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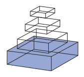

Circadian rhythms of sexual activities in moths: a review

Astrid T. Groot[1,2]*

[1] Department of Evolutionary Biology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands
[2] Department of Entomology, Max Planck Institute for Chemical Ecology, Jena, Germany

Edited by:
Emmanuelle Jacquin-Joly, Institut National de la Recherche Agronomique, France

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Monika Stengl, Universität Kassel, Germany
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***Correspondence:**
Astrid T. Groot, Department of Evolutionary Biology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, Netherlands
e-mail: a.t.groot@uva.nl

The circadian rhythm of behavior has interested many researchers in the past decades, yet amazingly little is known on the evolution of natural variation in circadian rhythms of behavior. Most research has been focused on identifying the circadian clock genes that form an intricate clock network, which turns out to be more complex with every discovery. To understand the importance of circadian rhythms of behavior in speciation, genetic analyses should be conducted on intra- and interspecific allochronic differentiation of behaviors. Many moth species show specific daily activity rhythms in their sexual activities, some species being sexually active early at night, while others are sexually active late at night. This differentiation has been suggested to have arisen to minimize communication interference between closely related species, as co-occurring and closely related species with overlapping sex pheromone blends show a temporal differentiation in their daily sexual activities. However, the genetic differentiation of this allochronic separation has barely been examined in any species so far. In this review I summarize studies conducted on timing of sexual activities in moths, and which factors have been found to influence this timing, with the aim to identify the gaps and challenges, to unravel the possible contribution of allochronic differentiation of sexual activities in moth speciation.

Keywords: sexual communication, diurnal rhythm, female pheromone, male response, sex pheromone production

INTRODUCTION

Virtually all life on earth experiences a 24-h circadian rhythm, which affects almost all behaviors, including sexual activity and mating. Circadian rhythms are governed by an endogenous circadian clock: their behavioral patterns are maintained even in the absence of direct cues (Edery, 2000; Sandrelli et al., 2008; Bloch et al., 2013). Circadian clocks are entrained by or synchronized to the 24 h light/dark cycle by external environmental cues, so-called Zeitgebers, such as light and temperature. Timing of mating also follows a daily rhythm in many species, which can be crucial not only to avoid predators, but also for finding the right mating partner, as separation in timing minimizes interference in sexual signaling between species. When species distributions change due to e.g., global warming or globalization, interactions between species with the same timing of activity may cause convergence through hybridization or divergence between populations. Thus, separation in timing of mating is a powerful isolation mechanism among species, and instrumental in speciation (Tauber et al., 2003; Coyne and Orr, 2004; Devries et al., 2008; Fergus et al., 2011; Rund et al., 2012). Yet, the role and importance of allochronic differentiation in the evolution of sexual communication and speciation is almost completely unknown.

Speciation through temporal isolation between *Drosophila* species has been linked to circadian clock genes (Kyriacou et al., 2008), but there is no known naturally occurring dimorphism in temporal timing of mating activity in fruitflies. The ideal species to investigate the importance of timing in speciation are the larger moths and butterflies (Lepidoptera, Apoditrysia), because natural variation in timing of sexual activity has been found within and between species (see **Table 1**). The Apoditrysia consist of ~145.000 species, the majority of which (~120.000) are moths (Bazinet et al., 2013), and thus the second most diverse group of insects after the Coleoptera.

In moths, reproductive isolation mostly results from species-specific sex pheromone blends (e.g., Roelofs and Carde, 1971; Roelofs et al., 1974; Cardé et al., 1977; Greenfield and Karandinos, 1979; Greenfield, 1981; Haynes and Birch, 1986; El-Sayed, 2014). Moth sexual communication seems to be under strong stabilizing selection, as deviations away from the mean in female signals as well as in the male response reduces the chance of finding a mating partner (Miller and Roelofs, 1980; Collins and Cardé, 1985; Löfstedt et al., 1990; Cossé et al., 1995; Linn et al., 1997; Zhu et al., 1997; Allison and Carde, 2008). Therefore, the evolution of moth sexual communication is an evolutionary mystery (Löfstedt, 1993; Gould et al., 2009). Additional mechanisms that have been recognized to contribute to species differentiation in Lepidoptera are habitat isolation (e.g., Roelofs and Carde, 1971; Haynes and Birch, 1986; Pashley, 1986), and seasonal and circadian variation in female signaling and male response (e.g., Roelofs and Carde, 1971; Cardé et al., 1975; Teal et al., 1978; Greenfield and Karandinos, 1979; Pashley et al., 1992; Monti et al., 1995; Sauman and Reppert, 1996; Monti et al., 1997; Froy et al., 2003; Santos et al., 2007, 2011; Zhu et al., 2008; Schöfl et al., 2009; Groot et al., 2010b; Zhan et al., 2011). However, how these factors may interact has not been explored systematically.

Table 1 | Timing of sexual activities (sex pheromone titers in female pheromone gland, female calling, male response and mating).

Family	Species	Occurrence[a]						T[b]	L:D[c]	Activity[d]	Time of day[e]							Pheromone[f]	Ref[g]
		I	II	III	IV	V	VI	°C			mid day	mid-late A	start S	early-mid S	mid-late S	end S	early-mid M	Major component	
Noctuidae	*Spodoptera exigua*							25	14:10	Pher								Z9 *E* 12-14:Ac	1
										Calling									
										Male									2
Noctuidae	*Spodoptera frugiperda - corn*							26-27	14:10	Calling								Z9-14:Ac	3, 4
										Mating									
	Spodoptera frugiperda - rice							26-27	14:10	Calling								*Z* 9-14:Ac	3, 4
										Mating									
Noctuidae	*Spodoptera descoinsi*							23	12:12	Calling								*Z* 9-14:Ac *Z* 9 *E* 12-14:Ac	5
Noctuidae	*Spodoptera latisfascia*							23	12:12	Calling								*Z* 9-14:Ac	5
Noctuidae	*Spodoptera littoralis*							25	16:8	Pher								*Z* 9 *E* 11-14:Ac	6
								24	16:8	Calling									7
								24	16:8	Calling–pre-exp									
								25	14:10	Pher									8
								25	14:10	Calling									
								25	14:10	Mating									
								22	17:7	Mating									9
								19	17:7	Male									
								19	17:7	Male-pre-exp									
Noctuidae	*Spodoptera litura*							20	16:8	Calling								*Z* 9 *E* 11-14:Ac	10
								25	14:10	Calling									11
								22	16:8	Male									2
								18	16:8	Male									10

(Continued)

Table 1 | Continued

Family	Species	Occurrence[a]						T[b]	L:D[c]	Activity[d]	Time of day[e]							Pheromone[f]	Ref[g]
		I	II	III	IV	V	VI	°C			mid day	mid-late A	start S	early-mid S	mid-late S	end S	early-mid M	Major component	
Noctuidae	*Agrotis ipsilon*							25	16:8	Pher								Z7-12:Ac	12
										Calling									
										Male									
Noctuidae	*Agrotis segetum*							23 D, 16 N*	17:7	Calling								Z7-12:Ac	13
								23	17:7	Male									14
	Heliotis virescens							26 D, 24 N	14:10	Pher								Z11-16:Ald	15
										Calling									
	Heliothis subflexa							26 D, 24 N	14:10	Pher								Z11-16:Ald	16
										Calling									
	Helicoverpa zea							25	14:10	Pher em.								Z11-16:Ald	17
								26 D, 20 N	16:8	Pher									18
										Calling									
	Helicoverpa armigera	R						25	14:10	Pher								Z11-16:Ald	19
										Calling									
								25	16:8	Calling									20
Noctuidae	*Helicoverpa assulta*							23	15:9	Pher								Z9-16:Ald	21
								25	16:8	Pher									22
								25	15:9	Pher									23
								23	15:9	Calling									21
								25	16:8	Calling									22
Noctuidae	*Trichoplusia ni*									Pher								Z7-12:Ac	24
								24	12:12	Calling									25
								O**	O**	Male									26, 27
										Mating									

(Continued)

Table 1 | Continued

Family	Species	Occurrence[a]						T[b]	L:D[c]	Activity[d]	Time of day[e]							Pheromone[f]	Ref[g]
		I	II	III	IV	V	VI	°C			mid day	mid-late A	start S	early-mid S	mid-late S	end S	early-mid M	Major component	
Noctuidae	*Autographa gamma*							26	14:10	Pher								*Z*7-12:Ac	28
										Calling									
Noctuidae	*Cornutiplusia circumflexa*							26	14:10	Pher								*Z*7-12:OH	28
										Calling									
Noctuidae	*Sesamia nonagrioides*							25	16:8	Pher								*Z*11-16:Ac	29
										Calling									
Noctuidae	*Pseudaletia/ Mythimna unipuncta*							25	16:8	Pher								*Z*11-16:Ac	30
										Calling									
								15	16:8	Calling									
								25	12:12	Pher									
										Calling									
Noctuidae	*Mythimna separata*							23	14:10	Calling								*Z*11-16:Ald	31
Noctuidae	*Mamestra configurata*							30	16:8	Calling								*Z*11-16:Ac	32
								20											
								10											
Noctuidae	*Euxoa declarata*							19-20	12:12	Calling								Z5-10:Ac	33
	Euxoa campestris																		
	Euxoa rockburnei																		
Pyralidae	*Dioryctria abietella*							27	12:12	Pher								*Z*3*Z*6*Z*9*Z*12 *Z*15-25Hy,	34
										Calling								*Z*9*E*11-14:Ac	

(Continued)

Table 1 | Continued

Family	Species	Occurrence[a] I	II	III	IV	V	VI	T[b] °C	L:D[c]	Activity[d]	Time of day[e] mid day	mid-late A	start S	early-mid S	mid-late S	end S	early-mid M	Pheromone[f] Major component	Ref[g]
										Male									
Pyralidae	*Plodia interpunctella*							28	14:10	Calling								*Z9E*12-14:Ac	35
								23	17:7	Calling									36
Pyralidae	*Ephestia kuehniella*							23	17:7	Calling								*Z9E*12-14:Ac	36
Crambidae	*Ostrinia nubilalis Z*							26	18:6	Pher								*Z*11-14:Ac	37
									18:6	Calling									
	Ostrinia nubilalis E									Pher								*E*11-14:Ac	
										Calling									
Crambidae	*Chilo suppressalis*							20	16:8	Calling								*Z*11-16:Ald	38
								30											
								20	16:8	Mating									
								30											
Crambidae	*Conogethes punctiferalis*							23	15:9	Pher								*E*10-16:Ald	39
										Calling									
Tortricidae	*Grapholita molesta*							25	16:8	Calling								*Z*8-12:Ac	40
								20	16:8										
								25	16:8	Male									
Tortricidae	*Platynota stultana*							24	16:8	Pher								*E*11-14:Ac	41
										Calling									
								20											
								14											

(Continued)

Table 1 | Continued

Family	Species	Occurrence[a]						T[b]	L:D[c]	Activity[d]	Time of day[e]							Pheromone[f]	Ref[g]
		I	II	III	IV	V	VI	°C			mid day	mid-late A	start S	early-mid S	mid-late S	end S	early-mid M	Major component	
Tortricidae	*Choristoneura rosaceana*							20	16:8	Pher								*Z*11-14:Ac	42
								20	16:8	Pher									43
										Calling									
Tortricidae	*Choristoneura fumiferana*							20	16:8	Pher								*E*11-14:Ald	43
										Calling									
Tortricidae	*Cydia pomonella*							23	16:8	Calling								*E*8*E*10-12:OH	44
								16											
								23		Male									
								16											
Tortricidae	*Argyrotaenia velutinana*							24	16:8	Calling								*Z*11-14:Ac	45
								16											
								24		Male									
								16											
Lymantriidae	*Lymantria dispar*							25	16:8	Pher								Z7,8-Epoxy-2-methyloctadecane (Disparlure)	46
								24	16:8	Calling									47
								O	O	Male									46
Arctiidae	*Holomelina lamae*							24	16:8	Pher								2me-17Hy	48
								24	16:8	Release									
										Calling									
Arctiidae	*Holomelina immaculata*							24	16:8	Calling								2me-17Hy	45
								16											

(Continued)

Table 1 | Continued

Family	Species	Occurrence[a]						T[b]	L:D[c]	Activity[d]	Time of day[e]							Pheromone[f]	Ref[g]
		I	II	III	IV	V	VI	°C			mid day	mid-late A	start S	early-mid S	mid-late S	end S	early-mid M	Major component	
Sesiidae	*Synanthedon pictipes*							27 - O	16:8	Calling								E3Z13-18:Ac	49
								14-O***											
Gelechiidea	*Phthorimaea operculella*							26	14:10	Pher									50
Pterophoridae	*Platyptilia carduidactyla*							21 D, 16 N	14:10	Calling								*Z*11-16:Ald	51
									12:12	Calling									
									10:14	Calling									
								O	O	Male									
Pterophoridae	*Platyptilia williamsii*							21 D, 16 N	14:10	Calling								*Z*11-16:Ald	51
									12:12	Calling									
									10:14	Calling									
								O	O	Male									
Sphingidae	*Manduca sexta*							24-26	16:8	Calling								E10Z12-16:Ald	52

[a]Occurrence in Ecozones: I, Neotropic; II, Nearctic; III, Afrotropic; IV, Palearctic; V, Indomalaya; VI, Australasia (R = recent introduction).

[b]T: Temperature in experiment, same in photophase and scotophase unless otherwise indicated.*D, temperature at photophase; N, temperature at scotophase; **O, outside trap catches; ***Females held at 14°C in the morning, after which they were moved to screen cages outside.

[c]L:D Light:Dark hours in experiment.

[d]Act, Daily activity patterns; Pher, Pheromone titers in the female sex pheromone gland; Pher-em, pheromone emission (gland extruded artificially by injecting females with EDTA-Na_4 so that females could not retract their gland once it was extruded); Release, airborne collection of pheromone collected from live females. Calling, female calling; Male, male response; pre-exp, pre-exposed to pheromone.

[e]Time of day: activity at specific times of the day, distinguished into the following periods. Midday, Mid-late Afternoon, Start Scotophase, Early-mid Scotophase, Mid-late Scotophase, End Scotophase, Early-mid Morning. White, no activity; Gray, some activity; Black, peak activity.

[f]Pheromone: The major sex pheromone component is given. For the full sex pheromone blends of each species, see Pherobase.com.

[g]References: 1 (Dong and Du, 2001 #1954); 2 (Saito, 2000 #1891); 3 (Pashley et al., 1992 #69); 4 (Schöfl et al., 2009 #293); 5 (Monti et al., 1995 #1677); 6 (Martinez and Camps, 1988 #1896); 7 (Sadek et al., 2012 #1173); 8 (Dunkelblum et al., 1987 #2007); 9 (Silvegren et al., 2005 #37); 10 (Kawasaki, 1986 #1892); 11 (Wei et al., 2004 #2065); 12 (Gemeno and Haynes, 2000 #1973); 13 (Löfstedt et al., 1982 #1862); 14 (Rosen et al., 2003 #39); 15 (Pope et al., 1982 #1231); 16 (Heath et al., 1991 #1311); 17 (Pope et al., 1984 #341); 18 (Raina et al., 1986 #351); 19 (Rafaeli and Soroker, 1989 #94); 20 (Kou and Chow, 1987 #1967); 21 (Kamimura and Tatsuki, 1993 #1966); 22 (Park et al., 1996 #2066); 23 (Choi et al., 1998 #2067); 24 (Hunt and Haynes, 1990 #1933); 25 (Sower et al., 1971 #1986); 26 (Saario et al., 1970 #1953); 27 (Birch, 1977 #2008); 28 (Mazor and Dunkelblum, 2005 #1926); 29 (Babilis and Mazomenos, 1992 #1983); 30 (Delisle and McNeil, 1987 #314); 31 (Han and Gatehouse, 1991 #1976); 32 (Gerber and Howlader, 1987 #1977); 33 (Teal et al., 1978 #1951); 34 (Fatzinger, 1973 #1952); 35 (Hirashima et al., 2001 #2014); 36 (Zavodska et al., 2012 #1574); 37 (Karpati et al., 2007 #1965); 38 (Kanno, 1979 #1905); 39 (Konno, 1986 #1899); 40 (Baker and Cardé, 1979 #457); 41 (Webster and Cardé, 1982 #303); 42 (Delisle and Royer, 1994 #1975); 43 (Delisle et al., 1999 #2068); 44 (Castrovillo and Cardé, 1979 #1948); 45 (Cardé et al., 1975 #302); 46 (Giebultowicz et al., 1992 #1901); 47 (Charlton and Cardé, 1982 #1935); 48 (Schal et al., 1987 #1580); 49 (Gorsuch et al., 1975 #2069); 50 (Ono et al., 1990 #1898); 51 (Haynes and Birch, 1986 #1944); 52 (Itagaki and Conner, 1988 #2073).

Moths show very specific daily activity patterns in their sexual activities; in some species, females start calling at the onset of scotophase and stop calling after midnight (e.g., *Spodoptera frugiperda corn-strain, S. descoinsi, Agrotis segetum, Chilo suppressalis*), while in other species females start calling after midnight and stop at the end of the scotophase (e.g., *Spodoptera frugiperda* rice-strain, *S. latisfascia*, *Heliothis virescens, Trichoplusia ni, Pseudaletia unipuncta, Sesamia nonagrioides, Manduca sexta*; see **Table 1**). These well-defined daily patterns have also been found for sex pheromone production (e.g., *Spodoptera exigua, S. littoralis, Heliothis virescens, H. subflexa, Agrotis ipsilon, Autographa gamma*) and for male response (e.g., *Spodoptera exigua, S. littoralis, S. litura, Agrotis segetum, A. ipsilon, Dioryctria abietella, Cydia pomonella, Argyrotaenia velutinana* (see **Table 1**).

Even though daily patterns of sexual activity (female calling, male response and mating) have been studied in a large number of moth species, virtually nothing is known on the evolution of allochronic differentiation, i.e., differentiation in daily patterns of sexual activity. For this we need to know the underlying physiological and genetic basis of variation in timing of daily sexual activities within and between closely related species. In this review, I summarize the knowledge that has been gathered on timing of sexual activities in moths, the identified genes and factors that have been found to affect timing of sexual behavior, which factors have been identified to affect circadian rhythms in moths, and the genetic basis of variation in timing of sexual activities. In this way, I aim to identify the gaps in our knowledge that we need to fill to understand how variation in timing of activity at night may contribute to the speciation process in moths.

PHENOTYPE: VARIATION IN TIMING OF DAILY SEXUAL ACTIVITY IN MOTHS

In the clock literature, a behavior is considered circadian only when this behavior (a) shows an endogenous free running period that lasts ∼24 h, (b) shows an entrainable period, i.e., the period can be reset by external stimuli, and (c) shows temperature compensation (circadian rhythm is maintained over a broad range of temperatures). In moths, the sexual behaviors that have been shown to have a 24-h rhythm are sex pheromone production in females, female calling, male response and mating. That this rhythm is truly circadian has been identified specifically in a few moth species, such as the cabbage looper *Trichoplusia ni* (Sower et al., 1971), the true armyworm *Pseudaletia unipuncta* (Turgeon and McNeil, 1982; Delisle, 1992), the oriental fruit moth *Grapholitha molesta* (Baker and Cardé, 1979), the codling moth *Cydia pomonella* (Castrovillo and Cardé, 1979) and the Egyptian cotton leafworm *Spodoptera littoralis* (Sadek et al., 2012). In these species the daily rhythm persisted in the absence of Zeitgebers, specifically light. In all moth species listed in **Table 1**, a daily rhythm in calling behavior has been found. Only few studies found that species become arrhythmic in constant darkness *and* in constant light. One such example is the Indian mealmoth *Plodia interpunctella* (Zavodska et al., 2012), so that its timing of sexual activities under normal L:D conditions does not seem to be regulated by an endogenous circadian clock. Maybe its endogenous clock is no longer functional, because it is a stored grain pest and is exclusively found indoors, i.e., in artificial light (Zavodska et al., 2012). Other possible explanations are that the functional clock may not remain synchronous or may be masked under constant conditions.

The calling rhythms overlap with the daily fluctuations in sex pheromone titer in some species but not in others, as described below. Since pheromone production is not always synchronous with calling behavior, these seem to be two different traits that may be regulated differently. Male response to sex pheromone has been shown to occur at specific hours at night as well (e.g., Fatzinger, 1973; Castrovillo and Cardé, 1979; Haynes and Birch, 1986; Kawasaki, 1986; Rosen et al., 2003; Silvegren et al., 2005; Merlin et al., 2007), and usually coincides with female calling time (e.g., Cardé et al., 1975; Castrovillo and Cardé, 1979), although not always (e.g., Saario et al., 1970; Cardé et al., 1974; Kawasaki, 1986). The timing of male response is thus a third trait in moth sexual communication that may have its own genetic basis.

FEMALE CALLING

Most research has been conducted on the time of female calling, probably because this is a relatively easy phenotype to measure, as females visibly extrude their sex pheromone gland from their abdomen when calling. Even though calling activity is affected by temperature, age and mating, as described below, in general some species are most active early at night, while other species start calling in the second part of the night and show peak calling activity toward the end of the scotophase. There is no phylogenetic correlation in the timing of calling, as within the same families and even genera early and late callers are found (see **Table 1**).

The variation in timing of female calling is most likely related to the level of overlap in sex pheromone composition between co-occurring species, because this minimizes possible communication interference (Roelofs and Cardé, 1974; Cardé et al., 1975; Baker and Cardé, 1979; Haynes and Birch, 1986). For example, *Spodoptera frugiperda* consists of two strains, the so-called corn and rice strain (Pashley, 1986), which co-occur throughout North and South America. Both strains differ somewhat in their sex pheromone composition (Groot et al., 2008; Lima and McNeil, 2009). However, the response of males to these differences did not differ much between the two strains, suggesting that divergence between these strains cannot be explained by their variation in sexual communication (Unbehend et al., 2013). These strains do differ significantly in their timing of sexual activity (Pashley et al., 1992; Schöfl et al., 2009), which is likely the most important contributor to their divergence (Groot et al., 2008, 2014). Other examples of overlapping pheromone but non-overlapping timing of sexual activity are *Spodoptera descoinsi* and *S. latisfascia* (Monti et al., 1995), *Platyptilia carduidactyla* and *P. williamsii* (Haynes and Birch, 1986), *Euxoa declarata*, *E. campestris*, and *E. rockburnei* (Teal et al., 1978) and *Lymantria monacha* and *L. dispar* (Roelofs and Cardé, 1974). The latter two species co-occur in Europe, where *L. dispar* is sexually active during the day, while *L. monacha* is active at dusk and at night (Roelofs and Cardé, 1974). In the USA, where *L. dispar* was introduced and *L. monacha* is absent, the timing of sexual activity in *L. dispar* expands into the night, which makes it likely that selection pressure from *L. monacha* has restricted the timing of sexual activity of *L. dispar* in Europe to the daytime (Haynes and Birch, 1986).

Conversely, examples of co-occurring species with overlapping timing of activity but non-overlapping sex pheromone are the E- and Z-strain of *Ostrinia nubilalis* (Karpati et al., 2007), *Heliothis virescens* and *H. subflexa* (Heath et al., 1991; Groot et al., 2009) and *Helicoverpa armigera* and *H. assulta* (Kou and Chow, 1987; Rafaeli and Soroker, 1989; Kamimura and Tatsuki, 1993). In the latter two species groups, one of the species (*Heliothis subflexa* and *Helicoverpa assulta*) produce and emit not only attractive sex pheromone compounds, but also compounds that specifically inhibit the attraction of heterospecific males, i.e., *Heliothis virescens* and *Helicoverpa armigera*, respectively (Kamimura and Tatsuki, 1993; Boo et al., 1995; Groot et al., 2006). The presence of such inhibitory compounds in the sex pheromone blend indicates that communication interference is an important selection force in the evolution of moth sexual communication (Groot et al., 2006).

Variation in female calling may also be related to the presence and timing of activities of predators and parasitoids (Baker and Carde, 1978; Cardé and Baker, 1984; Acharya and McNeil, 1998; Skals et al., 2005; Conner and Corcoran, 2012; Corcoran and Conner, 2012). A few studies have shown that attraction of male moths to female pheromone is disrupted by ultrasounds, indicating the presence of predatory bats (Baker and Carde, 1978; Acharya and McNeil, 1998), although there can be a trade-off in male response to pheromone and evasive behavior to sounds from predators (Skals et al., 2005). However, whether and to what extent timing of moth sexual activity is driven by timing of activity of predators and parasitoids is difficult to assess. In addition, female pheromone may adhere to plant leaves, so that day-active parasitoids may still home in on the eggs oviposited by night-active female moths, as the pheromone gland surrounds the ovipositor (Noldus et al., 1991; Xu et al., in press).

SEX PHEROMONE PRODUCTION IN FEMALES

In moths, pheromone production in females has been shown to be regulated by Pheromone Biosynthesis Activating Neuropeptide (PBAN) (Raina et al., 1989; Rafaeli and Jurenka, 2003; Jurenka, 2004; Jurenka and Rafaeli, 2011); (but see Tang et al., 1989). This neuropeptide is produced by three groups of neurons present in the suboesophagal ganglion (SOG) and released via the the corpus cardiacum (CC) into the hemolymph (Jurenka, 2004). When PBAN binds to the PBAN receptor (PBANr) in the sex pheromone gland, a calcium channel is opened and the influx of Ca^{2+} initiates pheromone production (Rafaeli et al., 2007) (see **Figure 1** for a simplified schematic overview). The sex pheromone precursors stearic acid, palmitic acid, and myristic acid may be stored first as triacyl glycerides, or directly converted to the end products, which are generally aldehydes, alcohols and acetate esters (Jurenka, 2004). PBAN may act on a late stage in the biosynthetic pathway, by activating fatty acid reduction (Arima et al., 1991) or by mobilizing the fats stored in triacylglycerols (Matsumoto et al., 2010) (pathway 1 in **Figure 1**), or PBAN may control the early stage of pheromone biosynthesis (pathway 2 in **Figure 1**) (Eltahlawy et al., 2007; Tsfadia et al., 2008; Jurenka and Rafaeli, 2011).

Whether the action of PBAN is a circadian humoral regulator seems to depend on whether the circadian rhythm of PBAN levels in the hemolymph is synchronized with pheromone production. In a number of moth species, sex pheromone production in females has been found to occur *de novo* every day, and has been found to be synchronous with female calling (e.g., Fatzinger, 1973; Coffelt et al., 1978; Pope et al., 1982; Raina et al., 1986, 1989; Rafaeli and Soroker, 1989; Raina, 1993; Ramaswamy et al., 1995; Iglesias et al., 1999, 2002; Foster, 2000; Dong and Du, 2001; Rafaeli and Jurenka, 2003; Xiang et al., 2010). However, in other species pheromone production seems to occur at different times, usually before calling (Coffelt et al., 1978; Bjostad et al., 1980; Webster and Cardé, 1982; Konno, 1986; Schal et al., 1987; Giebultowicz et al., 1992). For example, in *Platonota sultana*, pheromone levels were high before females started calling and then decreased significantly once the females called (Webster and Cardé, 1982). Alternatively, the pheromone levels in the gland may be relatively constant day and night, e.g., in *Trichoplusia ni*, *Pectinophora gossypiella,* and *Argyrotaenia velutinana* (Hunt and Haynes, 1990; Jurenka et al., 1994; Rafaeli and Klein, 1994). Hence, in these species biosynthesis of sex pheromone seems to occur independently from when females are actually calling, suggesting that pheromone can be synthesized rapidly during calling (Schal et al., 1987) and that pheromone can be stored in the gland before calling.

Pheromone precursors can be stored in the gland as glycerolipids, as mentioned above, which may be mobilized for pheromone biosynthesis, at least in *Bombyx mori* (Fonagy et al., 2001; Matsumoto et al., 2002, 2010). However, in other species (*Argyrotaenia velutinana*, *Ostrinia nubilalis*, and *Heliothis virescens*) these precursors seem to be dead end stores for excess precursor acids and not used for pheromone biosynthesis (Bjostad et al., 1987; Foster, 2004; Foster and Anderson, 2012). These differences are likely due to nutrient intake and pheromone biosynthesis control via PBAN: in *B. mori*, females do not feed and PBAN seems to act on a late stage in the biosynthetic pathway (Arima et al., 1991; Matsumoto et al., 2010). In *H. virescens*, females do feed on nectar, and can thus replenish carbohydrate resources to start pheromone biosynthesis from the basic building blocks acetyl CoA and malonyl CoA (Jurenka, 2003; Foster, 2009). In addition, in heliothine moths PBAN controls the early stage of pheromone biosynthesis (Eltahlawy et al., 2007; Jurenka and Rafaeli, 2011) and pheromone production coincides with female calling (Pope et al., 1982; Heath et al., 1991). Thus, it seems that in species that store pheromone precursors, pheromones biosynthesis is not in phase with female calling, while in species without such storage and with *de novo* synthesis every night, pheromone biosynthesis is in the same phase as female calling.

MALE ACTIVITY AND RESPONSE

That male response to female sex pheromone shows a circadian rhythm in moths has been shown for *Cydia pomonella*, *Agrotis segetum, Trichoplusia ni*, and *Spodoptera littoralis* (Castrovillo and Cardé, 1979; Linn et al., 1996; Rosen et al., 2003; Silvegren et al., 2005; Merlin et al., 2007): in the absence of Zeitgebers, these species showed persistent rhythms in their attraction to sex pheromone. Of course, sexual communication can only be effective if female calling and male response are synchronized. Such synchronization reduces metabolic costs and likely also predation

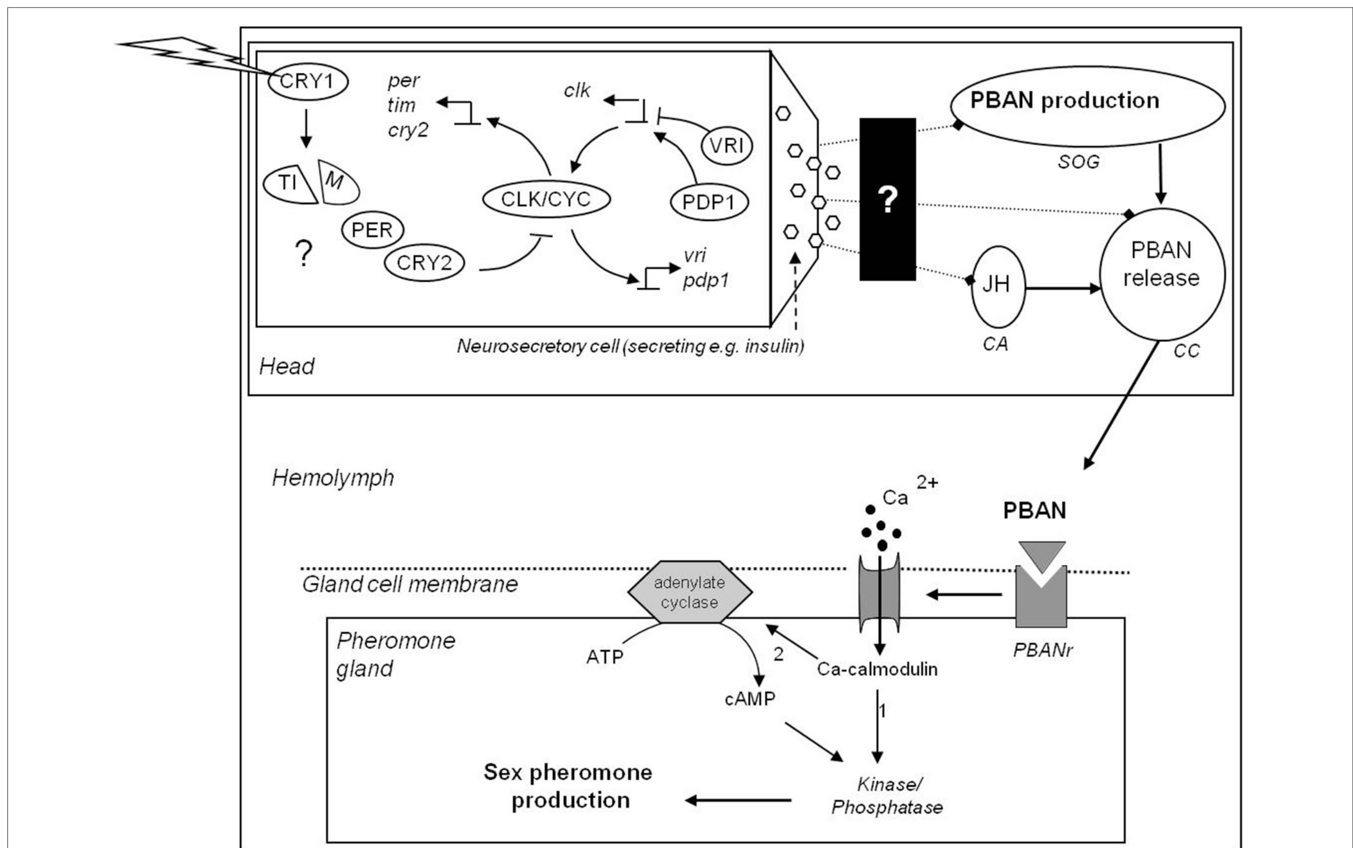

FIGURE 1 | Simplified flow diagram of circadian feedback loops in neurosecretory cells and their possible regulation of moth sex pheromone biosynthesis. Question marks are the outstanding questions for moths. Clock genes are expressed in neurosecretory cells [pars lateralis (PL) and pars intercerebralis (PI)], but maybe also in the subesophagal ganglion (SOG), corpus cardiacum (CC) and corpus allatum (CA) (see Sandrelli et al., 2008). CRY1 is activated by light and degrades TIM. CRY2 is light-independent and inhibits CLK/CYC mediated expression of *per/tim*. In both day-active and night-active insects, *per* and *tim* are transcribed mostly at night. The neurosecretory cells innervate the CA, CC and/or the SOG (indicated with dotted lines with diamond) (Bloch et al., 2013), activating JH production in CA. Exactly how this activation occurs is still a black box, although it is known that insulin is involved (Reppert et al., 2010). PBAN is produced in the SOG, likely continuously, so that it accumulates during the photophase in some moths (Rafaeli, 1994). PBAN transport to and its release from the CC into the hemolymph is regulated by a circadian clock (Rafaeli, 1994), but how exactly is not known. When PBAN binds to the PBAN receptor (PBANr, a G-protein coupled receptor) in the pheromone gland cell membrane, a Ca-channel opens. The influx of Ca^{2+} either stimulates phosphatases directly (in *B. mori*; path (1) or activates cAMP via adenylate cyclase, which in turn stimulates phosphatases and/or kinases (in Heliothines; path (2), after which pheromone is produced (either starting with acetyl CoA and malonyl CoA or acting on the final reduction of the pheromone precursors) (Blomquist and Vogt, 2003; Jurenka, 2004). The neurosecretory secretions act similarly as is shown for PBAN, i.e., by binding to receptors they cause a Ca^{2+} influx, which (de)phosphorylates proteins in the cytoplasm, affecting transcription of e.g., clock genes. Overall, it is not clear yet whether circadian rhythms in moth behavior or physiology are regulated by peripheral clocks and/or central pacemakers that act via neuronal and/or via endocrine signaling pathways, or through interactions between these factors (Bloch et al., 2013). See text for further explanations.

(Cardé and Baker, 1984; Acharya and McNeil, 1998; Silvegren et al., 2005; Skals et al., 2005). However, a wider temporal male response window could be advantageous for males to locate early as well as late calling females (Linn, 1997). As mentioned above, the timing of male usually coincides with female calling time (e.g., Cardé et al., 1975; Castrovillo and Cardé, 1979), but exceptions do occur (e.g., Saario et al., 1970; Cardé et al., 1974; Kawasaki, 1986).

GENOTYPE: IDENTIFIED GENES AND FACTORS UNDERLYING CIRCADIAN RHYTHMS OF SEXUAL BEHAVIOR

THE CORE CIRCADIAN CLOCK: TWO INTERACTING FEEDBACK LOOPS

The genes underlying variation in circadian rhythms of behavior in general has been extensively studied in *Drosophila melanogaster*, mostly through mutagenesis experiments (Konopka and Benzer, 1971; Hall, 2003; Zhang and Kay, 2010). The center of the clock represents the activation of *period (per)* and *timeless (tim)* and the binding of protein dimers to E-boxes that are found in the promoter region of many circadian genes, e.g., *per*, *tim*, *vrille*, *PAR domain protein 1e (pdp1e)* (Peschel and Helfrich-Forster, 2011). In *D. melanogaster*, two interlocked feedback loops form the clock gene network, centered around the rhythmic expression of *clk* (Cyran et al., 2003; Hardin, 2005). In one loop, *per* and *tim* transcription is activated by the binding of the CLOCK/CYCLE (CLK/CYC) to their promoter. After translation, PER/TIM heterodimerize in the cytoplasm and are translocated to the nucleus where PER

inhibits CLK/CYC activity in a ~24 h cycle (see also **Figure 1**). In a stabilizing loop regulating clock expression levels, v*rille* and *pdp1* are transcribed. The expression of *clock* is repressed by VRILLE that binds to the VRILLE/PDP1 binding box in the *clock* promoter, after which PDP1 accumulates and substitutes VRILLE in binding to the VRILLE/PDP1 binding box, which promotes *clock* expression (Cyran et al., 2003; Hardin, 2005).

In Lepidoptera, most work on clock genes has been conducted in the moth *Anthereae pernyi* (Prestwich et al., 1986; Reppert et al., 1994; Levine et al., 1995; Sauman and Reppert, 1996, 1998; Gotter et al., 1999; Sauman et al., 2000; Chang et al., 2003) and *Danaus plexippus* (Froy et al., 2003; Sauman et al., 2005; Zhu et al., 2008, 2009; Zhan et al., 2011), as well as in *Bombyx mori* (Sehadova et al., 2004) and *Manduca sexta* (Wise et al., 2002; Schuckel et al., 2007). These studies have focused on verification of the identified clock genes from *Drosophila* in lepidopteran species. In these comparative analyses, some essential differences have been found, as described below.

In *Drosophila melanogaster*, there are at least three light-input pathways for the daily light-input entrainment (Helfrich-Forster et al., 2001), one of which is through the circadian photoreceptor Cryptochrome (CRY) that is acting in the pacemaker cells themselves (Emery et al., 1998), and mediates the light-degradation of TIM (Young et al., 1996; Ivanchenko et al., 2001; Hall, 2003; Peschel et al., 2006). In constant light, flies become arrhythmic, which is likely due to light-dependent degradation of TIM (Konopka et al., 1989). TIM stabilizes PER in the cytoplasm after dark (see review Peschel and Helfrich-Forster, 2011).

In Lepidoptera (as well as in some other insects) there are two cryptochromes, CRY1 and CRY2 (Zhu et al., 2005, 2008) instead of one. CRY1 (CRY-d) is similar to the *Drosophila* CRY and seems to have a similar function as in the flies, while CRY2 (CRY-m) is homologous to vertebrate CRY and functions as a transcriptional repressor to *per* transcription (Merlin et al., 2013), replacing the function of PER (see review Sandrelli et al., 2008). Whether TIM has a similar function in Lepidoptera as described in *Drosophila*, i.e., stabilizing PER, seems thus unlikely but remains to be investigated.

Also, in contrast to *Drosophila*, PER has not been found in the nucleus in brain neurons in the investigated lepidopteran species so far (Sandrelli et al., 2008), although Schuckel et al. (2007) found it in the nucleus of olfactory receptor neurons in *Manduca sexta*. The inability to find PER in the nucleus in other studies may be due to a technical problem, e.g., a problem with the antibodies used (Schuckel et al., 2007). However, this is an unsatisfactory explanation as no clock proteins except monarch CRY2 has ever been found nuclear, and in *Danaus plexippus* all immunocytochemistry experiments, including those on PER, have been performed with species-specific antibodies. In night-active moths, it seems likely that activation of some core clock genes are reversed or that oscillators are differently coupled compared to day-active insects, such as *Drosophila* and day-active butterflies, although *per* and *tim* transcription levels are highest at night both in day- and night-active insects (Giebultowicz, 2000).

LOCALIZATION OF THE CLOCK CELLS

Clock genes are expressed in the central nervous system in the brain, where the circadian master clock is located (Sandrelli et al., 2008). In *Drosophila*, the photoreceptors are located in many clock neurons in the brain and directly respond to light stimuli (see review Peschel and Helfrich-Forster, 2011). The physical location of the Lepidoptera clock, at least in the species investigated, is in the dorsolateral protocerebrum, specifically in four large neurons clustered in the pars lateralis (Truman, 1972, 1974; Wise et al., 2002; Sehadova et al., 2004; Sauman et al., 2005; Zhu et al., 2008). These neurons are type 1a neurosecretory cells. In *Danaus plexippus* all four neurons co-express *tim* and *cry2*, while two of the four neurons also co-express *per* and *cry1* (Wise et al., 2002; Sehadova et al., 2004; Sauman et al., 2005; Zhu et al., 2008)

In insects, clocks in peripheral tissues (antennae, gut, reproductive tissues and even epidermis) also function independently of the core clock (Giebultowicz, 2000, 2001; Helfrich-Forster, 2004). For example, rhythmic release of sperm bundles has been found in the moth species *Cydia pomonella* (Gvakharia et al., 2000), *Lymantria monacha* (Giebultowicz et al., 1989; Riemann and Giebultowicz, 1991), and *Spodoptera littoralis* (Kotwica-Rolinska et al., 2013). *Per*-positive epithelial cells that surround the *vas deferens* lumen were found to have a daily cycle of secretory activity, and this circadian activity seems vital in moths, as disruption of this rhythm through constant light leads to male sterility (Giebultowicz et al., 1990). *Per* is also present at the base of chemoreceptor cells in the antennae (Plautz et al., 1997). In the monarch butterfly, antennal circadian clock coordinates sun compass orientation during migration (Merlin et al., 2009; Reppert et al., 2010), which seem to oscillate independently from the brain, as clock protein and mRNA levels oscillated even *in vitro* and continued to respond to light (Merlin et al., 2009; Reppert et al., 2010).

GENE REGULATORS: ENDOCRINE SIGNALS

The general regulators of clock genes are endocrine signals that, when bound to receptors (generally G-protein coupled receptors), cause an influx of Ca^{2+} or K^+, which (de)phosphorylates clock proteins in the cytoplasm, which in turn changes their stability and causes their degradation (Hardin, 2011; Peschel and Helfrich-Forster, 2011). Several kinases have been identified that phosphorylate PER, CLK, and TIM in *Drosophila* (Hardin, 2011).

The main neurotransmitter that has been studied most thoroughly is Pigment Dispersing Factor (PDF), which is a well-conserved neuropeptide present in master clock neurons of all insects studied so far, including Blattodea, Coleoptera, Hymenoptera and Lepidoptera (Hermann et al., 2013). The PDF receptor is located on most clock neurons (Shafer et al., 2008), and is considered to be the main output factor of the clock, acting as a neuromodulatory as well as a synchronizing signal between different clock neuron clusters (Petri and Stengl, 1997; Helfrich-Forster, 1998; Schneider and Stengl, 2005; Shafer et al., 2008). In *Drosophila*, PDF is co-expressed with PER, but this is not the case in other insects (Zavodska et al., 2003; Hermann et al., 2013). Zavodska et al. (2012) examined the location of PDF in the two moth species *Plodia interpunctella* and *Ephestia*

kuehniella, and found in both species PDF-positive cells in the pars intercerebralis, the superior lateral protocerebrum, the optic lob and the suboesophagal ganglion. However, in *P. interpunctella* no PDF-stained cells were found in the interior medial protocerebrum, which may at least partly be correlated to the fact that this species is arrhythmic or not synchronized in constant darkness *and* in constant light (Zavodska et al., 2012).

As mentioned in 1b, sex pheromone production is regulated by PBAN. At what time of the day or night PBAN is released from the SOG seems to depend on juvenile hormone (JH) (Cusson and McNeil, 1989; Gadenne et al., 1993; Cusson et al., 1994). JH is synthesized and released from the corpora alata (CA), which is innervated by neurosecretory cells that have their cell bodies in the brain, the corpora cardiaca (CC), or the suboesophagal ganglion (SOG) (Bloch et al., 2013). JH biosynthesis can be regulated via direct or indirect neuronal pathways coming from cells in the circadian network (Bloch et al., 2013) (see also **Figure 1**). In other insects, JH regulates production or release of sex attractants, i.e., in cockroaches (Schal et al., 1997) and bark beetles (Seybold and Tittiger, 2003). Also in some migratory moth species there is evidence that JH regulates PBAN biosynthesis or release (Cusson and McNeil, 1989; Gadenne et al., 1993; Picimbon et al., 1995). However, in non-migratory moth species, the exact role of JH in regulating daily sex-pheromone production is still poorly understood (Bloch et al., 2013). In the non-migratory *Helicoverpa armigera*, JH has been shown to prime the pheromone gland just before the females emerge, i.e., only during development (Fan et al., 1999).

JH may be involved in the circadian modulation of the male response to the female calling signals, as has been found in *Agrotis segetum* (Rosen et al., 2003). In the related species *A. ipsilon,* JH has been found to regulate male sensitivity to female sex pheromone in the antennal lobes, but not in the antenna (Anton and Gadenne, 1999). However, it is not clear whether JH titers in male *Agrotis* moths vary during the day. In addition, the temporal relationship between peak JH titers and male flight activity may differ between species. For example, the crickets *Gryllus rubens* and *Scapteriscus vicinus* have similar diurnal JH titer profiles, while *G. rubens* is active throughout the night and *S. vicinus* is only active for a short period directly after sunset (Bloch et al., 2013).

In addition to JH, biogenic amines, such as melatonin, octopamine, serotonin, and dopamine may affect diurnal activity patterns (reviewed by Bloch et al., 2013). For example, in *Tichoplusia ni* melatonin levels are highest at night and show rhythmicity in constant darkness but not in constant light (Linn et al., 1995). In *Manduca sexta*, serotonin levels also show a diurnal pattern, with peak levels when these moths are most active (Kloppenburg et al., 1999). Octopamine has also been indicated as controlling pheromone production, not through activation or release of PBAN, but through inhibition of pheromone production (Rafaeli and Gileadi, 1995; Rafaeli et al., 1999; Hirashima et al., 2001). Octopamine has also been proposed to work as an intermediate messenger during the stimulation of sex pheromone production in *H. virescens* (Christensen et al., 1991, 1992, 1994), although octopamine has been found to have pheromonotropic activity of PBAN in *H. armigera* (Hirashima et al., 2001). Thus, the exact role of octopamine in pheromone production is not clear yet (Jurenka, 2004).

FACTORS AFFECTING CIRCADIAN RHYTHMS IN MOTHS

The exogenous factors that affect timing of moth sexual communication are photoperiod and temperature (Sower et al., 1971; Cardé and Roelofs, 1973; Cardé et al., 1975; Baker and Cardé, 1979; Castrovillo and Cardé, 1979; Turgeon and McNeil, 1983; Haynes and Birch, 1984; Delisle and McNeil, 1986), which are the two main Zeitgebers in general. Other exogenous factors that have been investigated to a lesser extent are relative humidity (Royer and McNeil, 1993) and the chemical environment (Anderson et al., 2003, 2007; Silvegren et al., 2005; Sadek et al., 2012).

LIGHT AND LENGTH OF THE SCOTOPHASE

In moths, a change in daylength can affect timing of female calling, generally to calling later at night when the night gets longer (Delisle and McNeil, 1986; Gerber and Howlader, 1987), although exceptions may occur (e.g., Haynes and Birch, 1986). This may indicate that species in the north are more likely to be active earlier in the night than species closer to the equator. That the length of the scotophase affects the calling rhythm has been shown in *Mamestra configurata* (Gerber and Howlader, 1987) and in *Pseudaletia unipuncta* (Delisle and McNeil, 1986): the longer the night, the longer the calling period (Gerber and Howlader, 1987), and in longer nights (12L: 12D), calling started later that in shorter nights (16L: 8D), indicating a relationship between mean onset time of calling and the midpoint of scotophase (Delisle and McNeil, 1986). However, in *Platyptilia carduidactyla* and *P. williamsii*, a change in daily photoperiodicity did not affect the timing of female calling behavior much (Haynes and Birch, 1986), although in *P. williamsii* females called only in the mid-late scotophase under a light:dark (L:D) regime of 12:12 and 10:14, while they also called in the early morning when kept under 14:10 L:D.

TEMPERATURE

Temperature affects sexual activity of moths generally such that at lower temperatures females call earlier in the scotophase (see **Table 1**) (Cardé et al., 1975; Baker and Cardé, 1979). Interestingly, Baker and Cardé (1979) suggest that a decrease in temperature may lift inhibition of calling instead of inducing calling, while higher temperatures may delay expression and thus suppress calling until later in the night. Most likely, the extent to which such shifts occur depends on the possibility of communication interference with closely related species in the same area, as well as the risk of encountering predators (Cardé et al., 1975).

Even though synchronization between female calling and male activity would be most effective, some studies have shown that males respond differently to changes in temperature compared to females, which can result in asynchronous sexual activities in males and females (Baker and Cardé, 1979; Cardé and Baker, 1984; Giebultowicz et al., 1992; Linn, 1997). For example, in *Lymantria dispar*, females show a shift in pheromone titer to earlier in the day, i.e., from the evening to the early morning when mid-afternoon temperatures are high (33°C), while male response to pheromone shifts to later in the day, i.e., from

morning to mid-afternoon at higher temperatures (Giebultowicz et al., 1992).

The mechanism of how temperature can cause a temporal shift in sexual activity has not been investigated in Lepidoptera. In *Drosophila melanogaster* it was found that isolated brains are not able to synchronize to temperature cycles, so a circadian thermoreceptor is not located in the brain or in the clock neurons, but in the periphery (Sehadova et al., 2009). It seems that some *cry*-negative neurons are especially sensitive to temperature (Miyasako et al., 2007; Yoshii et al., 2009), which makes those neurons the likely candidates that receive temperature information from the periphery (Peschel and Helfrich-Forster, 2011). Whether such a peripheral circadian thermoreceptor is present in moths remains to be investigated. In *D. melanogaster* two genes have also been identified to influence circadian temperature reception: *norpA* which encodes for the phospholipase C, and *nocte* which encodes a large glutamine-rich protein of which the function is unknown (Glaser and Stanewsky, 2005; Sehadova et al., 2009).

RELATIVE HUMIDITY

A few studies assessed the effect of relative humidity on calling behavior and mating success in moths (Baker and Cardé, 1979; Kanno and Sato, 1979; Royer and McNeil, 1993). In the European corn borer *Ostrinia nubilalis* fewer females called at low relative humidity compared to high relative humidity when temperature and L:D was held constant and the moths emerged at three different but constant conditions of relative humidity until their sixth night of calling (Royer and McNeil, 1993). Females also began calling later at night, had fewer calling bouts, spent less time calling, and the mating frequency was lower at low RH (Royer and McNeil, 1993). At low relative humidity there may be a higher chance of desiccation, so that the surface area for desiccation can best be kept minimal (Royer and McNeil, 1993). However, other studies did not find an effect of relative humidity on the proportion of females calling or their timing of calling (Baker and Cardé, 1979; Kanno and Sato, 1979).

THE CHEMICAL ENVIRONMENT (PRE-EXPOSURE TO PHEROMONE)

That the chemical environment influences sexual communication in moths has been shown indirectly, by showing that in overlapping areas of two closely related species the sexual communication channel is more divergent than in non-overlapping areas (e.g., McElfresh and Millar, 1999, 2001; Gries et al., 2001), and directly by showing that females with an altered blend containing less inhibitory compounds attracted heterospecific males (Groot et al., 2006). Thus, reproductive character displacement does seem to occur in moths. However, this is probably a slow process, taking at least a number of generations. Whether the chemical environment can induce short-term plastic responses in moths has hardly been investigated. We found that *H. subflexa* females contain more of their inhibitory compounds (acetates) when emerged in the odor of the closely related species *H. virescens*, showing for the first time that phenotypic plasticity in moth sex pheromone blends can happen (Groot et al., 2010a). A few studies also showed that the timing of female calling is affected by previous exposure to pheromone, either by advancing the onset time of calling (Palanaswamy and Seabrook, 1978; Stelinski et al., 2006), delaying the onset time of calling (Noguchi and Tamaki, 1985), prolonging the calling time (Sadek et al., 2012) or not affecting their timing (Dunkelblum et al., 1987; El-Sayed and Suckling, 2005). In some species, females may aggregate upon detecting their own pheromone, most likely to increase their probability of mating success (Birch, 1977). These variable results may be due to experimental conditions or differences in lifestyles (Sadek et al., 2012).

Male response is also affected by previous exposure to pheromone (Anderson et al., 2003, 2007; Silvegren et al., 2005). Brief exposure of 2 min in the first night caused a significantly quicker and more sensitive response (i.e., to lower doses) the following nights (Anderson et al., 2003, 2007). This effect lasted for at least two nights and suggests that learning is involved in male response (Anderson et al., 2007), or that sensitization of the olfactory neurons occurs. Silvegren et al. (2005) also found that *S. littoralis* males show temporal variation in pheromone response when they were pre-exposed to female pheromone gland extracts a few hours before the expected scotophase, even though they were kept in constant darkness. Such a circadian rhythm was not found in non-pre-exposed males that were kept in constant darkness, suggesting that in the absence of the Zeitgeber light, female pheromone acts as a weak Zeitgeber synchronizing male sensitivity to pheromone with female preference of mating time (Silvegren et al., 2005). Also, the peak of male activity shifted to earlier in the scotophase in pre-exposed males compared to unexposed males (Silvegren et al., 2005). This may be due to male-male competition, as female moths generally mate once a night but every other night, while males mate once a night and every night (e.g., Raulston et al., 1975; Raina and Stadelbacher, 1990; Klepetka and Gould, 1996), so that the operational sex ratio is generally male-biased. The earlier response to sex pheromone can thus be explained as a trial to outcompete other, conspecific males. Whether pre-exposure to heterospecific pheromone affects male response has not been investigated so far. Possibly, this depends on the chance of being attracted to the "wrong" female.

OTHER FACTORS AFFECTING TIMING OF MOTH SEXUAL COMMUNICATION

Over the past five decades, factors such as age and mating status have been shown to affect daily rhythms in female calling and male response in moths as well.

Age

In most moth species, females and males start to become sexually active 1–2 days after emergence. In general, pheromone glands contain very low levels of pheromone on the first night after eclosion, which then increases sharply on the second and third night (Pope et al., 1982, 1984; Webster and Cardé, 1982; Heath et al., 1991; Gemeno and Haynes, 2000; Xiang et al., 2010). When females get older, pheromone production generally decreases. For example, in the black cutworm moth *Agrotis ipsilon* the quantity of the major pheromone component of Z7-12:OAc increased in 1- to 2-day-old females and decreased in 2- to 6-day-old females (Gemeno and Haynes, 2000).

The onset of female calling has been found to become earlier at night when females get older in a number of species

(e.g., Kanno, 1979; Turgeon and McNeil, 1982; Webster and Cardé, 1982; Howlader and Gerber, 1986a,b; Kou and Chow, 1987; Delisle, 1992; Kamimura and Tatsuki, 1993; Spurgeon et al., 1995). This is probably to increase the chance of getting mated, especially because older females seem to release suboptimal amounts of pheromone (Kanno, 1979; Webster and Cardé, 1982). Thus, female-female competition is likely to affect the timing of female calling as well. However, it is important to note that not all females may initiate calling on the night after emergence (Delisle and Royer, 1994). For example, in a population of 5-day-old females, some females call for the third, second or first night, while other females have not started calling yet (Turgeon and McNeil, 1982; Delisle and McNeil, 1986; Kou and Chow, 1987; Han and Gatehouse, 1991). Therefore, it is probably good to distinguish chronological age (age after emergence) from calling age (age at which females start calling), which likely indicates the day of sexual maturation (Turgeon and McNeil, 1982; Delisle and McNeil, 1986; Gerber and Howlader, 1987).

In contrast to an advance in timing of calling with increasing age, in some species a delay in their period of calling has been found as they get older (Castrovillo and Cardé, 1979; West et al., 1984; Delisle and McNeil, 1986; Schal and Carde, 1986). This may be due to costs that can be associated with shifting calling time if such a shift causes an overlap of timing with another species, causing interspecific communication interference and mating mistakes (Roelofs and Cardé, 1974; Haynes and Birch, 1986), and encountering environmental conditions that reduce mate-finding (Cardé and Baker, 1984; Gemeno and Haynes, 2000).

Mating status

After female moths are mated, pheromone production and release ceases, at least for the rest of the night, and in a number of species also for the following night (e.g., Raina et al., 1989; Raina and Stadelbacher, 1990; Foster and Roelofs, 1994; Rafaeli and Gileadi, 1995; Ramaswamy et al., 1996; Ahn et al., 2002). Only a few species have been found where the pheromone titer in mated females is reduced to very low amounts for longer periods (e.g., Shorey et al., 1968; Webster and Carde, 1984; Babilis and Mazomenos, 1992). The change in behavior from virgin to mated females has been suggested to be controlled by a male derived peptide, so-called Pheromone Suppressing Peptide (Kingan et al., 1993, 1995; Eliyahu et al., 2003). If male-derived peptides are controlling the change in female behavior, this would thus be better termed an exogenous factor. Virgin females and males have been found to mate earlier in the scotophase than mated individuals, at least in *Heliothis virescens* (Raina and Stadelbacher, 1990). However, it is unclear whether this is a general trend.

GENETIC BASIS OF VARIATION IN TIMING OF SEXUAL ACTIVITIES

Even though many genes and factors have been identified that make up the circadian clock in insects and mamals, surprisingly little research has been conducted on which gene(s) underlie variation in timing of sexual activities within and between closely related species. Assessing variation in the identified clock genes is of course very interesting, but it does not give insight in the first genetic changes that have led to differences in timing of activity between specific strains within species or between closely related species. Maybe this is because in *Drosophila* there are peak activities, but flies are or can be active throughout the day and even at night. In moths, sexual activities really show a daily on-off rhythm; females and males are completely inactive throughout the day and for some hours during the night, and their sexual activities start at specific times at night (see **Table 1**). This makes moths ideal species to study the genetic basis of within- and between-species variation in these very well defined activity patterns. Below I summarize what is known on the genetic basis of variation in circadian rhythms within and between species.

Variation in timing of sexual activities between species has been investigated by comparing fly species that differ in their timing of mating: e.g., *D. melanogaster* vs. *D. pseudoobscura*, the latter mating later (Tauber et al., 2003), *D. melangoster* vs. *D. simulans*, also mating slightly out of sync (Ritchie and Kyriacou, 1994; Sakai and Ishida, 2001), flies of the genus *Bactrocera*, i.e., *B. tryoni*, mating at dusk, vs. *B. neohumeralis*, mating at daytime (Tychsen and Fletcher, 1971; Smith, 1979), and two selection lines of *B. cucurbitae*, one line mating at dusk and one line mating at night (Miyatake, 2002).

Sakai and Ishida (2001) tested the mating rhythms of *D.melanogaster* per^{01} and tim^{01} null mutant lines that are arrhythmic in their adult emergence and locomoter activity, and found that these lines were also arrhythmic in their mating behavior, indicating the involvement of *per* and *tim* in timing of mating activity in *D. melanogaster*. However, when *D. melanogaster* per^{01} null lines were transformed with *per* from *D. simulans* (sim-transformed) or with *per* from *D. melanogaster* (mel-transformed), females did not discriminate between males from the different transformant lines, suggesting that *per* is not very important in the premating isolation between these two species (Ritchie and Kyriacou, 1994). On the other hand, when Tauber et al. (2003) transformed *per* from *D. pseudoobscura* and *per* from *D. melanogaster* in the per^{01} null mutants, they did rescue the species-specific mating times.

In the two *Bactrocera* species, An et al. (2002, 2004) found that *per* had the same cycling phase in the two species and could thus not explain the difference in mating time. C*ry* also showed a similar diurnal expression patterns in both species, being highest in the morning especially in the antennae, but *cry* transcript levels were significantly higher in the day-mating *B. neohumeralis* than in the dusk-mating *B. tryoni* (An et al., 2004). Miyatake et al. (2002) selected for young (Y) or old (O) reproductive age in *B. curcubitae*, and found that these selection lines also differed in their timing of mating, the Y-line mating at dusk and the O-line mating at night. The fluctuations of *per* expression levels in these lines reflected their different mating rhythms (Miyatake et al., 2002), again suggesting a role for *per* in timing of mating. However, since *per* is located on the sex chromosome and reciprocal hybrids did not differ in their mating rhythm (Miyatake et al., 2002), it is more likely that a trans-acting regulator of *per* on one of the autosomes is responsible for the variation in mating times.

The above-mentioned studies with their candidate gene approach can only determine whether the already identified clock

genes may be involved in inter- or intraspecific variation in the circadian rhythm of mating. To identify the exact genetic changes underlying variation in timing of sexual activities, quantitative trait locus (QTL) analysis is needed to identify the genomic location that explains most of the variance, which can also lead to the discovery of new clock components (Tauber and Kyriacou, 2005). In moths, genetic analysis of variation in female calling has been conducted by Monti et al. (1997), who hybridized two closely related *Spodoptera* species (*S. descoinsi* and *S. latisfascia*) and found that females of both reciprocal crosses were intermediate in their calling time. Hence, an autosomal factor is involved in the variation of timing of female calling in these species. We conducted QTL analysis on the variation in timing in the two strains of *Spodoptera frugiperda* and found that one chromosome, homologous to *B.mori* chromosome 27, explained most of the variance (Hänniger et al., unpublished results). Interestingly, this chromosome harbors the clock gene *vrille*, making this our main candidate gene. Even more interestingly, this same chromosome is also the QTL for the pheromone variation between the two strains (Hänniger et al., unpublished results), suggesting a possible genetic interaction or hitchhiking between the two traits.

CONCLUSIONS

Clearly, different moth species show different daily rhythms in their sexual activities, ranging from female sex pheromone production and female calling to male response and mating. After the vast amount of work in the past five decades to identify the daily activities and circadian rhythms within and between moth species, the current challenge is to determine the underlying mechanism and identify the genetic changes underlying natural variation in these circadian rhythms. Recent studies on behavioral patterns in *Drosophila* show that circadian behavior in natural populations may be quite different from circadian behavior measured under laboratory conditions (Menegazzi et al., 2012; Vanin et al., 2012), showing the importance of assessing the adaptive significance of rhythmic phenotypes in natural populations. The identified clock regulation and clock genes in *Drosophila* and Lepidoptera form an excellent basis to assess possible variation in and selection on these genes in moths. With QTL analysis, fine-scale mapping, mapping the clock genes to these genetic maps, and functional analyses, it will be possible to identify whether inter- and intraspecific variation in circadian timing of sexual activities in moths is due to mutations in these genes themselves, or in trans- or cis-acting regulatory elements in the clockwork. Identifying the exact genetic changes responsible for the species- or strain-specific timings will be necessary to determine whether and how the evolution of allochronic differentiation coincide or interact with the evolution of sex pheromone composition, which may have led to the enormous diverse group of ∼145.000 moth and butterfly species.

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