including *tim*, *per*, *cry-d*, and *cwo* (Lindestad et al. 2022). A comparison of two populations of the butterfly *Pieris napi* that differ in the propensity to enter diapause revealed a few genomic regions that showed a high divergence between populations. Genotyping diapausing and directly developing siblings (non-diapause) from backcrosses of these populations identified that a single genomic region, which contained the three major clock genes *cyc, Clk* and *per*, is associated with diapause induction (Pruisscher et al. 2021).

Conclusion

Figure 11 summarizes our current knowledge of the physiological modules and molecular elements regulating insect photoperiodism. Retinal and/or extraretinal photoreceptors are used for photoreception. Opsins in the retinal or extraretinal photoreceptors and CRY-d in the brain may play a role in photoperiodic regulation. However, only one study has directly confirmed the role of opsins in photoperiodism. Different opsin genes may play different roles. The possible involvement of CRY-d also needs to be further studied. The mechanism of transfer of photic information to photoperiodic time measurement and circadian clocks is still unknown. *S. similis*, in which photoperiods are assessed via external coincidence, may use distinct photoreceptors through distinct neural pathways. *N. vitripennis*, in which photoperiods are assessed via internal coincidence, may use opsins in the retinal or extraretinal photoreceptor to set the phase of circadian oscillators.

Clock genes are causally involved in photoperiodic time measurement, but they also play a crucial role in other processes downstream of photoperiodic time measurement. The role of each clock gene has to be verified to understand how the clock is involved in photoperiodic time measurement in each species. Although classic physiological studies have established photoperiodic time measurement models, little information is available on their molecular elements. The molecular dissection of φ_i in the external coincidence model and that of the active phases in the internal coincidence model need to be elucidated in future studies. The distinct photoperiodic response observed in local populations may provide us with some clues. Several genomic

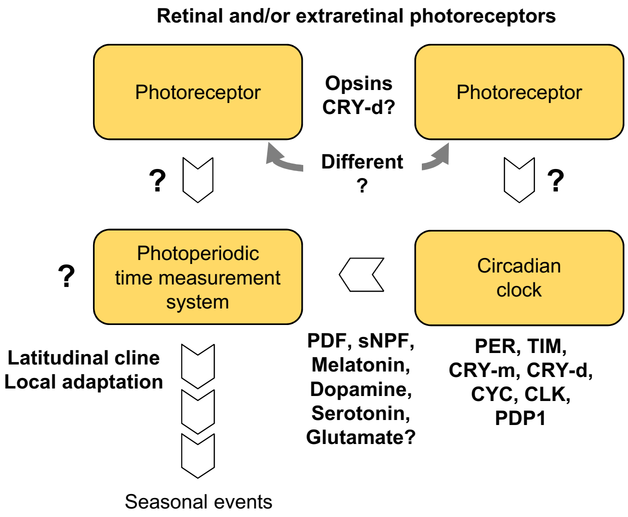


Fig. 11 Current knowledge of the physiological modules and molecular elements involved in photoperiodism in various insect species. For further explanation, refer to the main text

studies revealed the link between diapause characteristics and clock genes. In *S. similis*, a latitudinal cline in the CNL was linked with the qualitative difference in photoperiodic time measurement and/or circadian clock. Although we still do not know how their photoperiodic time measurements are different, the significance of *per* is also proposed in a latitudinal cline in *Nasonia*. Local populations possess a common tool kit, but the selection pressure has favored some alleles producing different responses. It is of great interest to see how the expressions or the functions of the genes detected are different among populations. This may be the first step for the molecular dissection of photoperiodic time measurement. This also clarifies the molecular elements that govern local adaptation.

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Declarations

Conflict of interest The authors declare no competing interests.

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