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ORIGINAL RESEARCH PAPER

Wing wear and body size measurements of adult spruce budworms captured at light traps: inference on seasonal patterns related to reproduction

Marc Rhainds[1]

Abstract Adult spruce budworms, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), were captured at light traps in New Brunswick (NB) in 2012, Québec (QC) in 2013, and Newfoundland (NL) in 2014; population densities were low in NB–NL, and moderate in QC. Morphological parameters (wing score index, wing length, dry weight, residual fecundity) were estimated for thousands of adults. A very large number of budworms were captured during the night of 15–16 July 2013. The heavy weight and low proportion of eggs laid by these females suggest a synchronized, pulsed emergence of local adults rather than mass immigration. Variation in sex ratio and adult morphology suggest that populations were 'closed' at all locations (resident moths ≫ immigrants), as indicated by an increasing proportion of females over time (protandrous emergence) and declining weight over time (reflective of the ageing of adults). The small size of adults in QC relative to NB–NL suggests that inverse-density-dependent fecundity affects population dynamics early in the transition between endemic and epidemic phases. Wing wear provides a useful proxy for the age of adults: individuals with fresh wings (limited wear) were heavier than those with damaged wings, which likely reflects the metabolic costs of survival and (for females) the accruing proportion of eggs laid over time.
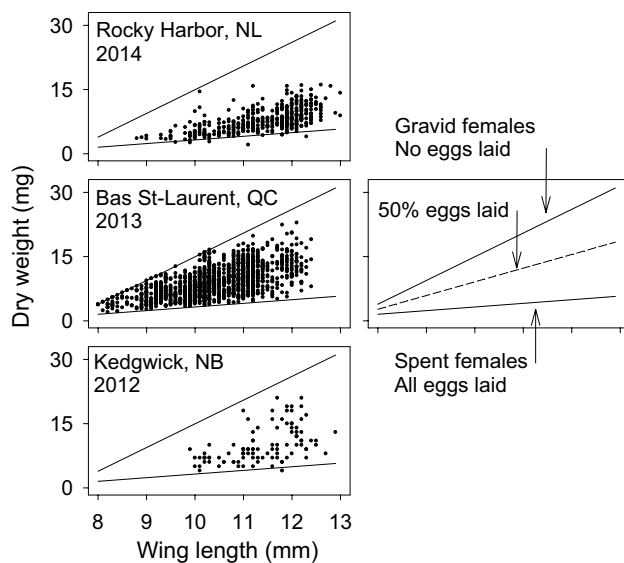
✉ Marc Rhainds
mrhainds@nrcan.gc.ca

1 Natural Resources Canada, Canadian Forest Service -
   Atlantic Forestry Centre, P.O. Box 4000, Fredericton,
   NB E3B 5P7, Canada

Introduction

The relation between body size at emergence and fecundity is ubiquitous in insects (Honěk 1993) particularly in Lepidoptera capital breeders whose females strictly rely on larval accumulated resources for reproduction (Heisswold et al. 2009; Leather 1988; Miller 2005; Tammaru et al. 2002). In these species, females rapidly lose weight after emergence as a result of egg-laying (Boggs 1997), and measurement of dry weight of field-collected specimens can be used to simulate the number and proportion of eggs laid by females relative to their potential fecundity (Lyons 1996). Equations describing the triangulation between potential fecundity (estimated using an indicator of body size), dry weight and realized fecundity (proportion of eggs laid by females at the time of sampling) are derived by rearing field-collected pupae to adulthood in the laboratory and allowing them to lay known numbers of eggs over different time intervals (Delisle et al. 1998; Rosenheim et al. 2008; Thomas 1978). The approach is depicted in Fig. 1 for the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). The realized fecundity (RF) of females of known body size (expressed here as wing length, WL) can be estimated based on their dry weight (DW); RF can be visualized in relation to two baseline equations describing WL-DW linear regression for gravid females at emergence (RF = 0) and spent females at death (RF = 1) (Fig. 1).

Fig. 1 Relation between the length of forewings (WL) and dry weight (DW) of female spruce budworms captured with light traps at different locations. The *regression lines* represent the equations for spent females that laid all their eggs (DW = 0.85 WL–5.27) and gravid females that did not lay any eggs (DW = 5.54 WL–40.44). The equations were derived from >1500 female pupae collected in the field in Fredericton in 1977 and allowed to oviposit in the laboratory (Thomas et al. 1980). The proportion of eggs laid by females was estimated using the ratio between realized fecundity (73.3 WL–13.2 DW–535.4) and potential fecundity (61.7 WL–465.7) (Thomas et al. 1980)

The spruce budworm (SBW) is the most severe defoliator of conifers in eastern Canada (Morris 1963). The negative socio-economic impact of SBW combined with the potential role of adult migration on outbreak dynamics, have prompted research efforts to understand its reproductive ecology. Short-lived female SBWs are typical capital-breeding moths that attract males with pheromone, mate early in life and oviposit shortly thereafter (Delisle and Hardy 1997, Outram 1971). One apparently unique strategy of SBW females is that they often migrate late in life after having laid more than 50 % of their eggs (Greenbank et al. 1980; Rhainds and Kettela 2013); young gravid females are incapable of flying because of their heavy wing load (Wellington and Henson 1947).

Conversion of estimates of body size and dry weight in terms of potential and residual fecundity have been used in three contexts for SBW: (1) emigrants captured while ascending above the tree canopy, to assess the residual fecundity of dispersing females (Greenbank et al. 1980); (2) dead females collected on drop trays, to assess the proportion of eggs laid by females that died from natural causes (Thomas 1978; Thomas et al. 1980); and (3) females captured at light traps versus resident females collected by fogging trees with insecticide, to quantify an oviposition

threshold for flight (Rhainds and Kettela 2013). The studies above were all conducted at locations with high densities of SBW; no data are available from low density (endemic) populations.

The condition of wings of females (wing wear) may help to contextualize their reproductive condition. In butterfly populations, wing wear is often used as a proxy to estimate the age and cumulative level of activity of field-collected adults; the technique is easy to implement and can be applied to thousands of individuals (Ehrlich et al. 1984). For unclear reasons, wing wear assessments have rarely been used for moths (Rhainds and Brodersen 2012) and never in the context of light trap studies. Assuming that wing wear is related to the age of SBW adults (as damage progressively accrues during the moth's life), two specific trends are expected: (1) young females with fresh wings have laid relatively few eggs and are thus heavier than old females with damaged wings; and (2) wing wear increases over time to reflect ageing of the local population of adults.

The present study was conducted to evaluate relationships between wing wear, length of forewing, and dry weight for male and female budworms captured at light traps in endemic and epidemic populations of SBW, with the objective of documenting seasonal variation in parameters related to the reproductive condition of adults. A holistic approach was used, taking into account multiple morphological parameters of moths captured at light traps to infer local processes related to the ecology and population dynamics of SBW and generate novel hypotheses for future research.

Materials and methods

Sampling procedure

The research was conducted in forest stands containing hosts of SBW (balsam fir and spruces) as dominant or co-dominant tree species. The experimental plots were located near Kedgwick in New Brunswick in 2012 (5 plots sampled within a 50-km^2 area between 9 and 31 July: 47.69°N, 67.20°W; 47.71°N, 67.08°W; 47.72°N, 67.19°W; 47.76°N, 67.15°W; 47.77°N, 67.11°W), near Mont-Joli in Bas Saint-Laurent in Québec in 2013 (3 plots sampled in a 30-km^2 area between 10 and 26 July: 48.41°N, 68.41°W; 48.44°N, 68.38°W; 48.51°, 68.18°W), and Rocky Harbor in Newfoundland in 2014 (3 plots sampled within a 5-km^2 area between 11 and 31 July: 45.58°N, 57.90°W; 45.59°N, 57.91°W; 45.60°N, 57.92°W). Densities of budworms, as provided by the Provincial Department of Natural Resources, were very low in NB [<0.2 overwintering larvae (L2) per branch], high in QC (>15 L2 per branch), and low in NL (1 L2 per branch).

In each plot, one stainless steel vane trap (Leptraps, Georgetown, KY, USA) with a 15-W neon tube as light source was suspended on a rope between two host trees, 3–4 m above ground: each trap was wired to a marine battery for power. Each day in late afternoon, ethyl acetate was placed in two 250-ml aluminium cans (with a sponge inserted through a slit on the top of the can) at the bottom of the trap to kill captured adults, and the moths were collected the next morning. For some days in 2014, strips of dichlorvos (Vapona) were used to kill the moths due to labor shortage (no worker was available to fill ethyl acetate cans in late afternoon between 17 and 19 July and 22–27 July): for these dates, wing wear was not measured.

Ethyl acetate was preferentially used as a killing agent because the moths rapidly died when exposed to its vapor: hence the condition of wings reflects that at the time of capture. Insecticide strips, on the other hand, result in slow deaths of moths, 'frantic' wing beating, and artificial wing damage. Ethyl acetate does not kill moths after it has evaporated from the aluminium cans, however, and it was unclear at the onset of the study whether ethyl acetate would kill moths over the entire night. For that reason, traps were emptied once or twice per night in 2012–2013, which indicated that ethyl acetate deployed in late afternoon is effective in rapidly killing moths through the entire night.

Moths captured at light traps were collected on a daily basis, transferred to plastic containers (labelled by plot and date) and stored at −20 °C. Within 72 h of capture, SBW were sorted from other moth species ('bycatch'); shortly after, SBW specimens were grouped into three classes based on wing wear: (1) damaged wings with a score of 1–3; (2) average wings with a score of 4–7; and (3) fresh (near mint) wings with a score of 8–10 (Fig. 1 in Rhainds and Brodersen 2012). Wing score assessments were standardized by grading the wings in late afternoon at the same physical location on a desk facing a window; a grid of moths with distinct wing scores served as reference during the grading process. [When traps became saturated with moths, as occurred during the night of 15–16 July in QC, ethyl acetate was ineffective at rapidly killing SBW so wing wear could not be determined]. The genitalia of specimens was visually inspected with a binocular microscope to segregate males and females, and the moths stored at −20 °C in separate paper bags labelled by location, date, sex, and wing score.

For most dates and locations, all females captured at light traps were processed to measure the length of one forewing (±0.1 mm) and dry weight (±0.0001, after an exposure at 60 °C for 48 h). Moths that had become damaged (loss of body parts) during the sorting-scoring-sexing processes were not included in measurements. Several thousand females were captured for some nights in 2013

(16–20 July, 24 July), and in these instances a subsample of >500 moths per night per location were grouped by wing score classes and sexed, of which >100 specimens were measured and dry weighed.

Measurement of individual moths is time consuming, and the major objective of the study was to assess the reproductive condition of females; males were also of interest but to a lesser extent. For that reason, the forewings of males were not measured in 2012; the dry weight was assessed cumulatively for groups of males by plot, date, and wing score index. In 2013, males were measured individually as recorded above for females. In 2014, males were assigned to one of four size classes based on the length of forewings: <9, 9–10, 10–11, and >12 mm; dry weight was assessed for groups of males for different plots, dates, and wing score.

Statistical analysis

Statistical analyses were conducted with the SAS software (SAS Institute, Cary, NC). The flight season was divided into three periods (early, peak, late) based on temporal variation in moth abundance (Fig. 2). For each location [New Brunswick (NB), Québec (QC), Newfoundland (NL)], numbers of males and females per trap per day [$y' = \log(y + 1)$] and average values of wing score per trap per day [each individual was assessed a grading of 1, 4, or 8] were analyzed with factorial ANOVA, treating sex and seasonal period as fixed factors, plot as a random factor, and date as a repeated measure; dates-plots with only one individual were deleted from analysis. Three morphological traits were further analyzed in relation to wing score and seasonal period using factorial ANOVA, with separate analyses for males and females: (1) wing length (WL, in mm), (2) dry weight (DW, in mg), and (3) proportion of eggs laid by females at the time of capture (equations in caption of Fig. 1). Because only 104 females were sampled in NB in 2012, data were pooled by plot for analysis. In NL in 2014, morphological attributes (WL, DW, eggs laid) of females with damaged wings (score 1–3) were not included in the analysis due to low sample size ($N = 9$ for the entire flight season).

One main objective of the study was to quantify parameters associated with the reproductive condition of female SBW in relation to wing wear. To that end, ANOVA was used to evaluate wing length and percentage of eggs laid by individual females captured at light traps in relation to location (NB, QC, NL) and wing score.

Results

The abundance of SBW captured at light traps was 70–100 times higher in epidemic populations in QC in
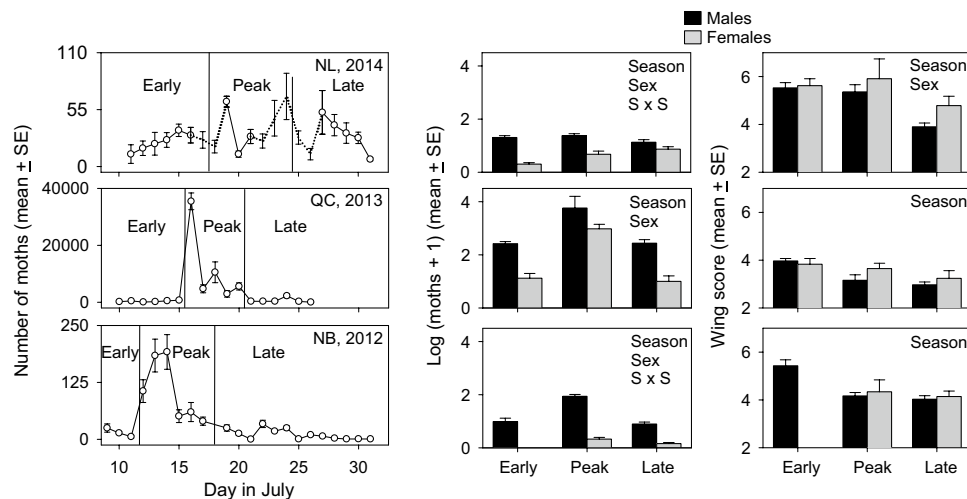
Fig. 2 *Left*: daily abundance of spruce budworms captured at light traps deployed near Kedgwick in New Brunswick in 2012, near Mont-Joli in Québec in 2013, and near Rocky Harbor in Newfoundland in 2014. The flight season was divided into three periods based on seasonal variation of moth abundance in 2012 and 2013; because moth abundance did not vary greatly as a function of time in 2014, the flight season was divided into three periods of 7 days. *Dotted line* segments in NL indicate dates for which wing score of moths was not measured. *Centre*: variation in abundance of male and female spruce budworms in relation to flight period (season). *Right*: variation in the wing score of males and females in relation to season: individual moths were assigned a score of 1–3 (damaged wings), 4–7 (average wings), and 8–10 (fresh wings) using the grading index depicted in Fig. 1 in Rhainds and Brodersen 2012. For the *centre* and *right* panels, significant parameters are represented in the *upper right corner* of each graph. S × S indicates a significant interaction between season and sex (factorial ANOVA); the effect of sex on wing score in NL was marginally insignificant ($p < 0.10$) (Table 1)

2013 (ca. 65,000 moths per plot) than in the two locations with endemic populations in New Brunswick (NB) in 2012 and Newfoundland (NL) in 2014 (900 and 625 moths per plot, respectively) (Fig. 2). Captures in QC were particularly high during the night of 15–16 July 2013 (>35,000 moths per plot). The abundance of adults increased sharply during the night of 11–12 July in NB and remained high for the three subsequent nights; in contrast, the abundance of moths remained relatively stable over time in NL (Fig. 2).

Males were more abundant than females at all locations, as indicated by the significant effects of sex in Table 1. In NB and NL, the interaction between season and sex was significant (Table 1) due to an increase in the proportion of females relative to males over time (Fig. 2). In QC, both males and females were more abundant during the peak flight period than early or late in the season, and the interaction between sex and season was not significant (Table 1; Fig. 2).

Wing score indices of adults declined over time at all locations (Table 1; Fig. 2). In NL, the wings of males were more damaged (low wing score) than those of females (Table 1; Fig. 2), although the effect was marginally insignificant ($p = 0.090$; Table 1). No difference in wing wear was observed between males and females in NB or QC, and the interaction between season and sex was not significant at any location (Table 1).

At both QC and NL, males with damaged wings (score 1–3) were smaller than those with fresh wings (score 8–10) (Fig. 3). The wing length of males declined over time in NL, an effect that was not observed in QC (Fig. 3). Trends related to dry weight of males were similar at all locations: (1) individuals with damaged wings were smaller relative to individuals with fresh wings, and (2) the dry weight steadily declined over time (Fig. 3); interactions between season and wing score were not significant (Table 1).

At NB, the dry weight of females declined over time, which corresponded to a higher proportion of eggs laid by females in late season (Fig. 4). For females in QC, the main effects of wing score and season were significant for all morphological traits (Table 1). The wing length of females declined over time and was lowest for females with damaged wings (Table 1; Fig. 4). Similarly, dry weight of females declined over time and was lower for females with damaged wings, but differences were more pronounced in early than late flight season, resulting in a significant interaction between season and wing score (Table 1; Fig. 4). The proportion of eggs laid by females clearly increased over time for females with high wing scores (i.e., low wing wear) but this trend was less evident for females with low wing scores, resulting in a significant season × wing score interaction (Table 1; Fig. 4). Early in the flight season, females with damaged wings had laid more eggs than females with fresh wings but this trend was not apparent in peak or late season (Table 1; Fig. 4). For females in

Table 1 Statistical effects of variables affecting morphological traits of spruce budworms captured at light traps [wing score, wing length (WL); dry weight (DW), proportion of eggs laid (equations in caption of Fig. 1)]

Dependent variable	Independent variable	Location					
		NB		QC		NL^t	
		F	P	F	P	F	P
Abundance^{tt}	Plot	ns		ns		5.87	0.0037
	Sex	295.15	0.0001	81.59	0.0001	98.04	0.0001
	Season	79.21	0.0001	65.90	0.0001	4.38	0.0146
	S × S	41.21	0.0001	ns		10.60	0.0001
Wing score	Plot	ns		3.12	0.0496	ns	
	Sex	ttt		ns		*2.98*	*0.0900*
	Season	12.23	0.0001	9.06	0.0003	11.27	0.0001
	S × S	ttt		ns		ns	
WL (♂)	Plot	ttt		ns		ns	
	Wing score	ttt		27.46	0.0001	13.19	0.0001
	Season	ttt		ns		4.15	0.0202
	WS × S	ttt		ns		ns	
DW (♂)	Plot	ns		ns		*5.27*	*0.0077*
	Wing score	32.29	0.0001	119.51	0.0001	29.27	0.0001
	Season	148.31	0.0001	57.88	0.0001	29.48	0.0001
	WS × S	ns		ns		ns	
WL (♀)	Plot	4.63	0.0195	ns		ns	
	Wing score	*3.34*	*0.0735*	6.88	0.0019	6.61	0.0144
	Season	ns		39.04	0.0001	4.46	0.0185
	WS × S	ns		ns		ns	
DW (♀)	Plot	*3.01*	*0.0666*	ns		ns	
	Wing score	ns		40.54	0.0001	*2.93*	*0.0961*
	Season	*4.61*	*0.0549*	48.33	0.0001	8.22	0.0013
	WS × S	ns		7.41	0.0001	ns	
Eggs laid	Plot	ns		4.13	0.0202	ns	
	Wing score	ns		5.13	0.0083	ns	
	Season	*3.61*	*0.0841*	36.58	0.0001	20.61	0.0001
	WS × S	ns		4.84	0.0001	ns	

F and *p* values are reported only for significant ($p < 0.05$) or marginally insignificant effects ($p < 0.10$; italicized characters). *ns* non-significant ($p > 0.10$)

Experiments were conducted at three locations: Kedgwick in New Brunswick in 2012 (NB), Bas Saint-Laurent in Québec in 2013 (QC), and Rocky Harbor in Newfoundland in 2014 (NL)

Abundance and wing score of adults were analyzed with factorial ANOVA using average values per plot per date and treating plot as random factor, seasonal period and sex as fixed effects, and date as a repeated measurement. Analyses on wing length, dry weight, and (for females) proportion of eggs laid were conducted separately for males and females; these analyses (factorial ANOVA) used average values per plot per day and treated plot as a random factors, seasonal period and wing score as fixed effects, and date as repeated measurements. S × S and WS × S denotes the interaction Sex × Season and Wing Score × Season, respectively

^{t} Morphological attributes (WL, DW, eggs laid) of females with damaged wings (score of 1–3) were not included in analysis due to low sample size ($N = 9$ females collected over the entire season; see Table 2)

^{tt} Data were subjected to logarithmic transformations [$y' = \log (y + 1)$]

^{ttt} The full ANOVA model could not be conducted because no females were captured in early season

NL, both wing length and dry weight declined over time and were lowest for individuals with worn wings: the interaction terms were not significant (Table 1; Fig. 4).

The proportion of eggs laid by females increased over time but was not significantly influenced by wing score (Table 1; Fig. 4).

Fig. 3 Variation in morphological traits of male spruce budworms captured at light traps deployed near Kedgwick in New Brunswick in 2012, near Mont-Joli in Québec in 2013, and near Rocky Harbor in Newfoundland in 2014. Indices of wing score (Score) and dates corresponding to different flight periods (Season) are represented in Figs. 2 and 3. Significant parameters are represented in the *upper right corner* of each graph (factorial ANOVA)
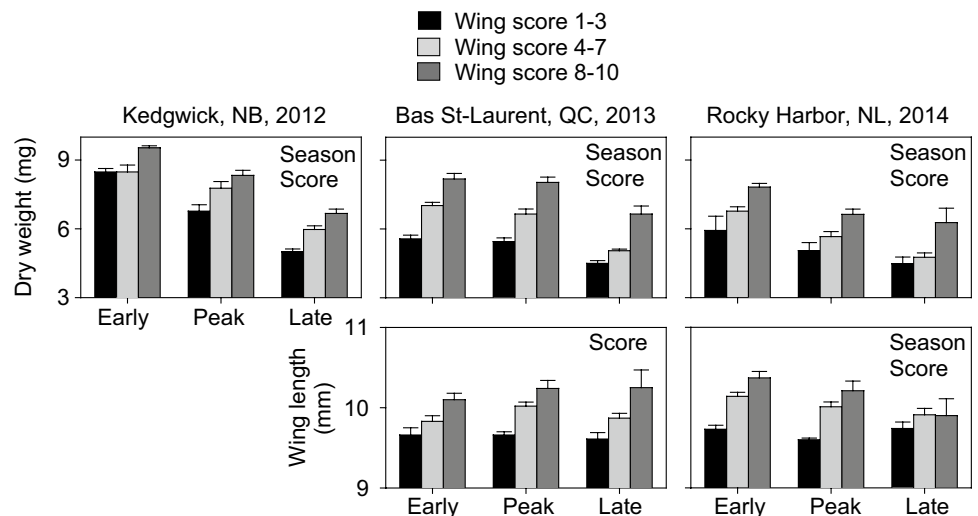
Fig. 4 Variation in morphological traits of female spruce budworms captured at light traps deployed near Kedgwick in New Brunswick in 2012, near Mont-Joli in Québec in 2013, and near Rocky Harbor in Newfoundland in 2014. The percentage of eggs laid by females was assessed using the equations in the caption of Fig. 1. Indices of wing score (Score) and dates corresponding to different flight periods (Season) are represented in Figs. 2 and 3. Significant parameters are represented in the *upper right corner* of each graph (factorial ANOVA in Table 1); *italicized characters* indicate marginally insignificant effects ($0.05 > p < 0.10$). In NL, females with wing score 1–3 are depicted but not included in analysis due to low sample size ($N = 9$ females collected during the entire flight season; see Table 2)
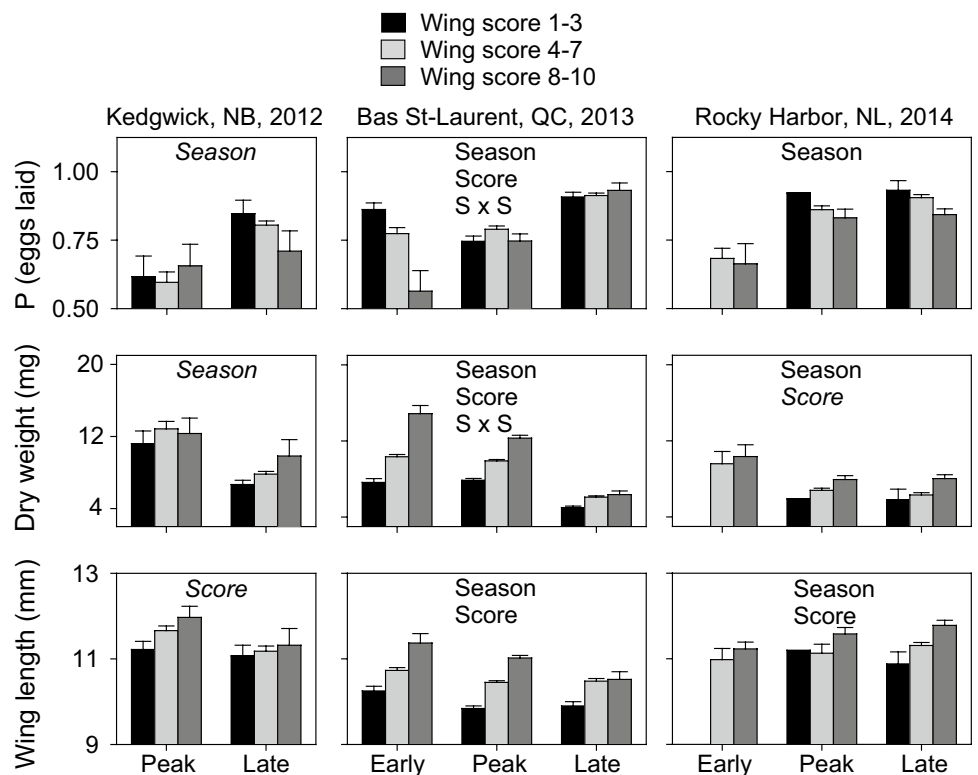
Wing length of females varied significantly between locations and in relation to wing score: females were smaller in QC than in NB or NL, and wing length increased with wing score (Table 2). The proportion of eggs laid by females declined in the following order: NL > NB > QC: females with damaged wings had laid more eggs than females with fresh wings at all locations (Table 2).

Females captured at light traps during the peak of flight in QC in 2013 (15–16 July) had laid considerably fewer eggs than for any other night (Table 3).

Discussion

Monitoring of SBW adults shifted in the 1980s from light traps to pheromone-baited traps, to a large extent because pheromone traps are species-specific and do not involve the time-consuming process of sorting budworms from other moths as in light traps; one disadvantage of pheromone traps is that they capture only males. The advantage of trapping females with light traps is illustrated by the high captures during the night of 15–16 July 2013 (Fig. 2), which may have resulted from either a

Table 2 Mean (±SE) wing length and estimated proportion of eggs laid (Fig. 1) of female spruce budworms captured at light traps in relation to their wing score (Fig. 2) at different locations: NB (near Kedgwick in New Brunswick in 2012), QC (near Mont-Joli in Québec in 2013), and NL (near Rocky Harbor in Newfoundland in 2014)

Location	Wing score	N	Wing length (mm)	p (eggs laid)
NB	1–3	20	11.13 ± 0.15	0.734 ± 0.050
	4–7	72	11.39 ± 0.08	0.714 ± 0.022
	8–10	12	11.64 ± 0.24	0.638 ± 0.052
QC	1–3	489	9.98 ± 0.04	0.642 ± 0.011
	4–7	876	10.53 ± 0.03	0.612 ± 0.007
	8–10	176	11.05 ± 0.05	0.517 ± 0.014
NL	1–3	9	10.66 ± 0.24	0.931 ± 0.009
	4–7	180	11.28 ± 0.06	0.862 ± 0.009
	8–10	56	11.62 ± 0.10	0.793 ± 0.014

Factorial ANOVA revealed the following significance levels: for wing length, Location ($F = 49.73$, $p < 0.0001$), Wing Score ($F = 17.73$, $p < 0.0001$), Location × Wing Score ($F = 1.21$, $p = 0.3056$); for the proportion of eggs laid, Location ($F = 59.60$, $p < 0.0001$), Wing Score ($F = 4.84$, $p = 0.0080$), Location × Wing Score ($F = 0.41$, $p = 0.8030$)

synchronized, pulsed emergence of local adults or a mass immigration event. Based on captures of males alone, it would have been difficult to segregate between the two scenarios. Considering that gravid females are physiologically incapable of migrating (Greenbank et al. 1980; Rhainds and Kettela, 2013), and that females on the night 15–16 July had laid a much lower proportion of their eggs than on any other night (Table 3), the scenario of immigration appears highly unlikely. In contrast, the heavy weight of females relative to their body size during the night of 15–16 July suggests that they were young at the time of capture, which implies a pulsed emergence of 'resident' females.

Females captured at locations with 'early epidemic' SBW populations in QC in 2013 were smaller than those at locations with endemic populations in NB and NL (Table 2), which is consistent with previous reports of inverse density-dependence of body size and fecundity of females (Blais 1953; Morris 1963; Régnière and Nealis 2007). What is surprising, however, is that defoliation was low (<10 %) in the 'early epidemic' locations in QC, which suggests that reduced size and fecundity of females operates on SBW population dynamics early in the transition phase between endemic to epidemic populations. If validated, this finding needs to be incorporated into existing models of SBW population dynamics (Ludwig et al. 1978; Régnière et al. 2001; Royama 1984; Stedinger 1984). At all locations, wings of large individuals (both males and females) were in better condition

than those of small congeners (Figs. 3, 4), which suggests that the level of activity among adults is inverse-size dependent: i.e., small moths are more active, hence their wings degrade more rapidly. The two findings above illustrate the importance of light rapping and body size measurements to generate novel hypotheses on the behavior, ecology and population dynamics of SBW.

The seasonal variations in sex ratio, wing length, and dry weight of specimens captured at light traps are consistent with 'closed' populations, whereby 'resident' moths largely outnumber immigrants: (1) temporal decline in the ratio male:female is due to protandrous emergence of local adults; (2) the small size of adults in late season is due to late emerging moths being smaller than early emerging moths (Miller 1957); and (3) the declining weights of adults over time likely reflects the metabolic cost of survival and (for females) depletion of eggs in the abdomen as females oviposit. Massive immigration events can be viewed as disturbances that superimpose themselves onto expected seasonal patterns of flight of resident moths and shift these patterns in predictable ways that result in three co-occurring trends: (1) high variation in moth abundance from one day to the next, (2) female-biased sex ratios (because females are more likely to migrate than males; Rhainds and Heard 2015), and (3) low residual fecundity of females (because gravid females are incapable of long-range flight; Greenbank et al. 1980). The spike in moth abundance during the night of 15–16 July 2013 did not reflect massive immigration because females had laid few eggs at the time of capture. It must be emphasized that 'closed' populations of SBW do not imply processes operating at a small spatial scale (the flight of adults may be synchronous over large areas) but rather relates to a small proportion of immigrants relative to resident local moths at a given location.

This study was initially designed to evaluate whether or not wing wear could be used to discriminate between 'resident' local moths and immigrants. Under circumstances when immigrants are numerically very abundant, wing wear could not be used to categorize migrants because ethyl acetate is not an effective killing agent when traps become saturated with moths. On the other hand, wing wear may provide a reliable indicator of the age of moths, as suggested by seasonal variation of morphological attributes of adults: (1) the score of wings steadily declined over time for both males and females at all locations, which is consistent with increased accumulated wing damage during the ageing process; (2) individuals with fresh wings were heavier and (for females) had laid fewer eggs compared with individuals with damaged wings (Figs., 3,4), as would be expected if the condition of wings reflect the age

Table 3 Estimated proportion of eggs laid by females for different locations and dates (Fig. 1)

Day in July	Proportion of eggs laid by females				
	<25 %	25–50 %	50–75 %	>75 %	Mean ± SE
Kedgwick, New Brunswick, 2012					
12–13	0 (0.000)	1 (0.091)	8 (0.727)	2 (0.182)	0.609 ± 0.041
13–14	2 (0.091)	8 (0.364)	11 (0.500)	1 (0.045)	0.535 ± 0.048
23–24	0 (0.000)	1 (0.032)	7 (0.226)	23 (0.742)	0.811 ± 0.019
Bas Saint-Laurent, QC, 2013					
9–10	1 (0.024)	7 (0.167)	23 (0.548)	11 (0.262)	0.642 ± 0.022
10–11	14 (0.154)	19 (0.209)	44 (0.484)	14 (0.154)	0.537 ± 0.025
13–14	3 (0.067)	16 (0.356)	15 (0.333)	11 (0.244)	0.584 ± 0.036
14–15	5 (0.069)	14 (0.194)	32 (0.444)	21 (0.292)	0.615 ± 0.025
15–16	91 (0.448)	83 (0.449)	23 (0.113)	6 (0.030)	0.289 ± 0.015
16–17	15 (0.070)	71 (0.330)	113 (0.526)	16 (0.074)	0.525 ± 0.012
17–18	46 (0.118)	164 (0.419)	148 (0.379)	33 (0.084)	0.480 ± 0.010
18–19	2 (0.017)	20 (0.169)	72 (0.610)	24 (0.203)	0.631 ± 0.013
19–20	13 (0.052)	47 (0.190)	114 (0.460)	74 (0.294)	0.616 ± 0.013
22–23	1 (0.018)	0 (0.000)	8 (0.140)	48 (0.842)	0.832 ± 0.019
23–24	0 (0.000)	1 (0.004)	31 (0.136)	196 (0.860)	0.854 ± 0.006
24–25	0 (0.000)	0 (0.000)	1 (0.091)	10 (0.909)	0.860 ± 0.021
Rocky Harbor, NL, 2014					
18–19	1 (0.038)	0 (0.000)	6 (0.231)	19 (0.731)	0.798 ± 0.034
22–23	0 (0.000)	1 (0.027)	5 (0.135)	31 (0.838)	0.841 ± 0.019
23–24	0 (0.000)	2 (0.020)	41 (0.410)	57 (0.570)	0.774 ± 0.012
24–25	0 (0.000)	0 (0.000)	6 (0.545)	5 (0.455)	0.789 ± 0.035
26–27	0 (0.000)	0 (0.000)	16 (0.258)	46 (0.742)	0.828 ± 0.011
27–28	0 (0.000)	0 (0.000)	6 (0.171)	29 (0.829)	0.843 ± 0.013
28–29	0 (0.000)	1 (0.024)	2 (0.049)	38 (0.927)	0.873 ± 0.017
29–30	0 (0.000)	0 (0.000)	1 (0.023)	43 (0.977)	0.927 ± 0.009
30–31	0 (0.000)	0 (0.000)	0 (0.000)	14 (1.000)	0.946 ± 0.016

A large number of (young) female moths with high residual fecundity were captured during the night of 15–16 July 2013. Nights with <10 females are not reported

of adults. An age-index based on wing wear may eventually help to model phenological parameters related to the emergence time and longevity of adults.

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