Temporal variation in abundance of male and female spruce budworms at combinatory associations of light traps and pheromone traps

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Abstract

A 3-year study (2014–2016) was conducted at Rocky Harbour near the west coast of Newfoundland, Canada, to record the abundance and phenology of adult spruce budworms captured at traps, using a factorial design (light traps and pheromone traps deployed contiguously or segregated spatially). Budworms were most abundant and occurred seasonally earlier in 2014 than in 2015 and 2016; these findings held generally true for males and females. The geographic setting of Newfoundland (large island isolated from the mainland by an oceanic barrier of >100 km across) provides an ideal location to discriminate local flight from long-range immigrations; in our study, however, immigrations cannot be ruled out for any single day of trapping due to broad overlap in emergence patterns at Rocky Harbour relative to forest stands with known populations of budworms on the mainland. Based on moderate daily variation in adult abundance, however, major immigration events (defined as external deposition of budworms with large numerical amplitude) likely did not take place at Rocky Harbor between 2014 and 2016. Males were more abundant at light traps coupled with pheromone traps, whereas abundance of males at pheromone traps was similar with or without contiguous light traps. This outcome may be mediated by lower range of attraction for light traps (usually <100 m) and (generally assumed to be several hundreds of meters). Females were equally abundant at light traps with or without pheromone traps. As expected, males were captured earlier in the season at pheromone traps than at light traps, and females occurred later in the season due to protandry. The onset of flight observed at light traps or pheromone traps in 2015 and 2016 occurred 10–15 days later than simulated predictions; caution is thus warranted as to conclusions derived on computer modeling of adult emergence.

Introduction

Spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), is the most serious defoliator of balsam fir, *Abies balsamea* (L.) Mill., and spruces (*Picea* spp.) (both Pinaceae) in the Nearctic boreal forest (Pureswaran et al., 2016; Bouchard et al., 2018). Univoltine

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adults emerge in late June–July over a span of 10–14 days, with a level of protandry of about 2 days (Bergh et al., 1988; Rhainds, 2015). Females attract conspecific males with sex pheromone and, upon mating, lay half their eggs in the natal patch (Silk et al., 1980; Delisle & Hardy, 1997; Rhainds & Kettela, 2013). Thereafter, partly spent females either oviposit locally for the rest of their life or ascend above tree canopies to migrate downwind (Greenbank et al., 1980; Boulanger et al., 2017), with some evidence of density-dependent dispersal (van Hezewijk et al., 2018; Moise et al., 2019).

Abundance of male budworms has been monitored for decades with light traps (Greenbank et al., 1980; Simmons & Elliot, 1985; Rhainds & Heard, 2015) and pheromone

traps (Houseweart et al., 1981; Ramaswamy et al., 1983; Allen et al., 1986; Sanders, 1988; Rhainds et al., 2016), generally with the objective of correlating catches with future population abundance. Few replicated studies have been carried out to document daily variation in budworm abundance (Régnière et al., 2012; Rhainds & Kettela, 2014; Rhainds, 2015), none of them using both light traps and pheromone traps. Factorial designs (light traps and pheromone traps deployed together or separately) have proven useful to understand various aspects of moth reproductive behavior: temporal variation in sex ratio, protandry, and late-season low response of males to female-produced sex pheromone (Henneberry et al., 1967; Yushima et al., 1973; Oloumi-Sadeghi et al., 1975; Delisle et al., 1998; Sambaraju & Phillips, 2008).

Understanding the phenology of adult budworm activity is important to implement mating disruption (Rhainds et al., 2012), recognize migration events ('out of phase' migrant moths; Sturtevant et al., 2013), and predict the impact of climate change on future patterns of emergence (Régnière et al., 2012). A phenology simulation model has been developed to forecast the life-history trajectory of individual budworms through successive developmental stages in relation to local weather conditions (BioSIM; Régnière, 1996). The model has never been formally validated for the adult stage, however, as it is intrinsically difficult to measure emergence time of budworms in natural conditions for two reasons: (1) time-consuming process of collecting large samples of pupae in the field and rearing them in the laboratory until emergence; and (2) individual variation in larval development rate and timing of pupation implies that multiple cohorts of pupae need to be collected and reared at a given site to reflect 'true' timing of emergence of budworm. The problem is most acute (near insoluble) in endemic, low-density populations with few pupae on tree branches (Régnière & Sanders, 1983).

As with other moths (Riedl et al., 1976; Knight, 2007; Carlos et al., 2018), the phenology of budworm emergence can be indirectly inferred by comparing captures of adults at traps with physiological process-based phenology models (Régnière, 1983; Régnière et al., 2012). Phenology simulations often yield broad windows of emergence relative to observed activity of adult budworms and tend to exhibit early season bias, that is, onset of flight tends to occur later than predictions (see, in particular, figure 6 in Régnière et al., 2012).

Phenology descriptors derived strictly from males captured at pheromone traps also exhibit systematic truncation toward early-flight seasonality. After all, pheromone traps are effective at trapping moths in early season but not so much in late season due to competition between synthetic pheromone sources and actively calling conspecific females (Oloumi-Sadeghi et al., 1975; McNeil, 1991; Delisle et al., 1998). Also, estimates of phenology strictly based on males are biased due to ubiquity of protandry in insects (late emergence of females relative to males) (Morbey & Ydenberg, 2001). In this study, we evaluate variation in day-to-day abundance of males and females at light traps and pheromone traps on the west coast of Newfoundland, Canada.

Materials and methods

Experimental procedure

The experiment was conducted at forest stands near Rocky Harbour (49.57°N, 57.88°W) in 2014 (10 July–1 August), 2015 (see below), and 2016 (10 July–14 August). The stands consisted predominantly of balsam fir with few overwintering larvae (<1 specimen per branch; Lavigne, 2016). The experiment was set up on July 3, 2015, but due to an unusually cold summer, budworms did not fly until July 28 (Figure 1); the experiment was discontinued on August 8.

Adult budworms were captured with stainless steel vane light traps (LT) (Leptraps, Georgetown, KY, USA) with a 15-W neon tube as light source. The LT were suspended on a rope 3–4 m above ground between the trunks of two firs. Each trap was wired to a 12-V marine battery for power, and batteries were replaced every 4–6 days to prevent discharge. Males were also captured using pheromone traps (PT: non-saturating Unitraps baited with 330 µg of pheromone released from a PVC cylinder) (Flexlure; Synergy Semiochemicals, Burnaby, BC, Canada). Traps were deployed on branches of fir 2.5 m above ground; the location of PT in relation to LT is specified below. Moths attracted to LT or PT were killed using strips of Vapona insecticide (Vaportape II; Hercon Environmental, Emigsville, PA, USA).

The study was conducted at the same three plots (spaced >1 km apart) each year. Three subplots were set up ca. 50 m apart at each plot, using the same trees each year. At the onset of experiment each year, a given subplot within a plot was randomly assigned to one of three treatments: (1) LT alone, (2) LT and PT <0.5 m apart, and (3) PT alone. Moths captured at LT and PT were collected daily in 2014–2015, and at intervals of 2–4 days in 2016. For any collection date, budworms were separated from other moth species ('bycatch'), and the abdomen of each budworm specimen was observed under a stereomicroscope to distinguish males and females.

Phenology of budworm flight was simulated with the BioSIM software (Régnière, 1996) at Rocky Harbour between 2014 and 2016, as well as three potential sources of migrants in the province of Quebec (Canada): known
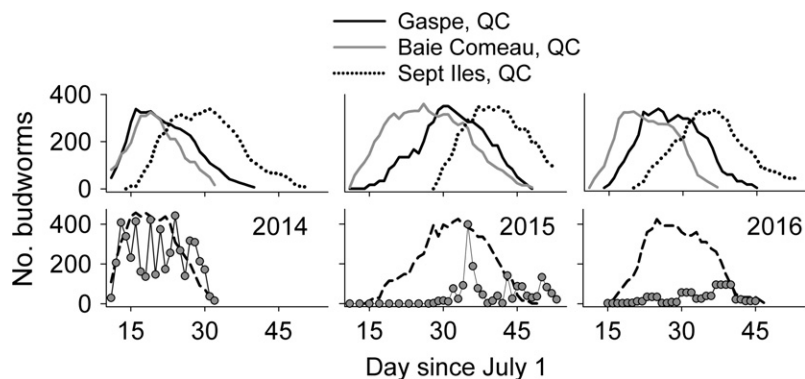
Figure 1 Predicted phenology of spruce budworm flight (upper panels) as determined with BioSIM at three potential sources of migrants: known forest stands with high densities of budworms in the province of Quebec, Canada, near Gaspé, Baie-Comeau, and Sept-Îles. Bottom panels: total numbers of adult spruce budworms (gray dots) captured at light traps and pheromone traps at Rocky Harbour along the west coast of Newfoundland in 2014, 2015, and 2016; dashed lines for each year represent simulated patterns of flight as determined with the BioSIM phenology software (Régnière, 1996).

forest stands with high densities of budworms near Gaspé (49.05°N, 64.62°W), Baie-Comeau (49.25°N, 68.22°W), and Sept-Îles (50.32°N, 66.46°W). Daily estimates of emerged adults were used as a proxy for predicted abundance.

Statistical analysis

Statistical analyses were conducted with the SAS software (SAS Institute, Cary, NC, USA). The dataset included two response variables: abundance of budworms: DENS = log [(adult/trap/plot/day) + 1], with day treated as a repeated measure, and phenology of flight: TIME = average date of capture of adults per trap per plot.

The experimental design was unbalanced (PT capture males but not females); the analyses were thus conducted separately along sex/ trap lines. For males, the effects of plot, year, trap, and treatment on DENS and TIME were evaluated with a generalized linear model, including two- and three-way interactions between year, trap, and treatment, and residual mean squares were used as error terms. The same procedure was used for comparison of males and females, with the variable 'trap' being replaced by 'sex'.

Results

General trends

Budworms were present in greater numbers and occurred seasonally earlier in 2014 than in 2015 and 2016 (Figure 1); these findings held generally true for males and females at LT and males at PT (Figure 2). Simulated and observed patterns of flight at Rocky Harbour on the island of Newfoundland broadly overlapped with the timing of flight at three locations on the mainland (Gaspé, Baie Comeau,

Sept-Îles) (Figure 1). The phenological match between observed and predicted temporal variation in adult abundance at Rocky Harbour was near perfect in 2014, whereas in 2015 and 2016 the onset of flight occurred 10–15 days later than predicted (Figure 1).

Abundance and phenology of males captured at pheromone and light traps

Males were more abundant at LT than at PT, with variable trap effects between years (trap, trap*year: both $P<0.0001$): high LT/PT ratio in 2016 (n = 705/82 = 8.6), intermediate ratio in 2014 (n = 3 839/629 = 6.1), and low ratio in 2015 (n = 705/195 = 3.6) (Table 1, Figure 2).

Experimental treatment (LT and PT deployed together or separately) influenced male abundance with variable effects between traps (treatment: $P = 0.013$; trap*treatment: $P = 0.0004$; Table 1). Separate analyses on a 'per trap' basis indicated higher captures of males at LT coupled with PT relative to LT alone (treatment: $P<0.0001$; Table 1), an effect that was consistent each year [$\sigma_{LT(PT)}$/$\sigma_{LT(0)}$ = 2 427/1 432 = 1.7 in 2014; 471/201 = 2.2 in 2015; 249/198 = 1.3 in 2016] (Figure 1). In contrast, the presence/ absence of LT near PT did not affect numbers of males captured at PT (Table 1, Figure 2). Males occurred earlier at PT than at LT (trap: $P<0.0001$), an effect that was consistent across years (year*trap: $P = 0.22$) and independent of experimental treatment (Table 1, Figure 2).

Abundance and phenology of males and females captured at light traps with or without pheromone traps

Males outnumbered females at LT to a variable extent between years (sex, sex*year: both $P<0.0001$; Table 2): the percentage of females was low in 2015 [(32/3 573) × 100% = 5.6%] and intermediate in 2014 (706/
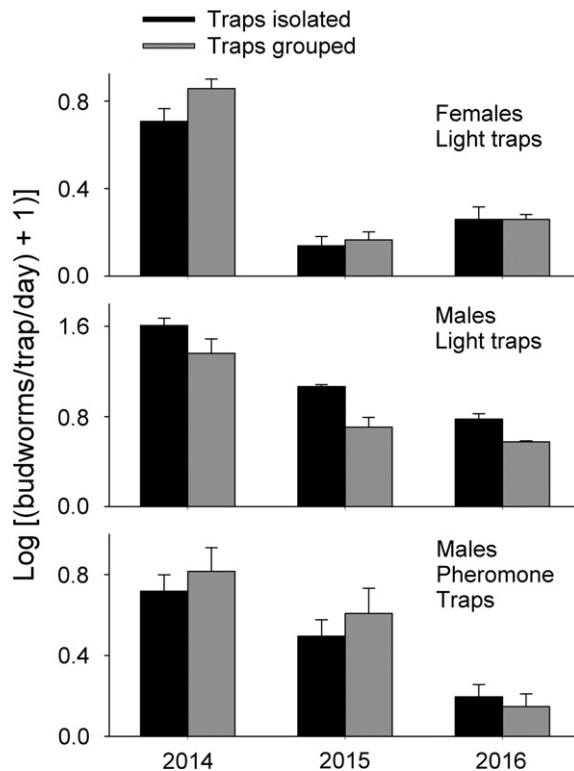
Figure 2 Mean (+ SE) abundance of male and female spruce budworms (no. individuals/ trap/ day) at light traps and pheromone traps either deployed alone or grouped together <0.5 m apart. The experiment was conducted at the same site on the west coast of Newfoundland (Rocky Harbour) between 2014 and 2016.

$4\ 565 \Rightarrow 15.5\%$) and 2016 ($150/855 \Rightarrow 17.5\%$) (Figure 2). Experimental treatment differentially affected abundance of males and females (treatment: P = 0.030; sex*treatment: P = 0.011; Table 1). As noted above, the presence of PT in the vicinity of LT increased the abundance of males (Figure 2). Separate model conducted for ♀ revealed no significant treatment effect (Table 2, Figure 2). Females flew later than males each year (P<0.0001) with a significant interaction term (year*sex: P<0.0001) that was due to between-year variation in extent of protandry [$TIME_♀ - TIME_♂$]: 4.5 days in 2014, 1.2 days in 2015, and 3.5 days in 2016 (Figure 3).

Discussion

Data obtained through this study shed light on several aspects related to spruce budworm adult stage, including sex-specific behavioral response to visual and olfactory stimuli, phenology of flight, and detection of immigration events.

Response of male spruce budworms to visual and olfactory stimuli

Male budworms exhibited asymmetric synergistic responses to light traps and pheromone traps deployed in close vicinity to each other or segregated spatially: males were more abundant at light traps 'baited' with a pheromone trap, whereas abundance of males at pheromone traps was similar with or without contiguous light traps. This outcome may be mediated, in part, by distinct ranges of attraction for light traps (usually <100 m; Baker & Sadovy, 1978; Bucher & Bracken, 1979; Truxa & Fiedler, 2012) and pheromone traps (generally assumed to be several hundreds of m; Wall & Perry, 1987; Phelan, 1997). In that context, pheromone sources may attract males from a long distance, and some of these males end up at light traps. On the other hand, the traps were deployed at a relatively short distance from each other in our experiment (50 m), thus relative abundance of males at light traps and pheromone traps likely involve multi-scale integrative neurophysiological responses to olfactory and visual stimuli (Nishino et al., 2018).

Synergistic interactions between light traps and pheromone sources have been demonstrated for some insects (Henneberry et al., 1967; Yushima et al., 1973; McQuate, 2014), but in others the effect is additive (Delisle et al., 1998; Sambaraju & Phillips, 2008). Based on recent reports that artificial light interferes with mate location (Otálora-Luna & Dickens, 2011; van Geffen et al., 2015), antagonistic interactions between visual and olfactory cues are also expected to occur in nature.

Response of female spruce budworms to visual and olfactory stimuli

The presence of PT in the vicinity of light traps had no statistical effect on the abundance or phenology of female budworms, which can be attributed to an inadequate bioassay. The short distance between light traps and pheromone sources (50 m) may, for example, have influenced the abundance of females independently of pheromone treatment. Although this hypothesis cannot be rejected, it must be noted that sex ratios of budworms at light traps in this study were well within the range of past studies (Rhainds & Heard, 2015).

Some level of behavioral response by female budworms to conspecific pheromone is expected, considering that females are physiologically capable of auto-detection, and exposure to conspecific pheromone alters behavior in laboratory conditions (Palaniswamy & Seabrook, 1978, 1985; Palaniswamy et al., 1979; Sanders, 1987; for a review of pheromone auto-detection in moths, see Holdcraft et al., 2016). The development of a field bioassay to detect direct or indirect response of female moths to their pheromone is much needed. In the absence of such an assay, the significance of pheromone auto-detection in nature remains

Table 1 Output of generalized linear model (glm procedure of SAS) evaluating multivariate effects on two response variables—DENS: log [(no. adults/trap/plot/day) + 1], with 'day treated' as a repeated measure; TIME: average date of capture of adults per trap per plot—for male spruce budworms captured at light traps or pheromone traps (trap) at three locations (site) near Rocky Harbour on the west coast of Newfoundland over a 3-year period (2014–2016). Experimental treatment consisted of light traps and pheromone traps, deployed contiguously or segregated spatially. For the variable DENS, separate analyses on a 'per trap' basis were conducted due to significant trap*treatment interaction

| | Response variables | | | | | | | |
| | DENS | | | | TIME | | | |
Independent variables	Type III SS	df	F	P	Type III SS	df	F	P
Site	5.20	2	2.53	0.080	3.61	2	1.50	0.25
Year	106.91	2	52.05	0.0001	1752.83	2	696.03	0.0001
Trap	188.69	1	183.74	0.0001	30.01	1	24.91	0.0001
Treatment	6.33	1	6.16	0.013	0.09	1	0.07	0.79
Year*trap	26.49	2	12.90	0.0001	3.89	2	1.61	0.22
Year*treatment	0.59	2	0.29	0.75	0.34	2	0.14	0.87
Trap*treatment	12.97	1	12.63	0.0004	0.36	1	0.30	0.59
Year*trap*treatment	1.89	2	0.92	0.40	0.30	2	0.12	0.89
Error term	540.17	526			26.51	22		
Light trap								
Site	13.26	2	5.66	0.0039				
Year	114.97	2	49.02	0.0001				
Treatment	18.71	1	15.95	0.0001				
Year*treatment	0.30	2	0.13	0.88				
Error term	307.26	262						
Pheromone trap								
Site	0.94	2	0.55	0.58				
Year	18.42	2	10.78	0.0001				
Treatment	0.59	1	0.69	0.41				
Year*treatment	2.18	2	1.28	0.28				
Error term	223.90	262						

unclear, even with regard to the directionality (attraction or repellence) of female response.

Phenology of spruce budworm emergence and flight

Although limited in scope, the data provided in this study suggest that phenology estimates derived from BioSIM exhibit early season bias, that is, the observed onset of flight in both 2015 and 2016 occurred 10–15 days later than simulated predictions (Figure 1; see also figure 6 in Régnière et al., 2012). It is also important to consider inherent 'bias' in phenology inference linked with sampling methodology. As documented in other species (Oloumi-Sadeghi et al., 1975; McNeil, 1991; Delisle et al., 1998), male budworms flew earlier at pheromone traps than at light traps for each of 3 years as a result of late-season competition between calling females and synthetic pheromone sources. As predicted, female budworms flew later than males at light traps, emphasizing the importance of sex ratio when assessing temporal windows of flight.

Early-stage development of a mathematic tool to discriminate resident/ immigrant budworms

Radar observations and aerial collections of windborne budworms have been used to document weather conditions conducive to migrations and sex ratios (males migrate but less frequently than females) (Miller et al., 1978; Greenbank et al., 1980; Dickison et al., 1983; Rhainds & Heard, 2015; Boulanger et al., 2017). One challenge in documenting immigration relates to the vastness of forest habitats and consequent 'homogeneous' niche of budworms with inter-locked populations, which makes it difficult to distinguish short-range flights of residents from long-range migrations. The geographic setting of Newfoundland (large island isolated from the mainland by an oceanic barrier >100 km across) provides an ideal location to discriminate local flight from long-range immigrations. In our study, immigrations cannot be ruled out for any single day of trapping due to broad overlap in emergence patterns at Rocky Harbour relative to forest stands with known populations of budworms on the mainland.

Table 2 Output of generalized linear model (glm procedure of SAS) evaluating multivariate effects on two response variables—DENS: log [(no. adults/ trap/ plot/ day) + 1], with 'day treated' as a repeated measure; TIME: average date of capture of adults per trap per plot—for male and female spruce budworms (sex) captured at light traps at three locations (site) near Rocky Harbour on the west coast of Newfoundland over a 3-year period (2014–2016). Experimental treatment consisted of light traps with or without a contiguous pheromone trap. The outcome of separate models for males at light traps are included in Table 1

Independent variables	Response variables							
	DENS				TIME			
	Type III SS	df	F	P	Type III SS	df	F	P
Site	7.92	2	3.96	0.020	1.70	2	2.52	0.10
Year	151.47	2	75.73	0.0001	1441.87	2	2138.18	0.0001
Sex	194.53	1	194.93	0.0001	76.36	1	226.47	0.0001
Treatment	5.92	1	5.92	0.015	0.50	1	1.47	0.24
Year*sex	10.87	2	5.43	0.0046	25.29	2	37.51	0.0001
Year*treatment	1.58	2	0.79	0.45	0.28	2	0.42	0.66
Sex*treatment	11.94	1	11.94	0.0006	0.04	1	0.11	0.74
Year*sex*treatment	1.23	2	0.61	0.54	0.00	2	0.00	1.0
Error term	490.02	490			7.42	22		
Females								
Site	1.79	2	1.15	0.32	3.73	2	5.23	0.028
Year	53.92	2	34.70	0.0001	606.12	2	851.23	0.0001
Treatment	2.54	1	6.75	0.027	0.13	1	0.37	0.56
Year*treatment	2.30	2	2.30	0.23	0.23	2	0.23	0.80
Error term	307.26	262			3.56	10		
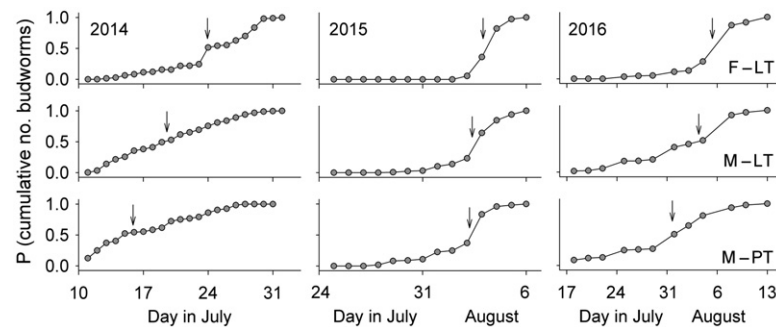
Figure 3 Cumulative abundance of male (M) and female (F) spruce budworms captured at light traps (LT) and males at pheromone traps (PT). The experiment was conducted at the same site on the west coast of Newfoundland (Rocky Harbour) between 2014 and 2016. The arrows in each plot correspond to the median date of capture.

Long-range immigrations from the mainland to the west coast of Newfoundland are expected to vary in intensity. Minor immigration events (those involving few individuals) are by nature difficult to tract and lead to a teleological trap: in assuming that minor immigrations occur everywhere, they become differentiable nowhere.

Immigration events are defined here as pulsed, external depositions of budworms with large numerical amplitude for both males and females (2–3 orders of magnitude in variation in moth abundance from one day to the next)

(Greenbank, 1957; Dickison et al., 1983; Rhainds, 2015). Based on moderate daily variation in abundance of adult budworms at Rocky Harbour between 2014 and 2016, we assume that few immigrations took place during the course of the study (no. resident budworms>>>immigrants). Long-term monitoring of budworm flight on the west coast of Newfoundland is needed to develop mathematical diagnostic tools to infer the likelihood of immigration events based on temporal patterns of adult abundance.

Acknowledgements

References

Allen DC, Abrahamson LP, Eggen DA, Lanier GN, Swier SR et al. (1986) Monitoring spruce budworm (Lepidoptera: Tortricidae) populations with pheromone-baited traps. Environmental Entomology 15: 152–165.

Baker RR & Sadovy Y (1978) The distance and nature of the light trap response of moths. Nature 276: 818–821.

Bergh JC, Eveleigh ES & Seabrook WD (1988) The mating status of field-collected male spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: tortricidae), in relation to trap location, sampling method, sampling date, and adult emergence. Canadian Entomologist 120: 821–830.

Bouchard M, Régnière J & Therrien P (2018) Bottom-up factors contribute to large-scale synchrony in spruce budworm populations. Canadian Journal of Forest Research 48: 277–284.

Boulanger Y, Fabry F, Kilambi A, Pureswaran DS, Sturtevant BR & Saint-Amant R (2017) The use of weather surveillance radar and high-resolution three dimensional weather data to monitor a spruce budworm mass exodus flight. Agricultural Forest Meteorology 234–235: 127–135.

Bucher GE & Bracken GK (1979) The bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae). An estimate of light and pheromone trap efficiency based on captures of newly emerged moths. Canadian Entomologist 111: 977–984.

Carlos C, Gonçalves F, Oliveira I & Torres L (2018) Is a biofix necessary for predicting the flight phenology of *Lobesia botrana* in Douro demarcated region vineyards? Crop Protection 110: 57–64.

Delisle J & Hardy M (1997) Male larval nutrition influences the reproductive success of both sexes of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Functional Ecology 11: 451–463.

Delisle J, West RJ & Bowers WW (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.

Dickison RBB, Haggis MJ & Rainey RC (1983) Spruce budworm moth flight and storms: case study of a cold front system. Journal of Climatology and Applied Meteorology 22: 278–286.

van Geffen KG, van Eck E, de Boer RA, van Grunsven RHA, Salis L et al. (2015) Artificial light at night inhibits mating in a geometrid moth. Insect Conservation and Diversity 8: 282–287.

van Hezewijk B, Wertman D, Stewart D, Béliveau C & Cusson M (2018) Environmental and genetic influences on the dispersal propensity of spruce budworm (*Choristoneura fumiferana*). Agricultural and Forest Entomology 20: 433–441.

Greenbank DO (1957) The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. II. The role of dispersal. Canadian Journal of Zoology 35: 385–403.

Greenbank DO, Schaefer GW & Rainey RC (1980) Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. Memoirs of the Entomological Society of Canada 110: 1–49.

Henneberry TJ, Howland AF & Wolf WW (1967) Combinations of blacklight and virgin females as attractants to cabbage looper moths. Journal of Economic Entomology 60: 152–156.

Holdcraft R, Rodriguez-Saona C & Stelinski LL (2016) Pheromone autodetection: evidence and implications. Insects 7: 17.

Houseweart MW, Jennings DT & Sanders CJ (1981) Variables associated with pheromone traps for monitoring spruce budworm populations (Lepidoptera: Tortricidae). Canadian Entomologist 113: 527–537.

Knight AL (2007) Adjusting the phenology model of codling moth (Lepidoptera: Tortricidae) in Washington State apple orchards. Environmental Entomology 36: 1485–1493.

Lavigne D (2016) Forest Insect and Disease: 2015 Control and Monitoring Activities and 2016 Outlook. FEIS Report 110. Government of Newfoundland and Labrador, Corner Brook, NL, Canada.

McNeil JN (1991) Behavioral ecology of pheromone-mediated communication in moths and its importance in the use of pheromone traps. Annual Review of Entomology 36: 403–430.

McQuate GT (2014) Green light synergistically enhances male sweetpotato weevil response to sex pheromone. Scientific Reports 4: 4499.

Miller CA, Greenbank DO & Kettela EG (1978) Estimated egg deposition by invading spruce budworm moths (Lepidoptera: Tortricidae). Canadian Entomologist 110: 609–615.

Moise ERD, Lavigne MB & Johns RC (2019) Density has more influence than drought on spruce budworm (*Choristoneura fumiferana*) performance under outbreak conditions. Forest Ecology and Management 433: 170–175.

Morbey YE & Ydenberg RC (2001) Protandrous arrival timing to breeding areas: a review. Ecology Letters 4: 663–673.

Nishino H, Iwasaki M, Paoli M, Kamimura I, Yoritsune A & Mizunami M (2018) Spatial receptive fields for odor localization. Current Biology 28: 1–9.

Oloumi-Sadeghi H, Showers WB & Reed GL (1975) European corn borer: lack of synchrony of attraction to sex pheromone and capture in light traps. Journal of Economic Entomology 8: 663–667.

Otálora-Luna F & Dickens JC (2011) Multimodal stimulation of Colorado potato beetle reveals modulation of pheromone response by yellow light. PLoS ONE 6: e20990.

Palaniswamy P & Seabrook WD (1978) Behavioral responses of the female eastern spruce budworm *Choristoneura fumiferana* (Lepidoptera, Tortricidae) to the sex pheromone of her own species. Journal of Chemical Ecology 4: 649–655.

Palaniswamy P & Seabrook WD (1985) The alteration of calling behaviour by female *Choristoneura fumiferana* when exposed

to synthetic sex pheromone. Entomologia Experimentalis et Applicata 37: 13–16.

Palaniswamy P, Sivasubramanian P & Seabrook WD (1979) Modulation of sex pheromone perception in female moths of the eastern spruce budworm, *Choristoneura fumiferana* by Altosid. Journal of Insect Physiology 25: 571–574.

Phelan PL (1997) Evolution of mate-signaling in moths: phylogenetic considerations and predictions from the asymmetric tracking hypothesis. The Evolution of Mating Systems in Insects and Arachnids (ed. by JC Choe & RJ Crespi), pp. 240–256. Cambridge University Press, Cambridge, UK.

Pureswaran DS, Johns R, Heard SB & Quiring DT (2016) Paradigms in eastern spruce budworm (Lepidoptera: Tortricidae) population ecology: a century of debate. Environmental Entomology 45: 1333–1342.

Ramaswamy SB, Cardé RT & Witter JA (1983) Relationships between catch in pheromone-baited traps and larval density of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist 115: 1437–1433.

Régnière JR (1983) An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist 115: 1371–1382.

Régnière JR (1996) Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology 25: 869–881.

Régnière JR & Sanders CJ (1983) Optimal sample size for the estimation of spruce budworm (Lepidoptera: Tortricidae) populations on balsam fir and white spruce. Canadian Entomologist 115: 1621–1626.

Régnière J, St-Amant R & Duval P (2012) Predicting insect distributions under climate change from physiological responses: spruce budworm as an example. Biological Invasions 14: 1571–1586.

Rhainds M (2015) Wing wear and body size measurements of adult spruce budworms captured at light traps: inference on seasonal patterns related to reproduction. Applied Entomology and Zoology 50: 477–485.

Rhainds M & Heard SB (2015) Sampling procedures and adult sex ratios in spruce budworm. Entomologia Experimentalis et Applicata 154: 91–101.

Rhainds M & Kettela EG (2013) Oviposition threshold for flight in an inter-reproductive migrant moth. Journal of Insect Behavior 26: 850–859.

Rhainds M & Kettela EG (2014) Monitoring spruce budworm with light traps: the effect of trap position. Psyche 2014: 450785.

Rhainds M, Kettela EG & Silk PG (2012) Thirty-five years of pheromone-based mating disruption studies with *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae). Canadian Entomologist 144: 379–395.

Rhainds M, Therrien P & Morneau L (2016) Pheromone-based monitoring of spruce budworm larvae in relation to trap position. Journal of Economic Entomology 109: 717–723.

Riedl H, Croft BA & Howitt AJ (1976) Forecasting codling moth phenology based on pheromone trap catches and physiological-time models. Canadian Entomologist 108: 449–460.

Sambaraju KR & Phillips TW (2008) Responses of adult *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) to light and combinations of attractants and light. Journal of Insect Behavior 21: 422–439.

Sanders CJ (1987) Flight and copulation of female spruce budworm in pheromone impregnated air. Journal of Chemical Ecology 13: 1749–1758.

Sanders CJ (1988) Monitoring spruce budworm population density with sex pheromone traps. Canadian Entomologist 120: 175–183.

Silk PJ, Tan SH, Wiesner CJ, Ross RJ & Lonergan CG (1980) Sex pheromone chemistry of the eastern spruce budworm, *Choristoneura fumiferana*. Environmental Entomology 9: 640–644.

Simmons GA & Elliot NC (1985) Use of moths caught in light traps for predicting outbreaks of the spruce budworm (Lepidoptera: Tortricidae) in Maine. Journal of Economic Entomology 78: 362–365.

Sturtevant BR, Achtemeier GL, Charney JJ, Anderson DP, Cooke BJ & Townsend PP (2013) Long-distance dispersal of spruce budworm (*Choristoneura fumiferana* Clemens) in Minnesota (USA) and Ontario (Canada) via the atmospheric pathway. Agricultural and Forest Meteorology 168: 186–200.

Truxa C & Fiedler K (2012) Attraction to light – from how far do moths (Lepidoptera) return to weak artificial sources of light? European Journal of Entomology 109: 77–84.

Wall C & Perry JN (1987) Range of action of moth sex-attractant sources. Entomologia Experimentalis et Applicata 44: 5–14.

Yushima T, Noguchi H, Tamaki Y, Fukazawa N & Sugino Y (1973) Mating and sex pheromone of *Spodoptera litura* F. (Lepidoptera: Noctuidae): an introductory report. Applied Entomology and Zoology 8: 18–26.