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REVIEW

Circadian rhythms of insect pheromone titer, calling, emission, and response: a review

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Abstract

Many insect species have circadian rhythms of pheromone production/titer, calling, emission, and response that are involved in intraspecific communication and impact pest management practices. Rhythms of pheromone biosynthesis, most studied in moths affecting forestry and agriculture, contribute to a periodicity of pheromone concentration or titer within glands or hemolymph. Calling rhythms by the pheromone-emitting sex are physical movements (pumping, vibrating wings) that aid in release and dispersion of the volatile pheromone components attractive to the opposite conspecific sex or both sexes. Circadian rhythms of emission of pheromone also occur as a result of an interaction between calling and the titer of pheromone available for release. Responding individuals usually show a coincidental rhythm of dispersal flight while seeking pheromone plumes in which, by orienting upwind, the insects find mates or food resources. However, some species begin searching an hour or more before the emitting sex initiates calling and emission, which benefits mass trapping control programs because the baited traps do not compete initially with natural pheromone sources. In our review, data of daily rhythms of moths and other insects were extracted from the literature by screen capture software to calculate mean time of activity and standard deviation and fit to normal curves. These methods are illustrated for various insects and as a basis for discussion of interactions of pheromonal circadian rhythms of the well-studied gypsy moth *Lymantria dispar*, spruce budworm moth *Choristoneura fumiferana*, turnip moth *Agrotis segetum*, and cabbage looper moth *Trichoplusia ni*. The various circadian rhythms are discussed in relation to application of species-specific sex and aggregation pheromones for benign biological control and management of pest insects.

Keywords Diel rhythms · Scotophase · Photophase · Insect communication · Calling · Pheromone titer · Pheromone emission · Photoperiod · Zeitgeber

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Key messages

- Pheromone production/titer, calling, emission, and response exhibit circadian rhythms affecting insect communication.
- Graphical data on insect circadian rhythms were analyzed by computer giving mean ± SD for fitting normal curves and quantitative evaluation.
- Knowledge of rhythms of pheromone emission and response are important for understanding insect mating systems and effective pest management.
- Pests where response begins before emission are most favorable for mass trapping control.

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Introduction

Circadian rhythms are innate biological rhythms of behavior or physiology occurring repeatedly every 24 h. In a broad sense, circadian just means about a day. In nature, the cycles are synchronized by exogenous environmental cues known as zeitgebers (German for time-givers). While temperature and humidity can act as zeitgebers, they can be affected by weather and vegetation and therefore are not as reliable as light intensity changes at dusk or dawn (Brady 1979; Cloudsley-Thompson 1980; Fleissner and Fleissner 2002). Strictly, circadian rhythms once entrained by several natural cycles of light:dark (L:D) must then repeat every day under constant light or dark under artificial conditions in the laboratory. Biological rhythms where there is as yet a lack of evidence of innate periodicity are termed diel. However, in cases where a diel rhythm has been reported, further experiments under constant light or dark for over 24 h have nearly always found that the periodicities continue several cycles and are in fact circadian rhythms. In nocturnal animals, most circadian rhythms are re-set each day by lights off (sunset as zeitgeber), and a specific rhythm becomes longer than a 24-h day in constant light, but shorter than a day in constant dark. In diurnal insects, on the other hand, circadian rhythms are usually re-set by lights on (sunrise is zeitgeber) while under constant light their rhythm becomes shorter than a day, but longer than a day in constant dark (Aschoff 1969; Cloudsley-Thompson 1980; Fleissner and Fleissner 2002). The zeitgebers for nocturnal and diurnal animals mentioned above and the free-running rhythms in constant light or dark have been called Aschoff's rule. However, Sower et al. (1971a) found evidence of a zeitgeber for a nocturnal insect that is contrary to Aschoff's rule. They found that female cabbage loopers *Trichoplusia ni* have a calling rhythm peak that occurs about 20.4 h after sunrise (lights on zeitgeber) regardless of L:D photoperiod ranging from 15L:9D to 9L:15D. Most research on circadian rhythms involving pheromones have not had the goal of determining the zeitgeber and effects of different L:D photoperiods, although some studies will be considered here. The main goal has rather been describing the time period when the insects were calling (body movements such as pumping the abdomen), emitting pheromone, or responding upwind so that this knowledge could be applied in pest management.

Numerous studies have found that the natural rhythms are modified in onset and length by environmental factors, foremost by changes from dark to light (morning) or light to dark (evening). In addition, different temperatures have been shown to modify pheromonal rhythms in onset and length (Sower et al. 1971a; Gorsuch et al. 1975; Bollinger et al. 1977; Baker and Cardé 1979; Castrovillo and Cardé 1979; Alford and Hammond 1982; Haynes and Birch 1984; Delisle and McNeil 1987; Gerber and Howlader 1987; Delisle and Royer 1994), but the modifications in the rhythms were relatively small over the usual temperature ranges where flight and mating occur most frequently (18 to 32 °C). Large changes in humidity had almost no effect on rhythms (Webster and Cardé 1982a), although low humidity and desiccation weakened European corn borer moths so that females called later in the night and for a shorter time (Royer and McNeil 1991). Very high-intensity light in the laboratory can also disrupt circadian rhythms (Fleissner and Fleissner 2002), but this is unnatural and not applicable to applied work. It is well known that some insect pests feeding on crops have high populations over several months each year due to multiple generations, while other insects have a relatively short flight activity period each year. The effects of seasonal photoperiod and temperature changes on pheromonal circadian rhythms are likely significant for insects that reproduce over an extended period, but less important for insects that fly over a short period each year under less variable conditions.

Circadian rhythms have likely evolved because they synchronize daily environmental changes (light and temperature) with activities that increase the reproductive fitness of individuals of each species, depending on their biology. Circadian rhythms are thus different in onset, peak, and duration with respect to photophase or scotophase for each species that occupy different niches. There can be several rhythms operating simultaneously with different periods and synchronies occurring at different times of the day, for example, emergence, feeding, calling, mating, oviposition, and anemotactic response rhythms. As mentioned above, studies in the laboratory have shown that varying environmental factors such as ratios of light:dark durations over 24 h can affect onset and lengths of circadian rhythms. Although the majority of laboratory studies attempt to replicate natural photoperiods and temperatures, some studies may not reflect the photoperiods and rhythms in nature. However, studies in the field such as observations of flying individuals responding to a source of pheromone are certainly under natural photoperiods and temperatures.

Probably all insect species have several different diel or circadian rhythms of various types, for example, emergence (Byers 1983; Kumara et al. 2015), feeding (Krupke et al. 2006), locomotion/flight (Bento et al. 2001; Jones and Gubbins 1979; Byers and Löfqvist 1989; Silvegren et al. 2005), and oviposition (Byers 1987; Pashley et al. 1992; Wang et al. 2002), that in some ways affect directly or indirectly pheromonal communication. This review will concentrate on pheromone-related rhythms of pheromone component titer in glands or bodies, calling (gland eversion, pumping, or wing flapping movements), emission of attractive sex and aggregation pheromones, similar rhythms of response of the attracted conspecifics, and mating (largely coinciding with calling, emission, and response). Because most studies have been on important forest and agricultural pest insects, we will discuss the natural biology in relation to applications in pest management. It is also important to note that studies of all insect circadian rhythms including those relating to pheromone communication are important in countering invasive species due to climate changes and global commerce (Hulme 2009). Knowledge of circadian rhythms of pheromone emission and response is important to (1) pheromone identification, (2) daily timing of control treatments such as insecticides when insects are most vulnerable, and (3) circadian application of pheromone dispensing to save costly pheromone and increase longevity. For example, use of automatic puffers (battery operated devices that dispense pheromone) that release pheromone during response periods can save costs of pheromone in mating disruption (McGhee et al. 2016).

Most studies on pheromone circadian rhythms of insects involve pests of food and fiber which drives the economics of entomological studies. For practical purposes, whether the reported rhythms of activity are diel or circadian does not matter much, only that the activity rhythms are consistent in order to design reliable management methods. Groot (2014) reviewed circadian rhythms of sexual pheromone activities in moths, which included female pheromone calling (usually the percentage calling of a sample of individuals) observed repeatedly over time, as well as circadian changes in pheromone quantity in glands (titer), and male responses (percentage of a group orienting) toward a source of pheromone, or numbers captured in the field. In Groot's review, graphs and data of circadian pheromone rhythms in the literature were transformed and shown in three increasing activity intensities of light, medium, and dark shades. While some earlier studies were quantitative and calculated a mean or median time of the rhythms entrained to a certain L:D photoperiod, very few studies have calculated a weighted mean time of peak activity and breadth as described by a standard deviation (SD) (Kochansky et al. 1977; Löfstedt et al. 1982; Byers 1987). Thus, we decided to model the reported pheromonal rhythms by a normal curve with a calculated mean and SD and a scaling factor, as was done for mean height and SD of vertical flight distributions of insects (Byers 2011).

We analyzed a database of 224 articles on pheromone-related circadian rhythms of insects (Supplementary information) and found moths (Lepidoptera) were represented most (152 papers, 67.9%) of insects. Of the Lepidoptera, most research has been done on the moth family Noctuidae (64 articles, 28.6%) followed by Tortricidae (21, 9.4%), Pyralidae (15, 6.7%), and Erebidae (Lymantriidae) (15, 6.7%) (Supplementary Table S1). Beetles (Coleoptera) were covered by 19 articles (8.5%), followed closely by sucking insects (Hemiptera) with 18 articles (8.0%), and flies (Diptera) with 14 articles (6.3%). There have been fewer articles on ants, bees, and wasps of order Hymenoptera with six articles (2.7%) which are the same as for cockroaches in order Dictyoptera, two articles on Ixodida (ticks), and only one article each on Trichoptera (caddisflies), Acarina (mites), and Araneidae (spiders). The orders with the most number of families:genera are Lepidoptera (18:62), Coleoptera (7:18), Hemiptera (7:16), Diptera (5:8), Hymenoptera (4:4), and Dictyoptera (4:5) (Table S1).

The database of articles was also examined for pheromone-related keywords that describe study areas regarding circadian-like rhythms. Keywords such as (a) production/biosynthesis, (b) titre (titer), (c) calling, (d) emission/release rate, and (e) response that are circadian (Table S2, supplementary information). In reviewing the literature, it became apparent that some keywords for behaviors were used improperly; for example, emission was used in titles where calling was actually measured. This problem is now less common with the advent of air collection of volatiles on absorbents and sensitive chemical analysis by gas chromatography-mass spectrometry (GC–MS). Therefore, one objective was to discuss the commonly used keywords and their interactions to aid understanding and development of improved control methods of pest management that utilize pheromones.

Rhythms of pheromone production

Pheromone titer in the body/gland may not be well correlated with either calling or pheromone production because of pheromone storage within the insect prior to rapid emission during calling (Fig. 1). Pheromone production or biosynthesis has been used in titles of articles in which only pheromone titer was determined (e.g., Gueldner and Wiygul 1987; Babilis and Mazomenos 1992; Kamimura and Tatsuki 1993, 1994; Foster and Roelofs 1994; Guldemond et al. 1994; Rafaeli and Klein 1994; Choi et al. 1998; Delisle et al. 1999; Foster 2000; Dong and Du 2001; Xiang et al.

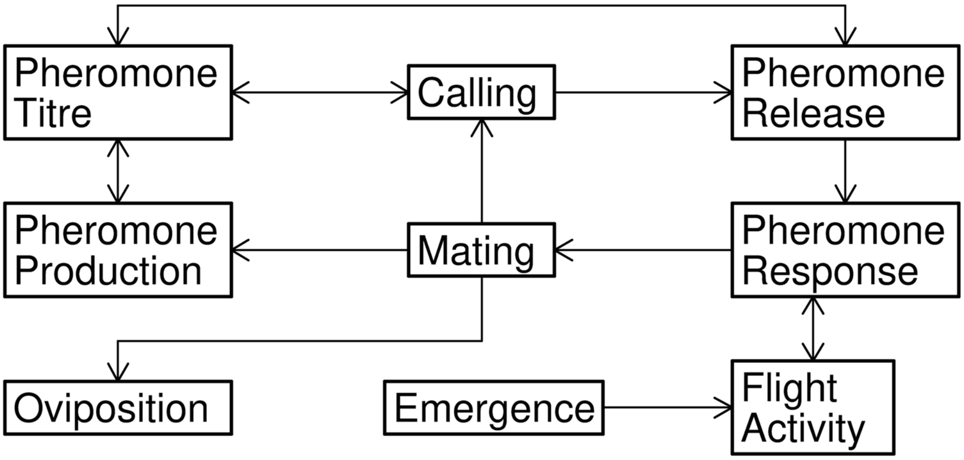

Fig. 1 Diagram of relationships between various circadian rhythms (boxes) affecting insect communication with pheromones

2010). Emission of pheromone during calling may outpace biosynthesis such that pheromone titer of female glands of omnivorous leafroller moths declined about 80% during the first half of a 6-h calling period in the scotophase (Webster and Cardé 1982b). Similarly, 10% of a group of female cabbage looper moths were calling at the onset of scotophase which increased linearly to 80% calling over 8 h, but at the same time pheromone emission increased about 50% over the first 4 h of scotophase and the pheromone titer of glands decreased from 1000 to about 300 ng per gland (Hunt and Haynes 1990). These results could mean that pheromone production declined during the scotophase, but more likely the emissions depleted titer faster than its replenishment. In contrast, over the first hour of scotophase female corn earworm moths had a fivefold increase in pheromone titer while calling increased concomitantly (Raina et al. 1991). An increase in pheromone gland titer during an increase in emission and calling during the day was also the case for gypsy moths until dusk when both emission and titer declined during the night (Charlton and Cardé 1982). Neither an increase or decline in titer of sex pheromone occurred in glands of virgin female peach twig borer moths during 24-h period even though there was a sharp 3-h emission in the morning (Schlamp et al. 2006).

Rhythms of pheromone titer

Many of the 224 studies we analyzed involved pheromone titer (Fig. 1) within the entire body, a major part such as abdomen, or most often a specific gland of an insect. In these studies, the amounts of pheromone components extracted from the tissues of the whole body or of dissected glands were quantified usually by GC or GC–MS at specific times during the day. The pheromone titer has been shown to vary on a daily rhythm in 52 articles (23.2%) (e.g., Webster and Cardé 1982b; Raina et al. 1986; Delisle and McNeil 1987; Dunkelblum et al. 1987; Schal et al. 1987; Ramaswamy et al. 1988; Ono et al. 1990; Heath et al. 1991; Giebultowicz et al. 1992; Tang et al. 1992; Delisle and Royer 1994; Rafaeli and Klein 1994; Del Mazo-Cancino et al. 2004; Mazor and Dunkelblum 2005; Liu et al. 2013; Lu et al. 2017).

Rhythms of pheromone calling

The most common topic with 82 papers (36.6%) is about the timing, duration, and percentage of a group of individuals exhibiting so-called calling behaviors (Fig. 1), represented mostly by studies on female moths with 66 publications (28.9%). Calling is the behavior of the emitting sex that appears to facilitate release and dispersion of the volatile molecules of the pheromone components away from the insect (Sower et al. 1971b). This usually involves pumping and exposure of glands in the abdomen and wing fanning in female moths or other exposure of their glands that can be discerned by the investigator. In moths this behavior is readily observed in females that exhibit a circadian-like rhythm of calling to males (e.g., Cardé 1974; Gorsuch et al. 1975; Baker and Cardé 1979; Castrovillo and Cardé 1979; Kaneko 1986; Konno 1986; Delisle and McNeil 1987; Gerber and Howlader 1987; Kou and Chow 1987; Itagaki and Conner 1988; Ramaswamy et al. 1988; Raina et al. 1991; Kamimura and Tatsuki 1994; Mozuraitis et al. 1997; Dong and Du 2001; Castrejón-Gómez 2010; Xiang et al. 2010; Sadek et al. 2012; Foster et al. 2020). In some moth species, males may release a sex pheromone, different from conspecific females, that attracts the latter from a short range of several centimeters and stimulates them to allow mounting and copulation by the male (e.g., Bento et al. 2001; Levi-Zada et al. 2014a). Circadian rhythms of calling have been investigated in only a few studies of species in order Coleoptera (Hammack and Burkholder 1976; Cross et al. 1977; Ma and Burkholder 1978; Leal et al. 1993), Diptera (Hendrichs and Hendrichs 1990; Epsky and Heath 1993; Quilici et al. 2002), and Hemiptera (Eisenbach and Mittler 1980; Thieme and Dixon 1996; Margaritopoulos et al. 2007; Stewart-Jones et al. 2007). However, calling may not be apparent in many insects (and thus not investigated) because either the observer is not aware of the specific behavior or there may be no movement and merely a release of pheromone (McNeil and Brodeur 1995).

Calling is usually observed for a cohort of insects, while individuals are usually not observed continuously. Thus, it is not known whether the 50% calling snapshot of a group of female moths at a particular hour is from half the individuals calling briefly multiple times during the night or the same individuals calling a few times for much longer periods. Multiple brief calling periods would likely make pheromone plumes shorter and might be an advantage at higher population densities to reduce interference by males. Kipp et al. (1995) observed a high population density where they caught a mean of 11 spruce budworm males per hour on a virgin female trap just before dusk. Individual female moths have not been reported to change their calling bout lengths or frequencies in response to pheromone concentration. However, Sadek et al. (2012) briefly exposed calling females to synthetic pheromone at the beginning of calling in scotophase and found the length of the group's usual calling period was extended and suggested this was in response to perceived competition among females to attract males.

Relatively few studies have looked at individual calling bout lengths of females. Castrejón-Gómez (2010) observed 20 virgin female sapodilla pod borer moths for several days, and the females appeared to call continuously for about 5 h with one or two not calling or only for an hour. In the codling moth, after the first day, virgin females appear to call for a mean of about 4-h duration, but the females were observed every 1–3 h (Castrovillo and Cardé 1979) which might bias results if observations coincided with shorter but frequent bouts. Females of true armyworm moths had a mean calling bout length of only 28 min on the first night of calling and then a mean bout of 54 min on the second night (Delisle and McNeil 1987). In the berth armyworm moth on the second calling night, Gerber and Howlader (1987) found that in a short 8-h scotophase the mean calling bout length was 1.5 h, which increased to 3.2 h in a 12-h scotophase, and to 4 h in a 16-h scotophase. Studies on virgin moths have found that mean calling bout time is several hours (Haynes and Birch 1984; Mazor and Dunkelblum 2005; Ming et al. 2007; Zarbin et al. 2007) or 6–9 h by a female cockroach (Smith and Schal 1991). However, some studies on individual variation in calling bout duration of female noctuid moths have shown that most have bouts of about 0.5 h while progressively fewer have bouts from 1 to 3 h (Monti et al. 1995). Individual cutworm moth females had bouts of 0.5 to 2 h (Teal 1985).

In contrast to female-calling moths, many species of beetles, cockroaches, fruit flies, solitary wasps, and plant bugs have males that are the calling sex (Halstead 1973; Jacobson et al. 1973; Chuman et al. 1987; Robacker 1988; Sreng 1990; Jarvis and Rutledge 1992; Brézot et al. 1994; Farine et al. 1994, 2007; Hoglund and Alatalo 1995; Hamilton et al. 1996; Khoo et al. 2000; Shelly 2001; McBrien et al. 2001, 2002; Field et al. 2002; Quilici et al. 2002; Hall et al. 2006; Borges et al. 2007; Wicker-Thomas 2007; Segura et al. 2007; Geiselhardt et al. 2008; Robacker et al. 2009; Cooperband et al. 2012). Models show that without pheromone traps (the native condition), the mate-finding success of both male-calling species and female-calling moth species is the same, but under mass trapping the species with calling males incur higher rates of female captures and less mating success (Byers 2012).

Rhythms of pheromone emission

Many reports on circadian rhythms have titles with keywords that promise pheromone release or emission (Fig. 1) but actually report only on calling activities (e.g., Sower et al. 1971a; Calvert and Corbet 1973; Fatzinger 1973; Eisenbach and Mittler 1980; Alford and Hammond 1982; Haynes and Birch 1984; Teal 1985; Chon et al. 1990; Thieme and Dixon 1996). Emission or release of pheromone should rather be used in reference to measurements of release rates of pheromone component amounts collected on absorbents from headspace air and chemically analyzed (Charlton and Cardé 1982; Morse et al. 1982; Pope et al. 1982; Haynes et al. 1983; Schal et al. 1987; Bestmann et al. 1988; Witzgall and Frérot 1989; Hunt and Haynes 1990; McLaughlin et al. 1990; Nation 1990; Heath et al. 1991, 1993; Valles et al. 1992; Epsky and Heath 1993; Leal et al. 1996; Bäckman et al. 1997; Bashir et al. 2003; Schlamp et al. 2006; Stewart-Jones et al. 2007; Fonseca et al. 2010; Byers et al. 2013; Skabeikis et al. 2016; Nojima et al. 2018). Relative emission rates can also be measured over the circadian day by solid-phase microextraction (SPME), which has been used for identifying pheromone components that when examined usually exhibit circadian cycles (Levi-Zada et al. 2012, 2013 2014a b, 2019, 2020a, b).

Pheromone release is a result of biosynthesis contributing to titer that is depleted by exposure of glands during calling. Release rates of pheromone can decline over the calling period if pheromone titer decreases due to inadequate biosynthesis or not decline due to compensation by increased biosynthesis. Schal et al. (1987) found that 13 of 16 female moths, *Holomelina lamae* (Erebidae = Arctiidae), had individual release rates that significantly declined during the calling period, while two other moths released more consistently, and only one female of 16 increased its release rate during calling. Schal et al. also measured pheromone emission from nine calling females of which seven emitted pheromone primarily for 30 min and by the next hour little was emitted, while in two females pheromone was emitted at levels of the first 30 min for another 2 h. In codling moths, however, shortly after dark the pheromone gland titer of codlemone in females increased slightly during calling which coincided with an increase in release rate (Bäckman et al. 1997). In the moth *Cacoecimorpha pronubana* (Tortricidae), individual females during the calling period had similar and consistent rates of emission of the main pheromone component (Witzgall and Frérot 1989). It is clear that the most relevant measure in regard to the chemical ecology of pest management would be the variation in circadian emission rate over 24 h and not necessarily the titer or calling rhythms. The release rate is what the responding individuals actually detect and respond to.

Rhythms of behavioral response to pheromone

The receiving individuals show an attractive pheromone response (walking or flying upwind) to sex and aggregation pheromone sources according to an odor-modulated anemotaxis (David et al. 1982) (Fig. 1). In some cases, the response period is wider and does not coincide fully with the emission period of the sending individuals, but usually the emission and response rhythms are well correlated (McLaughlin et al. 1990; Heath et al. 1993; Schlamp et al. 2006; Levi-Zada et al. 2014b, 2018). Calling and response also are usually well correlated (Cardé et al. 1974; Cross et al. 1977; Castrovillo and Cardé 1979; Quartey and Coaker 1996; Zhang et al. 1996; Sasaerila et al. 2000). However, male long-horned beetles emitted sex pheromone many hours after most females responded (Skabeikis et al. 2016). Some moth species have a response period that appears longer than the calling period of females (Haynes and Birch 1984; Kawasaki 1986; Zhang and Paiva 1998). Sometimes the responding sex begins flying and responds earlier in time than when pheromone is released (or calling as a proxy) by conspecific females (Fatzinger 1973; Cardé 1974; Baker and Cardé 1979; Cibrian-Tovar and Mitchell 1991; Zhang and Paiva 1998). Some studies have indicated that synthetic pheromone attracts insects earlier and over a more prolonged period than do virgin calling insects (Kawasaki et al. 1983; Hendricks 1985; Kaster et al. 1989; Stevenson and Harris 2009). This earlier than expected response window in male moths is termed *response protandry* or *protandrous response*, which can increase the effectiveness of mass trapping. This is because earlier each day for a period of time attractive traps have little competition from attractive females and thus males are readily trapped. Unmated female papaya fruit flies were attracted to synthetic pheromone of males earlier in the photophase than were mated females (Landolt and Heath 1988). Some ticks produce and respond to assembly pheromones throughout a 24-h period (Rechav 19781978). Generally, if the time window of response is larger than the emission window, then mass trapping should be more effective than otherwise.

The role of an antennal response rhythm in rhythms of behavioral response is uncertain. In a few studies, the antennal receptors are reported to show a circadian rhythm of depolarization magnitude of electrophysiological recordings in response to volatiles. Rymer et al. (2007) showed a dramatic increase in electroantennographic (EAG) response of cockroach *Leucophaea maderae* to non-pheromone volatiles 3-hydroxy-2-butenone or senecioic acid. Several male pheromone–related volatiles gave small but consistently higher EAG responses in the afternoon than in the morning for both males and females of the Mediterranean fruit fly (Sollai et al. 2018). However, in other studies on the turnip moth, there was no evidence of an EAG rhythm regarding sex pheromone (Rosén et al. 2003). Earlier work on the spruce budworm moth did not show an EAG rhythm to sex pheromone tested every hour of the day (Worster and Seabrook 1989). It is generally accepted that the insect's brain is mainly responsible for associating the various antennal signals and other sensory input in coordination with circadian rhythm contributions to effect orientation toward pheromone sources (Todd and Baker 1999). The odor-modulated anemotaxis response is based on the brain and visual responses to the movement below the flyer as well as olfactory response of the antenna/brain (David et al. 1982; Cardé and Willis 2008).

Rhythms of the central nervous system also impact response rhythms. A rhythm of electrical activities of neurosecretory cells involved in pheromonal activities is regulated by release of pheromone binding neuropeptide (PBAN) that stimulates calling in the silkworm moth and coincides with the first 75% of the scotophase and then PBAN levels drop precipitously (Ichikawa 1998). Konstantopoulou et al. (2006) found that a general odorant binding protein was lower in scotophase than in photophase in both sexes of a noctuid moth *Manduca sexta*, indicating a possible circadian rhythm. However, they found that the male's pheromone binding protein (PBP) did not change levels between day and night. Different clock genes in the antenna and brain of noctuid moth *Spodoptera littoralis* were found to cycle according to a circadian rhythm, and the EAG responses measured every 3 h were claimed to follow a daily rhythm (Merlin et al. 2007). However, only at the end of scotophase was the EAG response significantly less than at other times during the day which were nearly the same. Nagari et al. (2017) performed EAG on honeybee antennae with several volatiles and fit cosine curves through data during the day. They found consistent fits for foragers but not nurse bees, suggesting a circadian rhythm in foragers. However, the EAG potentials appear nearly the same for a particular chemical over the day. These changes in EAG could be due to other factors changing during the day and it remains a question whether these subtle changes in EAGs are biologically significant. A clock gene in *Drosophila melanogaster* was found using monoclonal antibodies to be in pheromone-sensitive sensilla and receptor neurons, and the gene expression varied daily (Schuckel et al. 2007).

Effects of mating, emergence, and oviposition rhythms

There is probably a feedback loop between pheromone production and pheromone titer. Mating (Fig. 1) often shuts down pheromone production and calling, which in turn reduces or terminates pheromone release (Byers 1981; Webster and Cardé 1984; Raina et al. 1986; Dunkelblum et al. 1987; Chon et al. 1990; Mbata and Ramaswamy 1990; Babilis and Mazomenos 1992; Tang et al. 1992; Foster and Roelofs 1994; McNeil and Brodeur 1995; Del Mazo-Cancino et al. 2004; Levi-Zada et al. 2014b). Some studies have indicated that calling and assumed pheromone release are not synchronous with mating. In the Mascarene fruit fly (Tephritidae), males exhibit a 5.5-h calling period starting at dawn, but mating began midway through the calling period and extended about 2 h after calling ended, possibly due to time needed for pre-mating courtships (Quilici et al. 2002). These courtships in fruit flies appear complex with both sexes of many species releasing different volatiles assumed to be involved in sexual selection and mating (Levi-Zada et al. 2020b).

Locomotor activity or flight activity (Fig. 1) usually also has a rhythm that influences attraction to pheromone (and trap catch). Obviously if the flight activity rhythm (which includes visiting flowers for nectar) is not completely correlated with pheromone release, this will preclude pheromone response and mating part of the time (Fig. 1). Thus, female moth pheromone titer plus female calling/exposure of gland will provide a pheromone release that interacts with male activity and male pheromone attraction (response) rhythms that result in mating or trap captures.

Emergence rhythms, which may affect pheromonal aspects mentioned earlier (Fig. 1), will also have an impact on flight activity and specifically on flight density. However, emergence often does not have an immediate effect on mating as it can take several days before a sex is ready to call and mate. Mating is usually prerequisite for oviposition rhythms (Fig. 1). Furthermore, as mentioned above, mating usually inhibits pheromone biosynthesis, calling, and mating because the female has an interest in finding oviposition sites and laying eggs on appropriate hosts. Oviposition rhythms (Fig. 1) occur at a different time than calling because the emitting sex (e.g., female moth) must remain stationary while calling so as to receive the responding opposite sex, while ovipositing requires searching for suitable host plants. For example, females of the turnip moth *Agrotis segetum* have an ovipositional rhythm that peaks at dusk (Byers 1987) and is over by the middle of scotophase when females peak in their calling (Löfstedt et al. 1982).

Analysis of pheromonal rhythms of insects

To achieve a quantitative analysis of insect daily rhythms (emergence, titer, calling, emission, response) reported in the literature, the data in figures of downloaded PDFs (Adobe Inc.) were screen-captured (Print Screen, Windows 10, Microsoft Inc.) and copied into software constructed in Java programming language (1.6 version, Oracle Inc.). The pixel coordinates of data in images were converted by the software to real values (Eq. 1 in Byers 2013). The values then were used to calculate the mean hour of a rhythm on X-axis and SD as weighted by activities on Y-axis (e.g., emergence, titer, emission) during the day from Eqs. 1 and 2, respectively, in Byers (2011), where hour of data observation replaces trap height and circadian activity replaces trap catch. A normal curve equation was fit to the circadian activity data using the calculated mean time of activity (X) and SD as found from the equation:

$$\boldsymbol{Y} = \boldsymbol{a}\left[\mathbf{exp}\left(-\frac{(\boldsymbol{X}-\boldsymbol{b})^2}{2\boldsymbol{c}^2}\right)/(\boldsymbol{c}(2\boldsymbol{\pi})^{0.5})\right] \tag{1}$$

where b = mean hour of activity during day (and converted to hour of photophase or scotophase as appropriate), c = SD of mean hour of activity, and a is a scaling factor found by computer iteration of Eq. (1) using an initial value for a from the following equation:

$$\boldsymbol{a} = 2\boldsymbol{M}/(\frac{1}{\boldsymbol{b}(2\boldsymbol{\pi})^{0.5}}) \tag{2}$$

where M is the maximum activity observed during the rhythm. The iterations proceed with a calculated above (Eq. 2) and then at each subsequent iteration of Eq. 1 reducing a by a/10,000 until stopping when $a \le 0.01$. The value of a at which the sum of the squared differences between the data points and the equation was least is the best-fitting normal equation corresponding to the given mean and SD (Byers 2011).

This analysis method was applied to pheromone circadian rhythms of calling, emission, and response of several insects from diverse families in non-lepidopteran orders (beetles, mealybugs, aphids, flies, bees, parasitic wasps, and cockroaches) (Table 1). Representative species of Coleoptera in five diverse families all had activity rhythms in the photophase (Bashir et al. 2003; Cross et al. 1977; Dobson and Teal 1986; Faustini et al. 1982; Fonseca et al. 2010; Gueldner and Wiygul 1978) except for a scarab species (Leal et al. 1996) with activity in the scotophase (Table 1). Generally, insects that are active in daylight or those that are nocturnal have mean times in the photophase or scotophase, respectively. In a dermestid beetle (Cross et al. 1977), female calling had a mean time 3.98 h into photophase that was identical to male response at 4.1 h, although the response rhythm appeared broader based on SD. Similarly in a grain weevil (Faustini et al. 1982), the male response rhythm was about the same as the female rhythm to male-produced aggregation pheromone (Table 1). In the order Hemiptera, emission of sex pheromone released by female citrus mealybug had a maximum at the end of night (Table 1), while in the vine mealybug female emission peaked in the morning (Levi-Zada et al. 2014a, b). In contrast, females of the spherical mealybug have a mean emission time of sex pheromone in the late afternoon (Levi-Zada et al. 2019). In an aphid, egg-laying females have a mean calling time in the photophase of 5.87 ± 2.94 h but their emission peak of sex pheromone occurs about 1.85 h later (Stewart-Jones et al. 2007). In fruit flies (Diptera: Tephritidae), species- and sex-specific volatiles are released in higher amounts during times of courtship and mating (usually in morning or late afternoon) (Table 1). In most fruit fly species, however, pheromonal functions of volatiles have been difficult to characterize apparently due to

Table 1 Mean time (hours) and SD in photophase or scotophase of pheromone activity rhythms calculated from graphical data in literature on non-lepidopteran insects. Data were fit to a normal equation from the mean time (b) and SD (c) by computer iteration to obtain the scaling coefficient a, allowing estimation of Y activity (emission, calling, or response) at any hour X (from Eq. 1 in text)

Species	Sex	Activity	Source	Mean h ± SD (P/S)[1]	a[2]	R^2 (N)
Coleoptera (beetles)						
Rhyzopertha dominica	Male	Emission	(1)[3]	7.94 ± 4.9 (P)	0.475	0.29 (7)
Trogoderma variabile	Female	Calling	(2)	3.98 ± 2.45 (P)	233.2	0.82 (27)
Trogoderma variabile	Male	Response	(2)	4.1 ± 3.7 (P)	566.8	0.55 (8)
Diabrotica barberi	Male	Response	(3)	4.23 ± 1.07 (P)	62.9	0.80 (14)
Sitophilus granarius	Male	Response	(4)	6.0 ± 4.94 (P)	444.9	0.34 (6)
Sitophilus granarius	Female	Response	(4)	6.7 ± 4.64 (P)	588.4	0.49 (6)
Hedypathes betulinus	Male	Emission	(5)	6.49 ± 1.98 (P)	696	0.76 (6)
Anthonomus grandis	Male	Emission	(6)	7.25 ± 4.23 (P)	24.7	0.97 (9)
Anomala albopilosa	Male	Emission	(7)	2.20 ± 2.05 (S)	45.95	0.58 (6)
Hemiptera (mealybugs, aphids, and sucking bugs)						
Planococcus citri	Female	Emission	(8)	11.93 ± 2.26 (S)	6.34	0.99 (11)
Planococcus ficus	Female	Emission	(8)	2.53 ± 5.05 (P)	6.02	0.90 (11)
Nipaecoccus viridis	Female	Emission	(9)	11.36 ± 2.32 (P)	167.3	0.99 (7)
Dysaphis plantaginea	Female	Calling	(10)	5.87 ± 2.94 (P)	858.5	0.48 (12)
Dysaphis plantaginea	Female	Emission	(10)	7.72 ± 4.27 (P)	69.7	0.84 (16)
Diptera (flies)						
Anastrepha suspensa	Male	Emission	(11)	11.36 ± 1.60 (P)	587.4	0.95 (8)
Ceratitis catoirii	Male	Calling	(12)	2.97 ± 1.23 (P)	85.95	0.90 (13)
Ceratitis catoirii	Male	Mating	(12)	5.27 ± 1.39 (P)	12.67	0.82 (12)
Bactrocera zonata	Female	Emission	(13)	10.06 ± 2.87 (P)	221.4	0.80 (6)
Bactrocera zonata	Male	Emission	(13)	7.97 ± 3.38 (P)	92.7	0.17 (9)
Hymenoptera (bees, ants, and wasps)						
Apis mellifera ligustica	Female	Titer	(14)	7.42 ± 4.36 (P)	9110	0.90 (6)
Aphidius nigripes	Male	Response	(15)	4.09 ± 2.95 (P)	80.3	0.50 (7)
Dictyoptera (cockroaches)						
Supella longipalpa	Female	Calling	(16)	6.58 ± 2.80 (S)	665.9	0.83 (14)
Supella longipalpa	Male	Response	(17)	6.98 ± 4.11 (S)	1124	0.92 (9)
Blattella germanica	Female	Calling	(18)	1.25 ± 5.78 (P)	1175	0.76 (24)
Blattella germanica	Female	Mating	(18)	11.44 ± 4.22 (S)	101.9	0.73 (23)

[1] Mean hour of circadian activity ± SD (P = photophase, S = scotophase)

[2] Scaling coefficient a, mean hour b, and SD c are used to calculate Y of activity (described in first column) at any hour X of photophase or scotophase according to the normal curve Eq. (1) in text

[3] Literature sources: (1) Bashir et al. (2003); (2) Cross et al. (1977); (3) Dobson and Teal (1986); (4) Faustini et al. (1982); (5) Fonseca et al. (2010); (6) Gueldner and Wiygul (1978); (7) Leal et al. (1996) (8) Levi-Zada et al. (2014b); (9) Levi-Zada et al. (2019); (10) Stewart-Jones et al. (2007); (11) Nation (1990); (12) Quilici et al. (2002); (13) Levi-Zada et al. (2020b); (14) Pain and Roger (1978); (15) McNeil and Brodeur (1995); (16) Smith and Schal (1991); (17) Liang and Schal (1990); (18) Liang and Schal (1993). More details are given in Supplementary information table S3

complex interactions among several volatiles, acoustic wing vibrations, visual displays, and mating-lek context (Nation 1990; Quilici et al. 2002; Levi-Zada et al. 2020a, b). In the European honey bee (Hymenoptera: Apidae), queen pheromone titer peaks midday (Pain and Roger 1978), while in a wasp parasitic of insects (Brachonidae), males respond to virgin females in mid-morning (McNeil and Brodeur 1995). The brown-banded cockroach (Dictyoptera) is nocturnal and female calling peaks at 6.58 h of scotophase, which is similar to the male response to female sex pheromone at 6.98 h scotophase (Table 1; Smith and Schal 1991; Liang and Schal 1990). The German cockroach is also nocturnal, and female calling occurs during the last half of night and into the morning, so the mean time occurs early in photophase (1.25 h) but has a broad SD of 5.78 h (Table 1). Mating of the German cockroach peaks about 15 min before dawn (11.44 h scotophase) and thus is not significantly different from calling (Table 1; Liang and Schal 1993). These examples indicate that mean time of pheromonal activity of different species can occur at any time of the day-night and can overlap L:D or D:L transitions. The different mean times of circadian rhythms of various species probably evolved to enhance fitness by reducing competition or interference with other sympatric species sharing their niche, although experiments to test this are largely lacking.

Several moth species (Lepidoptera) of immense economic importance including the gypsy moth *Lymantria dispar* (L.), spruce budworm *Choristoneura fumiferana* (Clemson), turnip moth *Agrotis segetum* (Schiff.), and cabbage looper *Trichoplusia ni* (Hübner) are among the insects most intensively studied regarding pheromonal rhythms. These four pest species with documented multiple circadian rhythms will be analyzed as above and discussed.

Gypsy moth *Lymantria dispar*

The gypsy moth (Lepidoptera: Erebidae = Lymantriidae) occurs across northern Eurasia and was introduced into Massachusetts about 1869 where it has spread to become a severe pest in eastern USA (Cameron et al. 1974; Cardé et al. 1996; Tobin et al. 2009). Females do not fly and thus oviposit close to their emergence site, while males fly in search of females. Dispersal is by larval ballooning, a term meaning larvae are carried by wind on long silken threads as are immature spiders (Tobin et al. 2009). The caterpillars feed upon 300 species of both deciduous and coniferous trees and can severely defoliate oak, willow, and aspen (Elkinton and Liebhold 1990; Tobin et al. 2009). Up to a half million ha of forests in the USA were infested in 1971 (Cameron et al. 1974). USDA programs to detect the gypsy moth used up to 250,000 pheromone traps annually across the USA from Minnesota to North Carolina in the first decade of 2000 (Tobin et al. 2009). These programs still continue today.

Gypsy moths have an emergence (or eclosion) rhythm with peak (or mean) at 5.8 h of photophase and SD = 2.5 h (Fig. 2A, Cardé et al. 1996). Odell (1978) also showed an emergence rhythm during the day. The mean time of adult emergence, as expected, was earlier than any other pheromonal rhythm. The titer of disparlure pheromone (*cis*-7,8-epoxy-2-methyloctadecane) in female glands measured by Tang et al. (1992) was modeled by a normal curve with a mean of 12.21 h of photophase and SD = 6.5 h (Fig. 2B) yielding a maximum Y of 23.2 ng/gland at the peak titer (solving Eq. 1 for Y at mean $X = 12.21$ and a, b, c parameters as in Fig. 2B). This normal curve has a mean time of pheromone titer that is about 6 h after the mean emergence time. The emission of disparlure from female gypsy moths (Charlton and Cardé 1982) appears to have a very similar rhythm to that of titer, with a mean of 12.6 ± 5.52 h (± SD) in photophase (Fig. 2C). We calculate that the peak emission rate of a 2-day-old virgin female was 29.6 ng/2 h based on the normal curve fit solving for Y in Eq. 1. It is not surprising that the emission closely follows the calling rhythm, although it is theoretically possible that different rates of pheromone biosynthesis and calling might cause the patterns to be unsynchronized. The normal curves fit well with coefficients of determination (R^2) 0.86 to 0.93 for pheromone-related rhythms (Fig. 2B–E). The emergence/eclosion rhythm fit less well with the data ($R^2 = 0.55$). After a single mating, female gypsy moths cease to call (Tang et al. 1992). As mentioned earlier, male attraction to virgin females is a

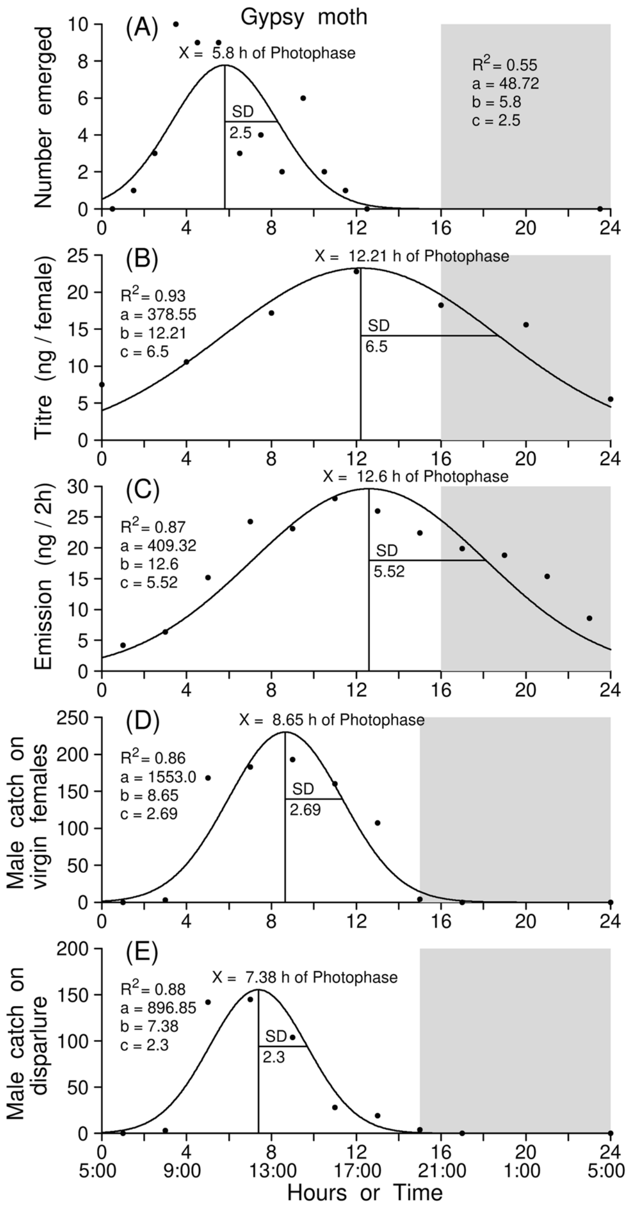

Fig. 2 Activity rhythms involved in pheromone communication of gypsy moth *Lymantria dispar* represented as normal curves with mean time (X) and SD. **A** Emergence from pupae (Cardé et al. 1996); **B** disparlure (*cis*-7,8-epoxy-2-methyloctadecane) pheromone titer of female gland (Tang et al. 1992); **C** emission of pheromone from female (Charlton and Cardé 1982); **D** male catch on virgin female traps (Cardé et al. 1974); and **E** male catch on disparlure-baited pheromone traps (Cardé et al. 1974). Calculation of R^2 and coefficients for corresponding normal curves explained in text

combination of emission (due to pheromone biosynthesis, titer, and calling) and the innate rhythm of male response to pheromone, the latter expected to be synchronized well with emission. Perhaps surprisingly, the mean time of catch on traps with virgin females (8.65 ± 2.69 h) was about 4 h earlier (Fig. 2D) than mean emission time (Fig. 2C). The peak catch at the mean time is not relevant to calculate from Eq. 1 as this depends on population levels. The mean time of male catch on traps releasing disparlure (Fig. 2E) is similar to catch on virgin females but was perhaps an hour earlier at 7.38 ± 2.3 h (protandry). The SD of male catch on both virgin females and disparlure is similar and considerably less than the SD of emission rate (Fig. 2). The protandry of male response would tend to aid mass trapping since males could be caught by traps before many females call and emit pheromone. It is notable that females called and emitted pheromone well into the night when hardly any males were responding to females or disparlure.

Spruce budworm *Choristoneura fumiferana*

The spruce budworm (Lepidoptera: Tortricidae) is a native insect with a wide distribution from eastern North America across the boreal and mixed coniferous forests into Alaska (Goodbody et al. 2018; Royama 1984). The larvae feed on spruce (*Picea* spp.) and fir (*Abies* spp.) accounting for 40 to 50% of Canada's timber losses from biological disturbances, or an average of 1.8 million ha of annual forest defoliation in Ontario since 1990 (Goodbody et al. 2018). Outbreaks of spruce budworm range in size, intensity, and duration occurring about every 30–40 years with a duration of 10–15 years (Royama 1984; Régnière and Nealis 2007). Population cycles of the spruce budworm appear regulated by an array of natural enemies interacting with host tree condition and climate (Royama 1984; Eveleigh et al. 2007; Régnière and Nealis 2007; Gray 2008; Nealis et al. 2015).

Spruce budworm adults exhibit an emergence rhythm in the afternoon, or a mean of 9.97 h of photophase and SD = 3.49 h (Fig. 3A, Kipp et al. 1995). Similar to the gypsy moth, emergence must occur before pheromonal activities can take place. The rhythm of pheromone titer appears flat during the scotophase with a mean of 2.67 ± 3.06 h (± SD) in the scotophase (Delisle et al. 1999, Fig. 3B). Using Eq. 1 and the parameters shown for the normal curve best fitting the mean and SD, the peak titer of the female's gland is 3.6 ng. Calling female spruce budworms have a very similar rhythm of calling (mean of 2.92 ± 2.37 h of scotophase) to that of gland titer, although data points are more peaked for calling compared to flat-topped for titer (Fig. 3B, C). It should be noted that titer and calling were measured under the same 16L:8D photoperiod while emission was measured under a 12L:12D photoperiod. Under this longer 12-h scotophase, the rhythm of pheromone emission of a female was 6.17 ± 2.28 h of scotophase. The peak emission of pheromone *E*11-14:Al is 30.7 ng/h from a virgin female (Fig. 3D, Morse et al. 1982). It can be seen that the rhythm of emission is approximately in the middle of scotophase, while titer and calling also are roughly in the middle of

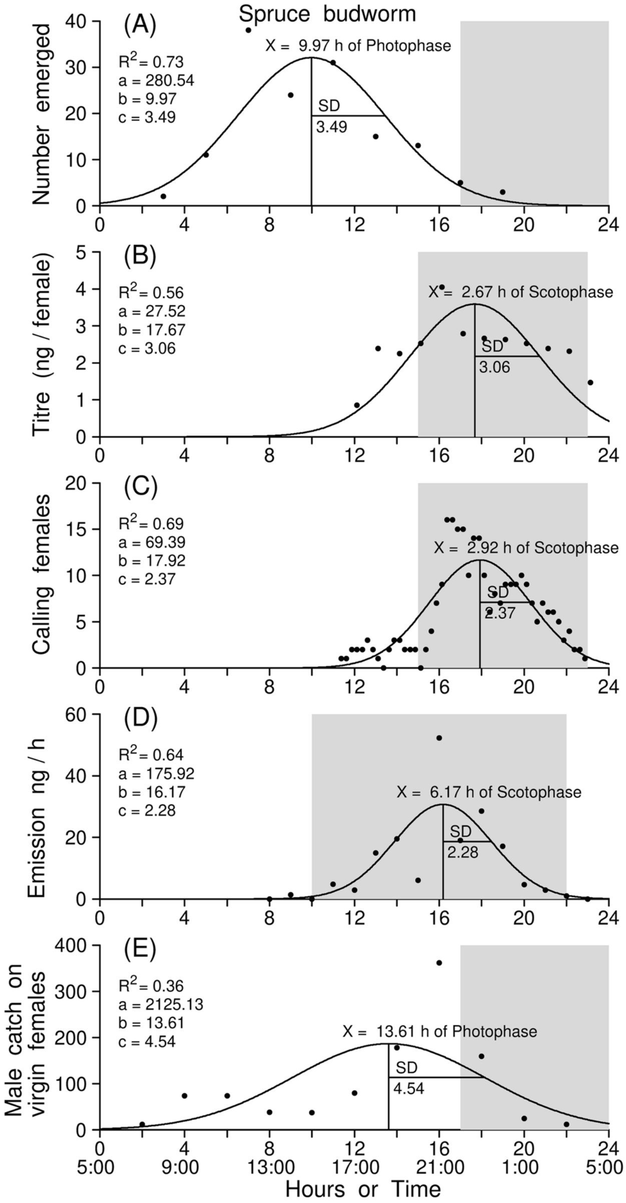

Fig. 3 Activity rhythms involved in pheromone communication of spruce budworm *Choristoneura fumiferana* represented as normal curves with mean time (X) and SD. **A** Emergence from pupae (Kipp et al. 1995); **B** *E*11-14:Al pheromone titer of female gland (Delisle et al. 1999); **C** calling females (Delisle et al. 1999); **D** emission of E11-14:Al pheromone from female (Morse et al. 1982); and **E** male catch on virgin females in high-density population (Kipp et al. 1995). Calculation of R^2 and coefficients for corresponding normal curves explained in text

scotophase but perhaps somewhat earlier in the night. It would be interesting to determine emission and calling under the same photoperiod. Under a shorter night 18L:7D photoperiod in the field, the mean male catch on virgin female spruce budworm moths was actually at 13.61 ± 4.54 h of the photophase (Fig. 3E, Kipp et al. 1995), which is significantly earlier than means for calling and emission (Fig. 3C, D). This appears to be a good example of protandry where the earliest males would mate in nature, but under mass trapping would be trapped more effectively than species where calling and response are better synchronized.

Turnip moth *Agrotis segetum*

The turnip moth (Lepidoptera: Noctuidae) is a cutworm that has a wide geographic distribution across temperature regions of Europe and Asia as well as Africa. Although the name implies that the moth feeds on turnips, the larvae feed on roots (including turnips) and lower parts of a very large number of host plants in many genera, ranging from corn and vegetables to conifers and some semi-toxic plants (Erasmus et al. 2010; Esbjerg and Sigsgaard 2014).

Female turnip moths oviposit in a rhythm with a mean at dusk (0.35 h ± 2.08 h in scotophase, Fig. 4A, Byers 1987). The egg laying occurs several hours before any of the pheromonal rhythms. For example, females have a mean calling time of 3.95 ± 0.93 h in the scotophase (Fig. 3B, Löfstedt et al. 1982) that occurs about 3.6 h after mean oviposition time. However, oviposition and calling rhythms should not interact since mating leads to oviposition in subsequent days. The reason for different peaks for oviposition and calling are unclear. The rhythm of calling appears more narrow than other rhythms such as titer, PBAN, or male response. Pheromone component *Z*7-12:Ac in 2-day-old virgin female turnip moths had a titer rhythm with mean 3.52 ± 2.33 h of scotophase (Fig. 4C, Rosén 2002). The peak titer of *Z*7-12:Ac was calculated as 0.96 ng per female. Male response to a four-component pheromone blend in the wind tunnel had a mean of 3.56 ± 1.86 h of scotophase (Fig. 4D, Rosén et al. 2003), similar to the mean times for titer and calling. PBAN concentration in female hemolymph had a mean at 4.03 ± 3.42 h of scotophase (Fig. 4E, Závodska et al. 2009), also similar to the mean times of male response and female calling and titer. The peak PBAN concentration in females at the mean time was 205 pM (Eq. 1). There is no evidence that males respond to pheromone before females call (i.e., no protandry that would benefit mass trapping). However, mass trapping with the four-component synthetic pheromone reduced males catch by 79% and female mating by 62% compared to control plots (Svensson et al. 2001).

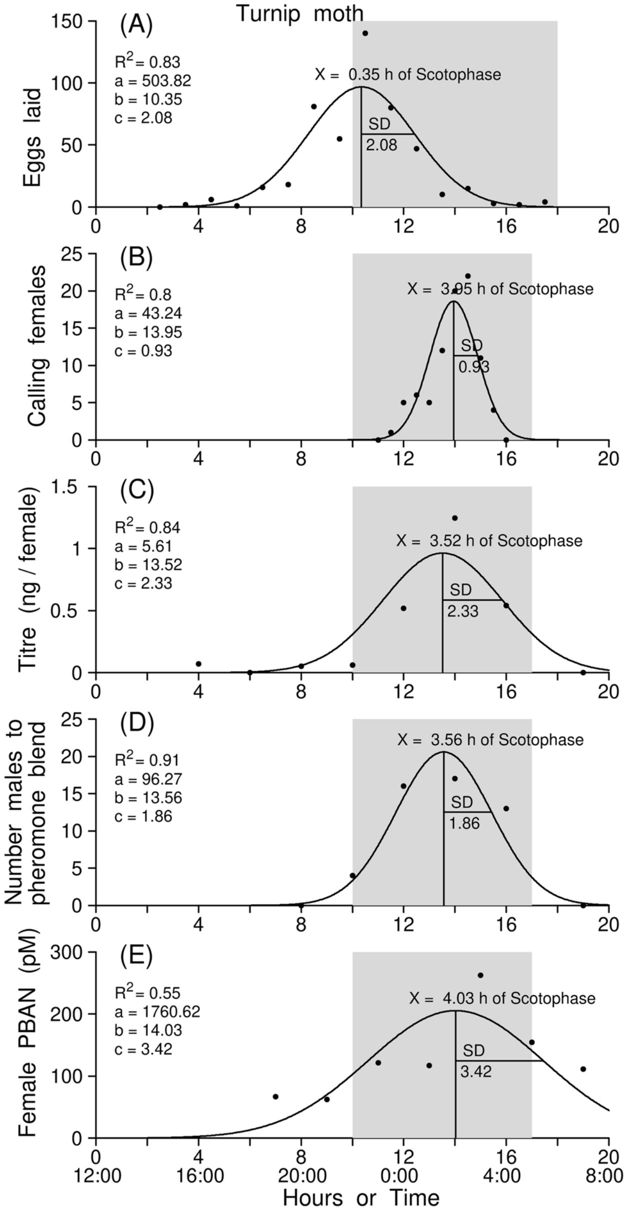

Fig. 4 Activity rhythms involved in pheromone communication of turnip moth *Agrotis segetum* represented as normal curves with mean time (X) and SD. **A** Eggs laid (Byers 1987); **B** calling females (Löfstedt et al. 1982); **C** pheromone component Z7-12:Ac titer of gland of 2-day-old females (Rosen 2002); **D** number males responding to pheromone blend in wind tunnel (Rosen et al. 2003); and **E** PBAN (pheromone biosynthesis activating neuropeptide) concentration of female hemolymph (Zavodska et al. 2009). Calculation of R^2 and coefficients for corresponding normal curves explained in text

Cabbage looper *Trichoplusia ni*

The cabbage looper (Lepidoptera: Noctuidae) is a major pest of cole crops (broccoli, Brussels sprout, collards, cabbage, cauliflower, kale, mustard, and turnip) and lettuce. The cabbage looper can also live on several weeds in agricultural areas and trap crops have not been effective in control (Cameron et al. 2007). In addition to the economic impact on plants in the family Brassicaceae, over 100 species of plants are eaten by cabbage looper (Hoo et al. 1984; Garcia et al. 2020). The female-produced sex pheromone consists of the primary component *Z*7-12:Ac and five additional minor components (Bjostad et al. 1984; Linn and Roelofs 1992). In response to female pheromone, males release a different sex pheromone from hair pencil glands in their wings that consists of *S*-linalool, p-cresol, and m-cresol, and probably acts to stimulate mating (Heath et al. 1992).

The major pheromone component *Z*7-12:Ac in female glands of cabbage loopers showed a rhythmic dip in titer during the scotophase as fit with a Gaussian equation (with non-linear regression, TableCurve2D, Systat Software Inc., Chicago, USA). This curve (Fig. 5A) has four coefficients, with $c = 14.1$ h (8.1 h of scotophase) that when $X = c$ (Eq. 1) gives the lowest titer $Y = 212$ ng, or using $X = 2$ h gives the highest titer of 780 ng (Hunt and Haynes 1990). The titer may decline after 2 h of scotophase due to pheromone biosynthesis not keeping pace with emission losses during calling (Fig. 5B). Calling by females was fit by a normal equation with mean time of 6.32 ± 2.01 h in scotophase. Almost identical with calling females, the response of males to virgin females in the field had a mean of 6.19 ± 1.97 h in the scotophase (Fig. 5C, Hendricks 1985). The catch of males on *Z*7-12:Ac baited traps in the field had a mean time of 4.03 ± 1.79 h (Fig. 5D, Saario et al. 1970), which indicates some protandry of males that could be caught by traps before finding females during mass trapping. Although a shorter dark period in the lab, Linn and Roelofs (1992) found males oriented to a 6-component blend of cabbage looper pheromone in a wind tunnel had a mean of 4.89 ± 1.78 h (Fig. 5E) that was similar to male catch to the main component in the field (Fig. 5D). Effects of increasing scotophase lengths on calling and response in the cabbage moth follow.

Sower et al. (1971a) provide interesting results with increasingly longer scotophases of photoperiods. Longer dark periods of entrainment of 9, 10.5, 12, 13.5, or 15 h during each 24 h caused mean calling times in the scotophase to change, respectively, from 5.32, 7.32, 8.49, 9.95, or 11.0 h (our calculations, Fig. 6A–E). The SD of mean times of the rhythms did not appear to change significantly as all five were between 1.59 to 2.16 h. According to Aschoff's rule for nocturnal animals, the mean calling time should be about the same time of night after dusk zeitgeber regardless of scotophase length, which is not the case here. Interestingly, the mean times of calling in all five different scotophase lengths were about 3–4 h before morning light. Sower et al. pointed out that the zeitgeber must be "lights on" (morning) since about 20–21 h later the peak of calling occurs in all five different photoperiods. It seems adaptive for cabbage loopers to call the same time before dawn regardless of the dark period length, and not in the middle or near the first part of the scotophase. Perhaps other moth species may follow Aschoff's rule if calling is adaptive to be synchronized with the earlier part of the night.

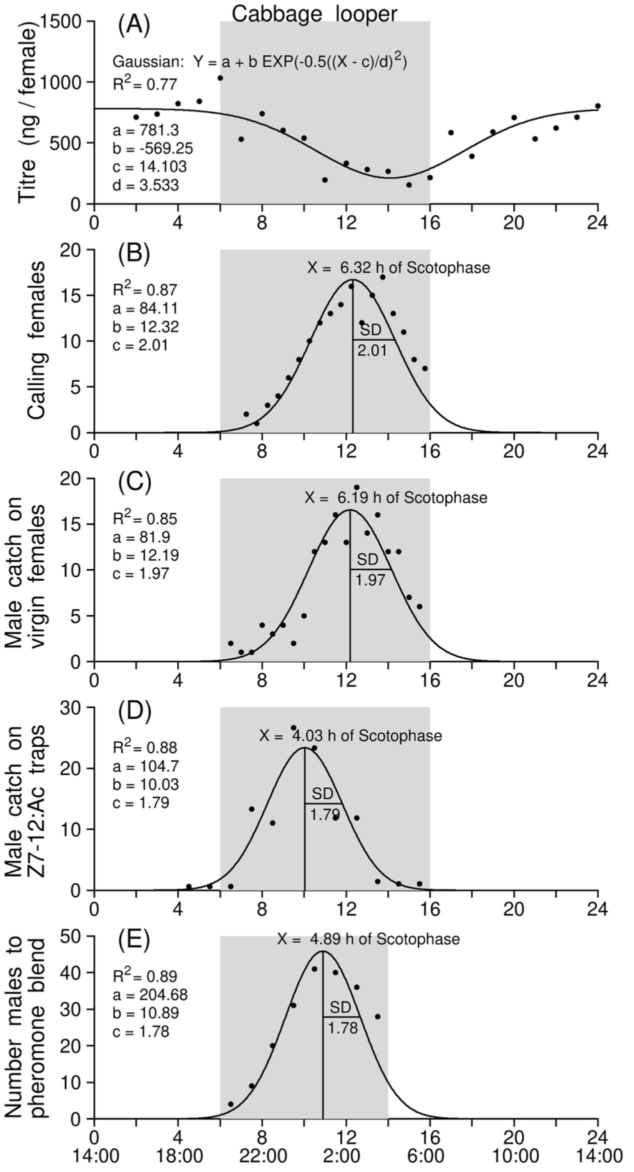

Fig. 5 Activity rhythms involved in pheromone communication of cabbage looper *Trichoplusia ni* represented as normal curves with mean time (X) and SD. **A** Pheromone titer of Z7-12:Ac in female gland (Hunt and Haynes 1990) follows a Gaussian curve; **B** calling females (Hunt and Haynes 1990); **C** catch of males on virgin females in traps in July (Hendricks 1985); **D** catch of males on Z7-12:Ac pheromone traps in July (Saario et al. 1970); and **E** male response to pheromone 6-component blend in wind tunnel (Linn and Roelofs 1992). Data in upper graph did not fit a normal curve but rather a Gaussian-like curve as indicated. Calculation of R^2 and coefficients for other graphs explained in text

In contrast to female calling rhythms above, Linn et al. (1996) studied effects of different photoperiods on rhythms of

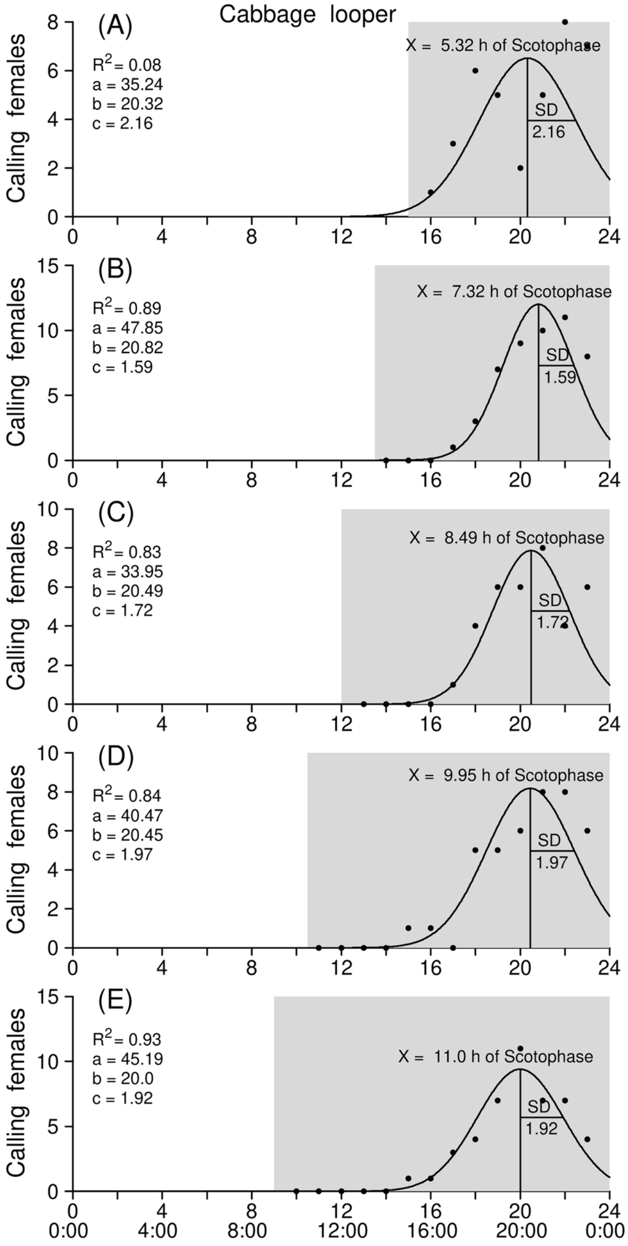

Fig. 6 Female calling rhythms involved in pheromone communication of cabbage looper *Trichoplusia ni* represented as normal curves with mean time (X) and SD under five different photoperiods (Sower et al. 1971a). **A** 15L:9D; **B** 13.5L:10.5D; **C** 12L:12D; **D** 10.5L:13.5D; and **E** 9L:15D. Calculation of R^2 and coefficients for corresponding normal curves explained in text

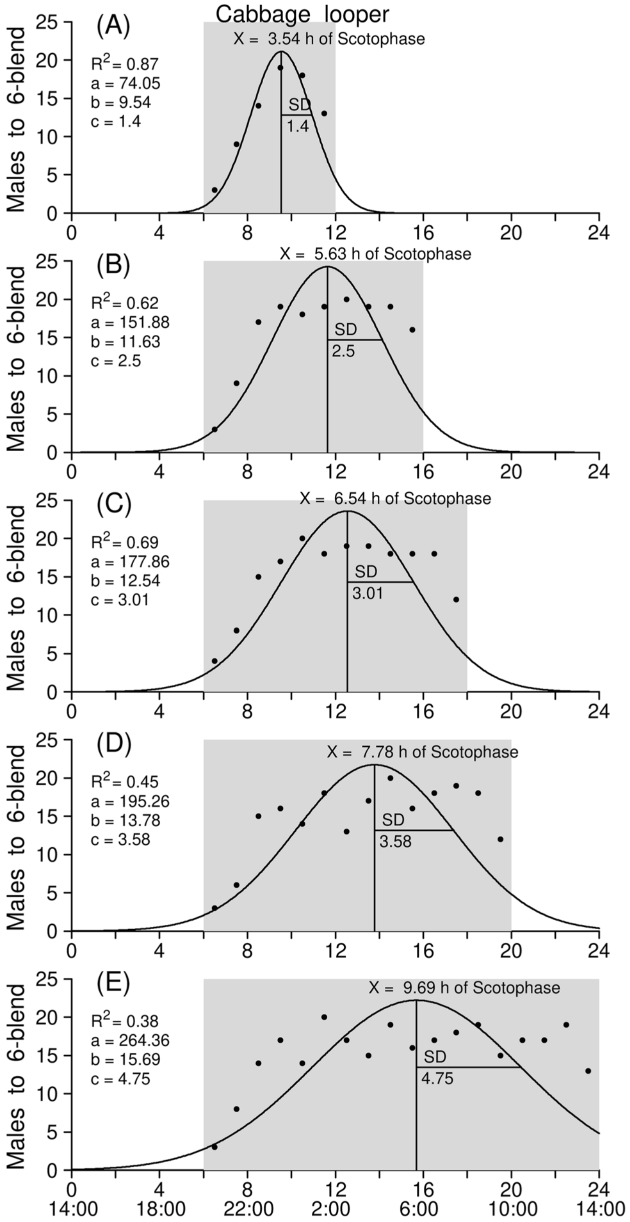

Fig. 7 Rhythms of male responses in wind tunnel involved in pheromone communication of cabbage looper *Trichoplusia ni* represented as normal curves with mean time (X) and SD under five different photoperiods (Linn et al. 1996). **A** 18L:6D; **B** 14L:10D; **C** 12L:12D; **D** 10L:14D; and **E** 6L:18D. Calculation of R^2 and coefficients for corresponding normal curves explained in text

male response in a wind tunnel to a 6-component pheromone blend of the cabbage looper moth (Fig. 7). The scotophases of experiments were of increasing duration: 6, 10, 12, 14, and 18 h per day and the mean times of response were 3.54, 5.63, 6.54, 7.78, and 9.69 h of scotophase, respectively (our calculations). The SD of mean time of response was proportional to the length of the dark period, ranging from 1.4 in the 6-h scotophase to 4.75 h in the 18-h scotophase. The SD of each mean time as a percentage of the scotophase was approximately 59, 56.3, 54.5, 55.6, and 53.8%, remarkably consistent (Fig. 7). Thus, the mean times of response were not the same time after lights off, nor were they a uniform time after lights on as was found for calling by Sower et al. (1971a). There does not seem to be a zeitgeber, rather the mean response time of males is just after the middle of the night regardless of night length. This appears due to an increase in response over the first 2 h of scotophase and then a uniform high level of response for the rest of the night except for perhaps a decline in the last hour or so of scotophase (Fig. 7A–E). Therefore, males have a wide response window during the night no matter its length. This wide response time of males would precede female calling (Fig. 6) and continue thereafter, a protandry effect and sustained response that is especially important in pest control for relatively longer scotophase periods in the spring and autumn. This pattern of male response is consistent with male catch on traps with virgin females that are likely calling (Hendricks 1985, Fig. 5C), but is not consistent with catch on *Z*7-12:Ac (Saario et al. 1970, Fig. 5D) where SD/10 h = 17.9% and attraction was low for the last 3 h of scotophase. However, the data of Linn et al. (1996) is consistent with earlier work (Linn and Roelofs 1992; Fig. 5E) where an 8-h scotophase caused a mean time of 4.89 h (intermediate between means of 3.54 and 5.63 h for 6- and 10-h scotophases above), although the SD/8 h = 22.3% is less than ~ 55% found above for other photoperiods (Fig. 7) but similar to 17.9% mentioned above (Fig. 5D).

Conclusions and future research

Basic studies of circadian rhythms of insects regarding pheromone communication should focus on determining the zeitgebers and consider the selective advantages for some nocturnal insects that use dusk while others use dawn to set their rhythms. It would also be interesting to survey more species and determine the zeitgebers for different rhythms. Studies of individual variation of circadian rhythms of pheromone emission and the responses have been far fewer than the number of studies on percentage of insects in groups calling, mean titer, or responses (catch each hour). The weighted mean time and SD of pheromonal rhythms in past studies has generally not been given as in the present review, although some studies reported median or mean times (although often the mean onset time of calling). This can be improved in future work using methods described here (Byers 2011). In addition to means of groups, individual variation in durations of calling bouts, emission bouts, and searching flights should be investigated to determine how this variation might impact the ecology and pest management of each species.

Sex and aggregation pheromones released from traps are used for detection of invasive species, in monitoring of population levels that trigger control, and in control methods of mass trapping (El-Sayed et al. 2006; Levi-Zada et al. 2018). Knowledge of the mean and breadth SD of rhythms of pheromone emission and of response indicate when each pest species is most vulnerable to control methods with pheromones and insecticides. This knowledge needs to be integrated with control programs that take advantage of when to activate pheromone puffer devices and smart release formulations in order to conserve pheromone and improving longevity of mating disruption. The use of pheromones in pest management has the advantage of being environmentally safe (not toxic and used in very low dosages) and not harmful to pollinating bees and generalist natural enemies of pest insects (El-Sayed et al. 2006). Because pheromones are critically advantageous for communication within a species, it has so far not been documented that heavy use of pheromones has caused a species to become resistant by evolving another pheromone (Haynes and Baker 1988). Mass trapping will be more effective with pest species in which the responding sex begins searching an hour or more before the emitting sex begins calling/emission, i.e., protandry in the case of male-searching moths and protogyny in the case of female-searching species. Pest species that additionally search for a period after most of the emitting sexes cease to release pheromone will also tend to be controlled better by mass trapping.

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