J. Acad. Entomol. Soc. 8: 61-67 (2012)

Temperature and humidity have limited effects on the daily activity patterns of adult pale-winged gray moths in nature (Lepidoptera: Geometridae)

Lauren Pinault, Jennifer Guy, Manon Vincent, Lucie Carrat, and Dan Quiring

ABSTRACT

This study presents the daily activity patterns of the adult pale-winged gray moth, *Iridopsis ephyraria* **Walker (Lepidoptera**: Geometridae), a defoliator of eastern hemlock, *Tsuga canadensis* (L.) Carrière (Pinaceae), in nature. Oviposition and mating were constrained to nocturnal hours. Most oviposition occurred between 21:00 and 23:00 and was weakly but positively correlated with warmer temperatures ($r^2 = 0.10$). Mating activity peaked between 02:00-04:00 and was negatively correlated to temperature and positively correlated to humidity, although these factors only explained 13.3 % of the variation in the timing of mating. Flight activity was highest between 22:00 and 01:00, although males and females often flew at different times. Hygrothermal stress has been previously cited as the most important factor affecting the timing of different moth behaviours, but the results of this study indicate that there are likely other factors that strongly influence the daily activity patterns of *Iridopsis ephyraria*.

RÉSUMÉ

Dans le présent article, nous présentons les tendances liées à l'activité diurne en milieu naturel des adultes de l'arpenteuse à taches (*Iridopsis ephyraria* **Walker) (Lepidoptera**: Geometridae), un défoliateur de la pruche du Canada (*Tsuga canadensis* (L.) Carrière) (Pinaceae). La ponte et l'accouplement ont été observés uniquement durant la nuit. L'activité de ponte a culminé entre 21 et 23 h et était faiblement mais positivement corrélée aux températures plus chaudes ($r^2 = 0{,}10$). L'activité d'accouplement a atteint son intensité maximale entre 2 et 4 h et était négativement corrélée à la température et positivement corrélée à l'humidité; ces deux facteurs n'ont cependant expliqué que 13,3 % de la variation associée au moment précis des accouplements. L'activité de vol a atteint son point culminant entre 22 et 1 h, mais les deux sexes ont souvent volé à des moments différents. Le stress hygrothermique a déjà été décrit comme le principal déterminant de la chronologie des différents comportements de l'arpenteuse, mais nos résultats démontrent que d'autres facteurs ont un impact déterminant sur les différentes composantes de l'activité diurne de l'*Iridopsis ephyraria*.

INTRODUCTION

Insects exhibit daily patterns of activity, where oviposition, mating, feeding, flying and/or resting occur during specific periods of the day or night (e.g., Prokopy and Hendrichs 1979; Quiring and McNeil 1987; Fellers 1989). Most studies of the daily activity patterns of nocturnal moths have been carried out in the laboratory (e.g., Crawford 1966; Hagstrum and Tomblin 1972; Solomon and Neel 1973), field cages (Richerson et al. 1976) or by carrying out repeated field collections in nets or traps (Raulston et al. 1975; Cardé 1976; Delisle et al. 1998; Schaefer et al. 1999). These studies generally

---

Received 11 April 2012. Accepted for publication 11 September 2012. Published on the Acadian Entomological Society website at www.acadianes.ca/journal.html on 16 October 2012.

Lauren Pinault[1]: Population Ecology Group, Faculty of Forestry and Environmental Sciences, PO Box 4400, 28 Dineen Dr., University of New Brunswick, Fredericton, NB Canada E3B 5A3 and Department of Biological Sciences, Brock University, St. Catherines, ON, Canada, L2S 3A1.

Jennifer Guy, Manon Vincent, Lucie Carrat, and Dan Quiring: Population Ecology Group, Faculty of Forestry and Environmental Sciences, PO Box 4400, 28 Dineen Dr.,University of New Brunswick, Fredericton, NB Canada, E3B 5A3

[1] Corresponding author (email lauren.pinault@gmail.com).

| Next Page | Full Screen

reported a peak in oviposition (Crawford 1966; Hagstrum and Tomblin 1972; Raulston et al. 1975) and calling (Cardé et al. 1974; Schaefer et al. 1999) in the early evening, and a peak in mating between 23:00. and 02:00. (Raulston et al. 1975). The only previous study to observe undisrupted adult moth behavior in nature over 24 h periods reported similar results; Quiring (1994), reported that the spruce bud moth, *Zeiraphera canadensis* Mutuura and Freeman (Lepidoptera: Tortricidae), oviposited during the few hours following sunset and mated primarily between midnight and 04:00.

The pressure to minimize hygrothermal (heat and desiccation) stress is believed to be the most important of the various biotic and abiotic factors that can influence the timing of Lepidoptera behaviour (Hagstrum and Tomblin 1972; Cardé et al. 1974; Dreisig 1976, 1986; Quiring 1994; Bento et al. 2001). Many moths rest in cool, humid and shady areas during the day and are active in the late evening and overnight when humidity is highest and temperatures are lower (Quiring 1994; Bento et al. 2001).

Although it is important to confirm daily patterns of moth activity observed in the laboratory with field studies to ensure that biases introduced by artificial environments are eliminated, it is also vital to understand the timing of reproductively important behaviours for pest species for the purposes of population control (Cardé and Minks 1995). To that end, we report results of a field-based, non-disruptive observational study to determine the daily activity patterns of the pale-winged gray moth, *Iridopsis ephyraria* Walker (Lepidoptera: Geometridae), in hemlock stands in Nova Scotia, Canada.

The pale-winged gray moth has a broad range, extending from Alberta to Nova Scotia and south to Texas (Ferguson 1954; McGuffin 1977) and recently has severely defoliated eastern hemlock trees, *Tsuga canadensis* (L.) Carrière (Pinaceae) in Nova Scotia (Pinault et al. 2007; Pinault and Quiring 2008). Eggs are laid in crevices in the tree bole, with increasing density in the upper bole (Pinault et al. 2007). By distinguishing moth genders during field observations, and by obtaining measurements of temperature and humidity, we were able to evaluate the influence of adult sex, hour of the day, temperature and humidity on activity patterns without noticeably disrupting moth behaviour. We also tested the hypothesis that hygrothermal stress (warmer temperatures and lower humidity) would have a significant influence on the timing of mating and oviposition. We, therefore, predicted that the timing of mating and oviposition would correspond to the cooler, more humid hours of the evening.

METHODS

This study was conducted during 2004-2006 in mature eastern hemlock stands in Queen's and Annapolis counties, Nova Scotia, Canada (Table 1). Study sites were composed primarily (ca. 60%) of eastern hemlock and were selected based on high caterpillar abundance earlier in the summer. Most trees were 20-30 m in height and were separated by approximately 2-5 m, although smaller understory trees (<10 m in height) were interspersed within the site. Moths were studied during the 1.5 week period of adult activity in late July and August (Pinault et al. 2007). Table 1 summarizes the overnight and 20-24 hour sessions. Since moths were very difficult to find during rainy conditions, observations were constrained to dates and times when it was not raining. Although it is likely that moths flew at higher elevations within the forest canopy, we were constrained to make our observations at eye to ground level due to the practical difficulty of overnight observations. However, we did not observe large densities of flying moths at higher elevations during our observation periods.

Table 1. Summary of study locations where pale-winged gray moth behavior was observed on mature hemlock trees in southern Nova Scotia, Canada. The dates and time periods of observations are also listed.

Year	Site Coordinates	Start Date(s)	Hours	Duration (h)
2004	44°23′N, 65°15′W	August 10	15:30—15:30	24
		August 12	13:30—9:30	20
	44°26′N, 65°12′W	August 18, 19	21:00—5:00	8
2005	44°23′N, 65°00′W	August 7, 8, 9, 10	21:00—6:00	9
		August 12 – 14	12:00—6:00 6:00—12:00	[a] 24
2006	44°23′N, 65°05′W	July 30	21:00—6:00	9

[a] A 24h session started on 12 August 2005, but was terminated at 06:00 on 13 August due to rain. The remaining 6 h was completed 14 August 2005.

At each site in both years, 20 mature hemlock trees (at least 2 m apart) were selected along a circular path and numbered using fluorescent flagging tape, with the knot placed on the north face of the tree. Each hour during the observation period, researchers moved from tree to tree along the circuit, remaining for 2 min. at each tree before moving to the next. Observers moved very slowly and silently and used red-filtered headlamps to minimize disturbance to moths. At each tree, the visible area across the north face of the trunk (0.5-1.5 m from the ground) was observed, along with a 1 × 1 m area on the ground at the base of the tree (2005 only).

The number of live adults was counted, and activity assigned to one of the following five behavioural categories: mating, ovipositing, flying, walking or resting. Based on results from observations in the lab, females were only categorized as ovipositing if ovipositors were inserted into bark crevices for >10 sec. Similarly, adults were only categorized as flying if they were flying within 30 cm of the study surface of the tree or ground. Adults were sexed by morphological characters (i.e., abdominal width, and plumose versus filiform antennae). Hourly temperature and humidity data were obtained from the nearby Kejimkujik weather station (Environment Canada), approximately 2.2-15.6 km from the different study sites.

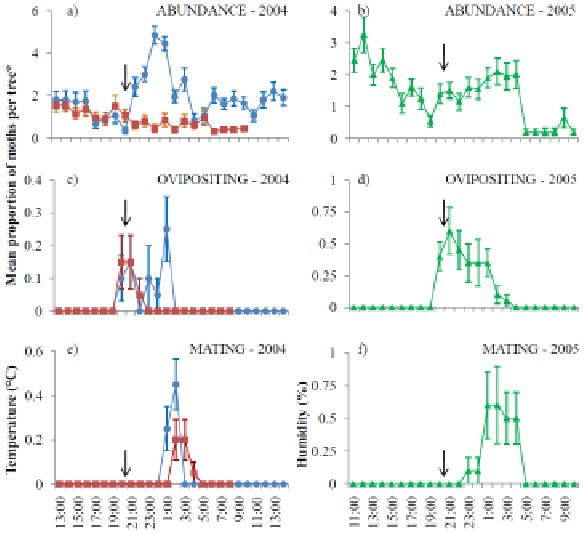
Student's t-tests were used to evaluate the influence of year and location (trunk versus ground) on moth abundance per overnight session. As moth abundance was substantially greater in 2005 than in 2004 (see results), only 2005 data from the four 9 h overnight sessions were used for the following analyses. A nested General Linear Model was used to evaluate the variation in moth abundance observed by sex, hour(date), date, and the interaction of sex × hour(date) and sex × date. A MANOVA with repeated measures on individual trees was used to evaluate the effects of sex, hour, date and the interaction of sex × hour and sex × date on the numbers of moths ovipositing, mating, flying, walking and resting. A Roy-Bargmann stepdown analysis was conducted with the MANOVA to evaluate the influence of each specific effect on each moth activity. To evaluate the potential role of hygrothermal stress on mating and oviposition, a stepwise (forward) regression analysis was used with temperature, humidity, and hour × date included as predictive factors in the model.

RESULTS

During the three 20-24 h observations sessions, there was a large and inconsistent variation in the abundance of moths, indicating that moths spent considerable periods of time in locations other than on the lower tree bole and on the ground (Figures 1a, b). However, all oviposition and mating activity occurred during the evening, following sunset, and early morning (Figures 1c-f).

The temporal distribution of moth abundance and of specific moth behaviors during the overnight sessions was generally similar in both study years (Figures 2 and 3). Fewer moths were observed per session in 2004 than in 2005 ($t_{1,7}$ = 9.43, P<0.05; Figures 2a ,b and 3a, b). Pale-wing gray moths were much more abundant on tree trunks (94.79 adults/m^2), than on the ground (6.62 adults/m^2) ($t_{1,88}$ = 158.12, P<0.001). During most evenings, moth abundance increased from the onset of darkness until 23:00-midnight, after which it gradually declined (Figures 2a, b and 3a, b; Table 2). In 2005, more males were observed on 7 August than on other study dates, especially early in the evening (Figure 3a), whereas a similar number of females was observed on all study dates (Figure 3b), leading to a significant interaction between sex and date (Table 2). There was also a significant interaction between sex and hour (Table 2): males were more abundant before 01:00 on most study dates (Figure 3a) but female abundance remained relatively constant from 21:00 to 04:00 (Figure 3b).

Figure 1. Temporal distribution of *I. ephyraria* adults in hemlock stands, showing mean ± SE number of moths per tree as a proportion of the daily mean: (a, b) total abundance; (c, d) females ovipositing; and (e, f) adults mating on 10 August (blue circles) and 12 August (red squares) 2004, and 12/14 August (green triangles) 2005. The break in sample dates in 2005 is indicated by a break in the line. Overall moth abundance was 2.24 moths/tree on 10 August and 0.66 moths/tree on 12 August, 2004 and 1.39 moths/tree on 12/14 August 2005. Timing of sunset is indicated with a black arrow.



*Adjusted for total daily abundance.

Prior to oviposition, females walked along the bark surface while probing for potential sites with their ovipositors, and appeared to initiate oviposition when a crevice of suitable depth was located. Oviposition activity was only observed between 20:00-05:00, but usually peaked between 21:00-23:00 (Figures 1c, d and 3f; Tables 3, 4). Oviposition patterns are not presented for 2004 since only two females were observed ovipositing during the overnight sessions. Very low densities of ovipositing females were observed on 7 August (Figure 3f), during the coldest night in 2005 (Figure

Figure 2. (a-e) Overnight activity patterns of *I. ephyraria* on 18 August (blue circles) and 19 August (red squares), 2004. The mean ± SE number of moths per tree as a proportion of the daily mean are shown for: a) males; b) females; c) flying males; d) flying females; and e) mating adults. Hourly fluctuations in f) temperature and g) percent humidity are plotted for comparison. Sunset occurred at ca. 20:20 and the overall moth abundance was 1.17 moths/tree on 18 August and 0.68 moths/tree on 19 August.

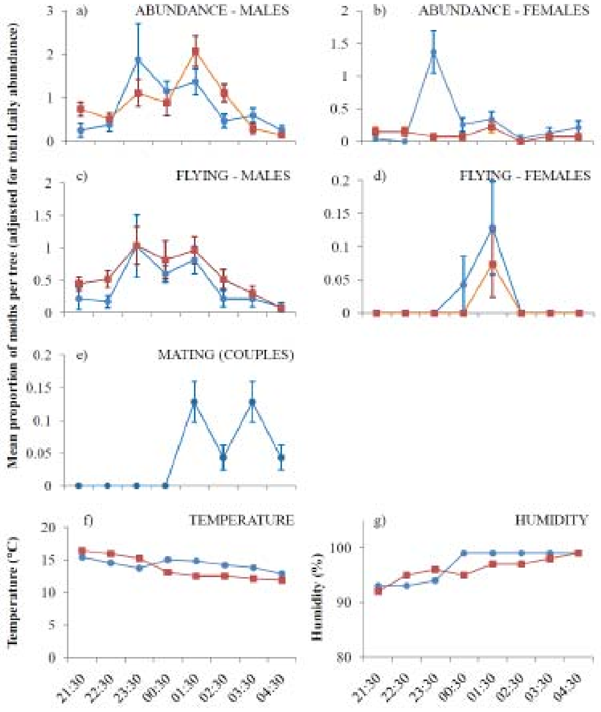
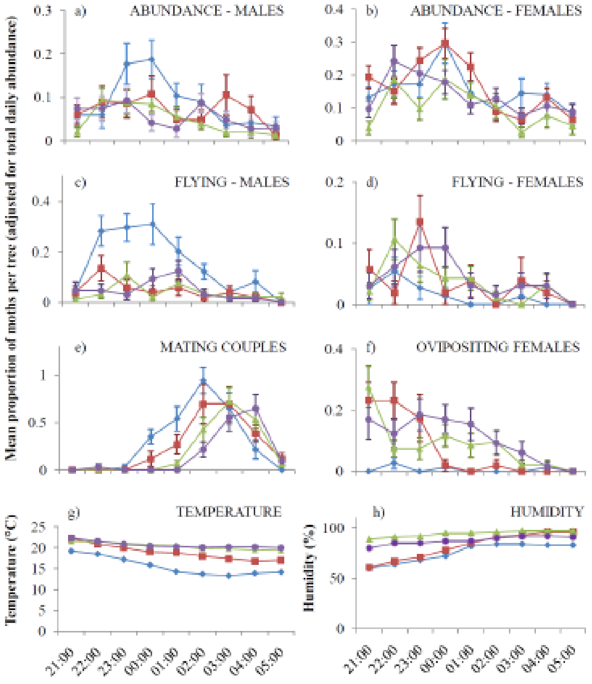


Figure 3. (a-f) Overnight activity patterns of *I. ephyraria* on 7 August (blue diamonds), 8 August (red squares), August (green triangles), and 10 August (purple circles), 2005. The mean ± SE moths per tree as a proportion of the daily mean for each hour are shown for: a) males; b) females; c) flying males; d) flying females; e) mating adults; and f) ovipositing females. Hourly fluctuations in g) temperature and h) percent humidity are plotted for comparison. Sunset occurred at ca. 20:35 and overall moth abundances were 3.72, 2.59, 4.71 and 3.24 moths/tree on 7, 8, 9, and 10 August, respectively.



3g), resulting in a significant influence of date (Tables 3, 4). As oviposition is only carried out by females, the influence of sex and interaction of sex × date and sex × hour were all significant factors in the Roy-Bargmann Stepdown Analysis (Tables 3, 4). In the stepwise regression, the number of ovipositing moths was significantly associated with hour ($t_{32,682}$ = 2.06; P=0.039) and warmer temperatures ($t_{1,682}$ = 7.02; P<0.001), although only 10% of variation was attributable to these factors ($s_{1,719}$ = 0.572; r^2 = 0.10).

During copulation, males and females were attached by the posterior tips of their abdomens and oriented vertically on the tree bole, or occasionally on branches. When disturbed, copulating pairs dropped to a lower level on the tree, or flew away, remaining attached. The density of mating couples varied significantly by hour (Tables 3, 4) as moths only mated between midnight and 05:00, with a peak in mating activity between 02:00 and 04:00 (Figures 1e, f, 2e and 3e). During the coldest study date in 2005, 7 August (Figure 3g), the peak in mating activity occurred an hour earlier (Figure 3e), which explains the significant effect of date in the Roy-Bargmann Stepdown Analysis (Tables 3, 4). In the stepwise regression, mating was significantly affected by hour × date ($t_{35,682}$ = -3.04; p=0.002), associated with colder temperatures ($t_{1,682}$ = -5.19; P<0.001) and more humid conditions ($t_{1,682}$ = 3.05; P=0.002), although the model only explained 13.3% of the data ($s_{1,719}$ = 1.59; r^2 = 0.13).

The abundance of flying moths fluctuated by hour (Tables 3, 4), with a peak in flight activity between 22:00-01:00 (Figures 2c, d and 3c, d). On 7 August 2005, many more males flew in the early evening than males on subsequent nights (Figure 3c), resulting in a significant effect of date (Tables 3, 4). As well, more males flew on 7 August 2005 (Fig. 3c) than females (Figure 3d), leading to a significant effect of sex and interaction between sex and date (Tables 3, 4). The interaction between sex and hour also explained some of the variation in densities of flying moths (Tables 3, 4).

Low numbers of moths were observed walking during different parts of the evening (Tables 3, 4), without any specific peak in walking activity. The number of walking moths was influenced by the effect of sex (Tables 3, 4), most likely due to variation in the relative abundance of the sexes and their activities on the different dates.

Females were observed resting more often than males (0.77 females/tree/hour ± 0.039; 0.37 males/tree/hour ± 0.03) and a higher proportion of both genders rested between 22:00-02:00, resulting in significant main effects of sex, hour, and date, and the interaction of sex and hour (Tables 3, 4).

Table 2. Summaries of analysis of variance evaluating the variation in *I. ephyraria* moth abundance per tree attributable to date, hour (date), sex, sex × date and sex × hour (date), in South Brookfield, Nova Scotia, Canada, in 2005. Degrees of freedom (df), mean sums of squares (MS), F and P-values are provided.

Influence	df	MS	F	P
sex	1	94.30	3.43	0.161
date	3	31.20	2.80	0.056
hour (date)	32	11.16	6.52	<0.001
sex x date	3	27.51	11.04	<0.001
sex x hour (date)	32	2.49	1.46	0.049
error	1367	1.71		

Table 3. Summary of a MANOVA analysis evaluating the difference in variation of moth abundance attributed to sex, date, hour, and the interactions of sex × date and sex × hour for five moth activities. Pillai's trace, F-values, degrees of freedom (df) and p-values are presented for each effect.

Effect	Pillai's trace	F	df	P
Sex	0.158	53.12	5, 1411	<0.001
Date	0.094	9.09	15, 4239	<0.001
Hour	0.431	16.66	40, 7075	<0.001
Sex × Date	0.084	8.18	14, 4239	<0.001
Sex × Hour	0.072	2.57	40, 7075	<0.001

Table 4. Summaries of multivariate Roy-Bargmann Stepdown analyses following MANOVA (Table 3), evaluating the variation in *I. ephyraria* moth abundance per tree attributable to sex, date, hour, sex × date and sex × hour, in South Brookfield, Nova Scotia, Canada, in 2005. Degrees of freedom (df), mean sums of squares (MS), Stepdown F and P-values are provided. Significant p-values (95% confidence) are indicated in bold typeface.

Effect	Activity	df	MS	Stepdown F	P
Sex	Flying	1, 1415	6.78	32.84	<**0.001**
	Walking	1, 1414	2.59	18.49	<**0.001**
	Resting	1, 1413	54.19	75.14	<**0.001**
	Mating	1, 1412	0.17	0.31	0.575
	Ovipositing	1, 1411	20.24	124.39	<**0.001**
Date	Flying	3, 1415	2.92	14.13	<**0.001**
	Walking	3, 1414	0.26	1.85	0.137
	Resting	3, 1413	4.92	6.82	<**0.001**
	Mating	3, 1412	5.36	10.04	<**0.001**
	Ovipositing	3, 1411	2.11	12.98	<**0.001**
Hour	Flying	8, 1415	2.54	12.28	<**0.001**
	Walking	8, 1414	0.31	2.19	<**0.026**
	Resting	8, 1413	9.73	13.49	<**0.001**
	Mating	8, 1412	33.81	63.32	<**0.001**
	Ovipositing	8, 1411	0.99	6.10	<**0.001**
Sex × Date	Flying	3, 1415	5.55	26.88	<**0.001**
	Walking	3, 1414	0.26	1.87	0.134
	Resting	3, 1413	0.01	0.01	0.998
	Mating	3, 1412	0.00	0.01	0.999
	Ovipositing	3, 1411	2.16	13.26	<**0.001**
Sex × Hour	Flying	8, 1415	0.51	2.47	**0.012**
	Walking	8, 1414	0.15	1.09	0.362
	Resting	8, 1413	1.58	2.19	**0.026**
	Mating	8, 1412	0.00	0.00	1.000
	Ovipositing	8, 1411	1.18	7.24	<**0.001**

DISCUSSION

Our study suggests that the ovipositing and mating activity of *Iridopsis ephyraria* can be modified by ambient fluctuations in temperature and/or humidity. However, as these two parameters only explained a small proportion of the variation in these behaviours, the timing of these activities is likely also strongly affected by other factors. It is also likely that the resolution of temperature and humidity readings from the local weather station would not have accurately reflected the microclimatic variations present in the field site, which limits the scope of our conclusions.

Oviposition, which may require more energy than mating as females must probe for suitable oviposition sites, occurred during the warmest part of the evening. However, it is likely that other factors, such as falling light intensity, which is known to trigger oviposition activity in other moth species (Crawford 1966; Bell 1981; Fedosov 1992) strongly influences the timing of reproductively important activities.

During the evening, the abundance of male and female moths increased slightly during the few hours following sunset, after which they declined gradually until morning, suggesting that moths moved to areas other than the bole and the ground. Fewer moths were observed in 2004 than in 2005, probably due to a lower population density at the study site. However, general activity patterns were similar in both years, despite differences in moth density.

In 2004, many more males than females were observed during the overnight sessions. As mating but almost no oviposition was observed during these sessions, it is probable that the higher proportion of males resulted from protandry, which is common in many Lepidoptera (Wiklund and Fagerstrom 1977; Fagerstrom and Wiklund 1982). The sex ratio was more male-biased during the first overnight session than on other days in 2005, supporting this interpretation.

In 2005, females oviposited in early evening on all study days except 7 August 2005 (Figure 3f), probably due in part to the colder and less humid conditions. Like oviposition, mating of *Iridopsis ephyraria* was also restricted to a narrow temporal window. Mating occurred several hours after peak oviposition activity. Limiting mate-searching and mating to a narrow temporal window can improve mate-finding success and is common among other Lepidoptera (Solomon and Neel 1973; Cardé et al. 1974). For example, the ghost moth *Hepialus humuli* Linnaeus (Lepidoptera: Hepialidae) forms male leks that use female-attractive pheromones to entice mates (Mallet 1984). Alternatively, some Lepidoptera time mating events for predator avoidance of subsequent generations of caterpillars (Visser et al. 2006).

The current study shows that the temporal distribution of different activities of a geometrid moth are very similar to that previously reported for a tortricid moth observed continuously for 24 hour periods in nature (Quiring 1994). These activity patterns are also similar to moth activity patterns reported in laboratory studies and in field studies carried out using field cages or traps (e.g., Crawford 1966, Cardé 1976, Raulston et al. 1975). When united, these studies suggest that many nocturnal moths oviposit during the few hours following sunset and mate during several hours between midnight and sunrise. Further studies are required to determine why so many different species of moths exhibit such temporally similar daily patterns of activity.

ACKNOWLEDGEMENTS

We thank Ryan Jameson and Antoine Davy for field assistance, Chris McCarthy (Parks Canada), Jim Crooker and Andrew Ross for providing study sites, and Heidi Fry, Chris Lucarotti, Blair Pardy, Jean Richardson, Graham Thurston, Jess Vickruck, and two anonymous reviewers for helpful discussion. This project was supported by a NSERC IPS scholarship to L.P. with support from Forest Protection Limited. Financial and logistical support was also provided by the Canadian Forest Service, Parks Canada, Environment Canada (weather station), the University of New Brunswick, NSERC (Discovery Grant), and the Nova Scotia Department of Natural Resources.

REFERENCES

Bell, C.H. 1981. The influence of light cycle and circadian rhythm on oviposition in five pyralid moth pests of stored products. Physiological Entomology **6**: 231-239.

Bento, J.M.S., Parra, J.R.P., Vilela, E.F., Walder, J.M., and Leal, W.S. 2001. Sexual behavior and diel activity of citrus fruit borer, *Ecdytolopha aurantiana*. Journal of Chemical Ecology **27**: 2053-2065.

Cardé, R.T., Comeau, A., Baker, T.C., and Roelofs, W.G. 1974. Moth mating periodicity: Temperature regulates the circadian gate. Experientia **31**: 46-48.

Cardé, R.T. 1976. Utilization of pheromones in the population management of moth pests. Environmental Health Perspective **14**: 133-144.

Cardé, R.T., and Minks, A.K. 1995. Control of moth pests by mating disruption: successes and constraints. Annual Review of Entomology **40**: 559-585.

Crawford, C.S. 1966. Photoperiod-dependent oviposition rhythm in *Crambus teterrellus* (Lepiodoptera: Pyralidae: Crambinae). Annals of the Entomological Society of America **59**: 1285-1288.

Delisle, J., West, R.J., and Bowers, W.W. 1998. The relative performance of pheromone and light traps in monitoring the seasonal activity of both sexes of the eastern hemlock looper, *Lambdina fiscellaria fiscellaria*. Entomologia Experimentalis et Applicata **89**: 87-98.

Dreisig, H. 1976. Phase shifting the circadian rhythms of nocturnal insects by temperature changes. Physiological Entomology **1**: 123-129.

Dreisig, H. 1986. Timing of daily activities in adult Lepidoptera. Entomologia Generalis **12**: 25-44.

Fagerstrom, T., and Wiklund, C. 1982. Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. Oecologia **52**: 164-166.

Fedosov, S.A. 1992. The diurnal rhythm of emergence from the pupa, oviposition and flight to light and to pheromone of the fall webworm (*Hyphantria cunea*) in nature and under laboratory conditions. Zoologichesky Zhurnal **17**: 53-60.

Fellers, J.H. 1989. Daily and seasonal activity in woodland ants. Oecologia **78**: 69-76.

Ferguson, D.C. 1954. The Lepidoptera of Nova Scotia. 1. Macrolepidoptera. Proceedings of the Nova Scotia Institute of Science **23**: 161-375.

Hagstrum, D.W., and Tomblin, C.F. 1972. Oviposition by the almond moth, *Cadra cautella*, in response to falling temperature and onset of darkness. Annals of the Entomological Society of America. **66**:809-812.

Mallet, J. 1984. Sex roles in the ghost moth, *Hepialus humuli* (L) and a review of mating in the Hepialidae (Lepidoptera). Zoological Journal of the Linnaean Society **80**: 67-82.

McGuffin, W.C. 1977. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. Memoirs of the Entomological Society of Canada **191**.

Pinault, L., Georgeson, E., Guscott, R., Jameson, R., LeBlanc, M., McCarthy, C., Lucarotti, C., Thurston, G., and Quiring, D. 2007. Life history of *Iridopsis ephyraria*, (Lepidoptera: Geometridae), a defoliator of eastern hemlock in eastern Canada. Journal of the Acadian Entomological Society **3**: 28-34.

Pinault, L.L., and Quiring, D.T. 2008. Sampling strategies and density-defoliation relationships for the pale-winged gray moth, *Iridopsis ephyraria*, on mature eastern hemlock. Forest Ecology and Management **255**: 2829-2834.

Prokopy, R.J., and Hendrichs, J. 1979. Mating behavior of *Ceratitis capitata* on a field-caged host tree. Annals of the Entomological Society of America **72**: 642-648.

Quiring, D.T, and McNeil, J.N. 1987. Daily patterns of abundance and temporal distributions of feeding, mating and oviposition of the dipteran leaf miner, *Agromyza frontella*. Entomologia Experimentalis et Applicata **45**: 73-89.

Quiring, D. T. 1994. Diel activity of a nocturnal moth, *Zeiraphera canadensis*, in nature. Entomologia Experimentalis et Applicata **73**: 111–120.

Raulston, J.R., Snow, J.W., Graham, H.M., and Lingren, P.D. 1975. Tobacco budworm: effect of prior mating and sperm content on the mating behavior of females. Annals of the Entomological Society of America **68**: 701-704.

Richerson, J.V., Cameron, E.A., and Brown, E.A. 1976. Sexual activity of the gypsy moth. American Midland Naturalist **95**: 299-312.

Schaefer, P.W., Gries, G., Gries, R., and Holden, D. 1999. Pheromone components and diel periodicity of pheromonal communication in *Lymantria fumida*. Journal of Chemical Ecology **25**: 2305-2312.

Solomon, J.D., and Neel, W.W. 1973. Mating behavior in the carpenterworm moth, *Prionoxystus robiniae* (Lepidoptera: Cossidae). Annals of the Entomological Society of America **66**: 312-314.

Visser, M.E., Holleman, L.J.M., Gienapp, P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia **147**: 164-172.

Wiklund, C., and Fagerstrom, T. 1977. Why do males emerge before females? Oecologia **31**: 153-158.