

# Fecundity and recruitment of eggs during outbreaks of the spruce budworm

VG Nealis<sup>1</sup>

Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre,  
506 W Burnside Road, Victoria, British Columbia, Canada V8Z 1M5

J Régnière

Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre,  
PO Box 3800, Sainte-Foy, Quebec, Canada G1V 4C7

*The Canadian Entomologist* **136**: 591 – 604 (2004)

**Abstract**—Field data from outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), in Ontario and Quebec show that current-year defoliation is the single greatest determinant of variation in fecundity. The species of tree that served as the foodplant and infections by the microsporidian *Nosema fumiferanae* (Thomson) (Microsporida) had little effect on mean lifetime fecundity in field populations. During a prolonged outbreak at one location (Black Sturgeon Lake, Ontario), annual lifetime fecundity was inversely related to observed defoliation in the same year, with the highest mean fecundity recorded at the beginning and the end of the outbreak when defoliation was least severe. The overall trend in yearly rate of change in egg density in a population time series at Black Sturgeon Lake was associated more closely with generational survival than with fecundity. Measured fecundity of local moths was greater than estimated per capita rates of recruitment in most years of the outbreak at Black Sturgeon Lake. This suggests that in these years of the outbreak at Black Sturgeon Lake there was a net emigration of egg-carrying moths.

Nealis VG, Régnière J. 2004. Fécondité et recrutement des oeufs au cours d'une épidémie de la tordeuse des bourgeons de l'épinette. *The Canadian Entomologist* **136** : 591–604.

**Résumé**—Nous avons établi, à partir de données provenant de populations naturelles en Ontario et au Québec, que la défoliation du feuillage de l'année est le facteur le plus influent sur la fécondité des populations naturelles de la tordeuse des bourgeons de l'épinette *Choristoneura fumiferana* (Clem.) (Lepidoptera : Tortricidae) au cours d'une épidémie. L'essence hôte de laquelle provient l'insecte, ou l'infection par *Nosema fumiferanae* (Thomson) (Microsporida), ont peu d'effet sur la fécondité des populations naturelles. Au cours d'une épidémie prolongée à Black Sturgeon Lake (Ontario), la fécondité était en relation inverse avec la défoliation observée au cours de la même année. La plus forte fécondité a été enregistrée au début et à la fin de l'épidémie lorsque la défoliation était la moindre. La tendance générale du taux de changement intergénérationnel de densité au stade oeuf dans la série temporelle relevée à Black Sturgeon Lake était plus étroitement associée au taux de survie intra-générationnelle qu'à la fécondité. La fécondité des papillons était plus élevée que le taux de recrutement annuel pour la plupart des années de l'épidémie à Black Sturgeon Lake. Ceci suggère une émigration nette de papillons féconds dans la plupart des générations au sein de la population de Black Sturgeon Lake.

<sup>1</sup> Corresponding author (e-mail: vnealis@pfc.forestry.ca).

## Introduction

Intergenerational rates of change in population densities of insects are determined by the net balance of births and deaths. The per capita birthrate or natality, the number of eggs that a female lays under field conditions, is determined largely by fecundity, the reproductive potential of an organism, modified to some extent by factors that influence the realization of that potential, such as mating success (Delisle and Simard 2002), adult longevity (Leather 1988), and movement (emigration and immigration). Fecundity is therefore a fundamental parameter in the analysis of population dynamics. It is important to understand sources of variation in fecundity to interpret observed patterns of recruitment in natural populations.

Populations of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), erupt periodically and cause widespread defoliation in the spruce–fir forests of North America east of the Rocky Mountains. Intensive research on the biology and population dynamics of the spruce budworm was carried out during outbreaks in eastern Canada in the 1950s and, as a result, much is known about the basic biology of this species (Sanders 1991). Population data from this period were presented first by Morris (1963) and reanalyzed by Royama (1984). These studies emphasize generational survival as the primary determinant of the 35-year periodicity of the fluctuations in spruce budworm populations.

Intergenerational recruitment rates in analyses of spruce budworm population dynamics have been estimated as the ratio of egg to moth densities ( $E/M$  ratio) (Royama 1984). The  $E/M$  ratio represents the apparent per capita fecundity of local moths. Comparisons between the  $E/M$  ratio and direct measures of actual fecundity of local moths can be used to infer immigration and emigration of moths (Greenbank 1963; Royama 1984) and can help our understanding of fluctuations in population density and our interpretation of the genesis and spatial relationships of extensive outbreaks.

Despite the high profile afforded the spruce budworm over the past half century, there has been little new information on fecundity in natural populations of this insect since the original publications of Blais (1952, 1953) and Miller (1957, 1963). In this paper, we reexamine fecundity in spruce budworm populations using what we consider to be important methodological improvements relevant to population dynamics. First, mean lifetime fecundity is estimated directly from individual female moths collected as pupae in the field rather than by using surrogate measures such as pupal size (Miller 1957). Second, fecundity of individuals collected from different host trees in the same mixedwood stand is compared and the effect of defoliation of these trees on fecundity determined. Third, we account for the influence of sublethal infections by the ubiquitous micropathogen *Nosema fumiferanae* (Thomson) (Microsporida). Fourth, data from widely dispersed field sites are compared. Finally, and most importantly, an unusually long time series of annual measurements of fecundity, population density, and survival from a single outbreak has been compiled. These estimates of fecundity are compared with observed intergenerational recruitment rates to deduce the patterns of immigration and (or) emigration with respect to changes in budworm populations and forest condition.

## Methods

### Field sites

Data were obtained between 1983 and 1997 from a mixedwood stand near Black Sturgeon Lake, Ontario (49°18'N, 88°52'W, 260 m altitude), between 1982 and 1984 from Lake Superior Provincial Park (hereafter called Gargantua), Ontario (47°35'N,

84°49'W, 305 m altitude), and in 1985 in stands in Quebec near Armagh (46°43'N, 70°37'W, 312 m altitude) and Lac à l'Épaulé (hereafter called Épaulé) (47°18'N, 71°12'W, 750 m altitude). Descriptions of all sites are given in Lethiecq and Régnière (1988). Data were collected from Black Sturgeon Lake throughout the outbreak period (Nealis and Régnière 2004), whereas observations at the other three sites were made only during the declining phase of the outbreaks.

## Fecundity

Direct estimates of fecundity were obtained from insects collected as pupae from branches at the study sites and incubated individually in glass tubes at 20 °C, 16L:8D. Upon emergence, female moths were caged with at least one male moth and a shoot of fresh balsam fir (*Abies balsamea* (L.) (Pinaceae)) foliage in a 500-mL glass jar shrouded in brown paper and covered with a mesh lid. Moths were provided with water daily and the foliage was changed twice weekly until the female died. All egg masses were removed from the foliage or container walls, and the total number of eggs in each egg mass was recorded. The total number of eggs laid by a female moth was considered to be her lifetime fecundity. No attempt was made to estimate the number of eggs remaining in female cadavers, as we were interested only in the number of eggs actually laid, given variation in longevity (Miller 1957; Leather 1988). The egg masses from each female were transferred to a clean, dry container at 20 °C, 16L:8D to observe eclosion. At least one eclosion from an egg mass was used as the criterion to establish fertility of moths. Only the data from fertile females were used in the analysis. Mating success under these conditions ranged from 55% to 80%. There was one exception to this procedure. In 1988, fecundity at Black Sturgeon Lake was estimated indirectly by measuring wing area of captured moths and using an established regression of wing area on fecundity (Sanders and Lucuik 1975). No measurements of either fecundity or size of spruce budworm are available for the 1986 generation at Black Sturgeon Lake.

The mean number of eggs per egg mass was estimated from egg masses recovered from branch samples collected during annual sampling. These samples consisted of a single 45-cm branch tip removed from the mid-crown of each of 20 to 60 codominant host trees at each location (Nealis and Régnière 2004). Egg masses that produced no viable larvae were considered infertile and not included. This was, however, so rare in field-collected egg masses as to be inconsequential.

At Black Sturgeon Lake, pupae were collected from balsam fir each year beginning in 1983, from white spruce, *Picea glauca* (Moench) Voss, beginning in 1984, and from black spruce, *Picea mariana* (Mill.) BSP, beginning in 1989. The host plant of origin of each individual was recorded. Estimates of fecundity on balsam fir and white spruce were also obtained from Gargantua (1982 to 1984) and Armagh (1985).

The rate of infection by *N. fumiferanae* for a generation of spruce budworm was estimated from live insects frozen immediately after collection from foliage at various intervals throughout the feeding period (Nealis and Régnière 2004). These insects were later smeared individually in a drop of distilled water on a slide and examined using a compound microscope with an oil-immersion objective (1000×). When *N. fumiferanae* is present in wild populations of spruce budworm, the density of spores is usually very high (>10<sup>6</sup> spores/mg dry mass) and their presence is detected readily (Nealis and Smith 1986). We calculated annual infection rate as the overall proportion of insects examined that contained spores. For the purposes of this study of fecundity, the rate of infection of adult moths collected in the field as pupae was used whenever available. Otherwise, we pooled all samples containing spruce budworm in the late larval (*i.e.*, fourth instar or later) and pupal stages to estimate the rate of infection. This selection

provided adequate sample sizes and avoided inclusion of observations from early in the season when rates of infection may have been changing rapidly (Wilson 1987).

Annual estimates of current-year defoliation at each site were obtained by the Fettes (1950) method, using 25 shoots from one mid-crown, 45-cm branch tip from at least 20 trees per site.

The influence of host plant species ( $S$ ), current-year defoliation ( $D$ ), and proportion of the spruce budworm population infected by *N. fumiferanae* ( $N_f$ ) on fecundity of spruce budworm moths ( $\Phi$ ) was tested with a General Linear Model (GLM procedure, SAS Institute Inc 1999) using the following initial model:

$$\Phi = a_0 + a_1(S) + a_2D + a_3(S \times D) + a_4N_f + a_5(S \times N_f) + a_6(D \times N_f) \quad [1]$$

where  $a_0$ – $a_6$  are parameters. This model was reduced by removing nonsignificant terms ( $P > 0.05$ ), starting with interactions.

Measurements of spruce budworm density were made several times in each generation by sampling foliage (Nealis and Régnière 2004) and were expressed as the number of insects per kilogram of fresh branch mass (Régnière et al. 1989). The life stage of each budworm in each sample was indexed from 1 (hatched eggs) to 8 (empty pupal integument). Using this system of indices, the age distribution of spruce budworms in each sample date was summarized as an average instar (Hardy et al. 1976). In this analysis, we use density estimates obtained during the pupal and egg stages. The density of pupae was estimated by pooling samples in which the average instar was between 6.5 and 7.5 (Nealis and Régnière 2004). Egg mass samples were taken in mid-August of each year after oviposition and hatch were complete but before there was appreciable loss of egg masses from the foliage. The density of eggs recruited to each new generation was the product of egg mass density and the mean number of eggs per egg mass. It was transformed to a log scale and designated  $E_{t+1}$ .

The estimates of pupal and egg densities were used to calculate the recruitment rate as follows. First, the estimate of pupal density was reduced by the observed survival of these pupae to eclosion in rearing (Nealis and Régnière 2004) to obtain an estimate of moth density. This measure of moth density was divided by 2 to estimate reproducing female density, assuming a 1:1 sex ratio (Royama 1984), then transformed to a log scale and designated hereafter as  $M_t$ . The recruitment rate or log  $E/M$  ratio is the difference between the estimated log density of eggs recruited to generation  $t + 1$  ( $E_{t+1}$ ) and the estimated log density of local moths surviving in the previous generation ( $M_t$ ). This  $E/M$  ratio was compared with lifetime fecundity for each year in the series from Black Sturgeon Lake.

### Recruitment rates

The log intergenerational rate of change in egg density,  $R_t$ , is the difference between log egg densities in successive generations, or  $R_t = E_{t+1} - E_t$ . The log generational survival rate,  $G_t$ , is the difference between the log density of surviving moths in generation  $t$  ( $M_t$ ) and the log density of eggs initiating generation  $t$  ( $E_t$ ), or  $G_t = M_t - E_t$ . The log egg recruitment rate,  $F_t$ , is the difference between the log egg density in generation  $t + 1$  and the log density of surviving moths in generation  $t$ , or  $F_t = E_{t+1} - E_t$ . Thus, we can write

$$R_t = E_{t+1} - E_t = G_t + F_t = (M_t - E_t) + (E_{t+1} - M_t) \quad [2]$$

Despite the 15 years of observations reported here, our data do not cover the period of sustained increase in population density of spruce budworm at Black Sturgeon Lake before 1983. Sanders (1988) reported annual estimates of larval densities for this

area in the years before our study began. We used the larval densities in Figure 1 of Sanders (1988) to construct yearly rates of change in population density from 1978 to 1984 to provide an extended historical context to our analysis.

## Results

### Fecundity

The annual mean number ( $\pm$ SE) of spruce budworm eggs per egg mass averaged  $16.3 \pm 0.67$  ( $n = 12$ ) throughout the series at Black Sturgeon Lake (Fig. 1a); this mean was consistently less than the value of 20 eggs per mass suggested by Miller (1957, 1963). There was a positive correlation between mean number of eggs per egg mass and fecundity (Table 1;  $r = 0.80$ ,  $P = 0.002$ ,  $n = 12$ ). Evidently, females that are more fecund also produce larger egg masses (Miller 1957). However, egg mass size was less variable than fecundity: the latter varied by a factor of four at Black Sturgeon Lake, whereas the difference between the minimum and maximum egg mass sizes at the same location was less than 50% (Table 1, Fig. 1a, 1b).

Mean ( $\pm$ SD) lifetime fecundity of female spruce budworm moths during this study (all plots and years combined) was  $154.9 \pm 44.9$  ( $n = 19$ ) (Table 1) and was within the range reported by Blais (1952) for northern Ontario and by Miller (1957) for New Brunswick. However, it varied considerably over the years, especially at Black Sturgeon Lake, with the highest fecundity at the beginning and the end of the outbreak period (Fig. 1b). In 1990, fecundity of spruce budworm collected from balsam fir was 53.9 eggs/female ( $n = 14$ ), which is less than the minimum spruce budworm fecundity estimated by Miller (1963) under extreme starvation conditions recorded during the Green River infestation in the 1950s. The maximum fecundity observed in this study was among females collected from balsam fir at Épaule in 1985 (220.2 eggs/female,  $n = 49$ ) and from Black Sturgeon Lake at the end of the outbreak in 1997 (230.7 eggs/female,  $n = 16$ , host not recorded) (Table 1). These values are as high as that obtained by Campbell (1962) under controlled conditions with ample food.

The lowest mean fecundity values (pooled over hosts) at Black Sturgeon Lake were observed in 1984 and from 1987 to 1993 (Fig. 1b), when annual defoliation exceeded 70% (Table 1, Fig. 1c). Fecundity increased temporarily in 1985 when defoliation decreased to less than 50% following a sharp reduction in budworm density as the result of a fungal epizootic at the end of the larval feeding period in 1984 (Perry and Régnière 1986). Fecundity increased again after 1993, at the end of the outbreak when the spruce budworm population was decreasing and defoliation of current-year foliage was less severe (Fig. 1b, 1c).

In fitting model [1] to fecundity ( $\Phi$ ), no interaction between host species ( $S$ ) and current-year defoliation ( $D$ ) was detected ( $F_{S \times D} = 0.43$ ,  $P = 0.66$ ), so this term was removed from the model. With the reduced model, the effects of host species and defoliation on fecundity ( $\Phi$ ) were highly significant ( $F_S = 9.35$ ,  $P = 0.001$ ;  $F_D = 17.42$ ,  $P < 0.001$ ). Whereas the immediate effect of current-year defoliation on fecundity is clear (Fig. 1b, 1c), the effect of host species is more complex. Estimates of least square means from model [1] indicated no difference in mean ( $\pm$ SD) fecundity of spruce budworm collected from balsam fir ( $158.6 \pm 5.67$ ) or white spruce ( $157.6 \pm 6.92$ ) at a given level of defoliation. Mean fecundity of moths collected from black spruce, however, was much lower ( $106.9 \pm 11.0$ ) for the same level of defoliation. In the field, however, defoliation of black spruce was always lower than that of either balsam fir or white spruce (Table 1) so that the host-plant effect on fecundity was compensated by the effect of defoliation on fecundity. The result was that the overall mean fecundity of

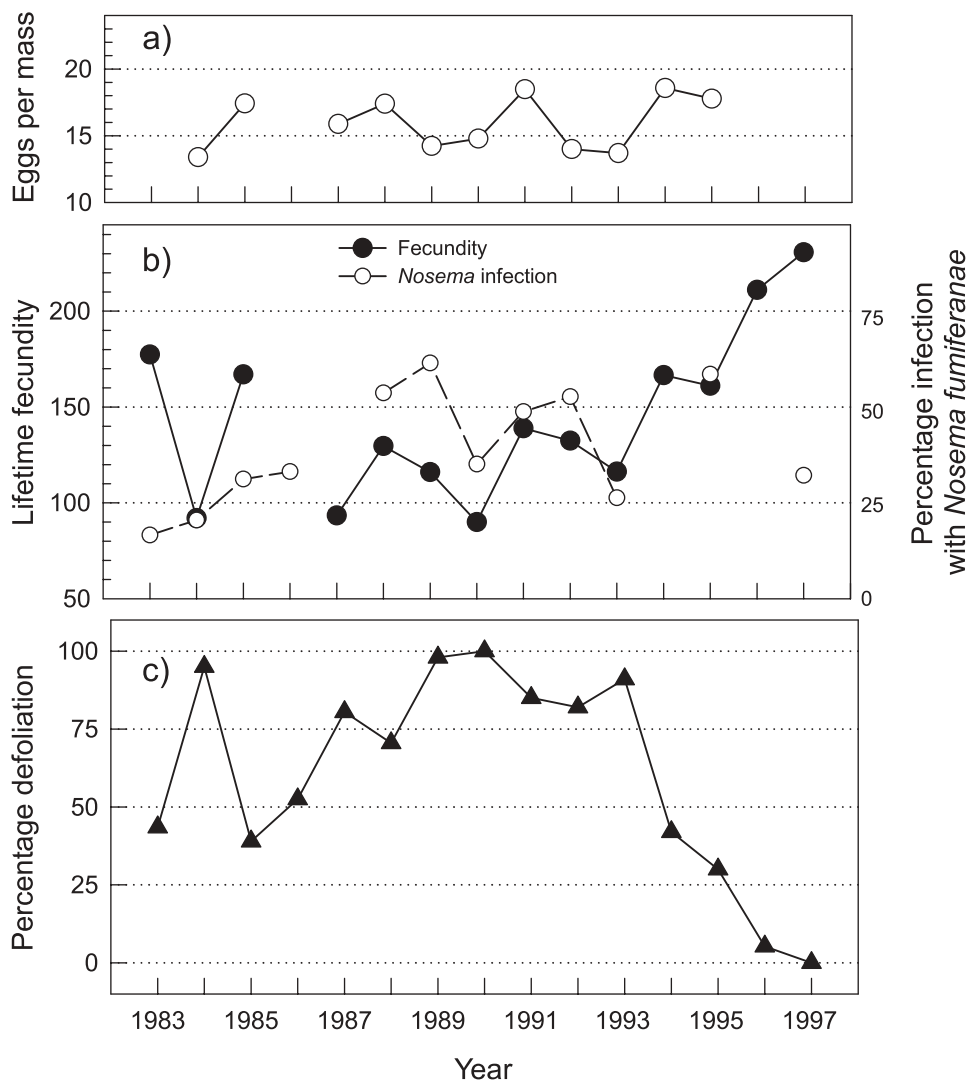


FIGURE 1. Annual estimates (1983–1997) of mean number of eggs per egg mass (a) and mean fecundity and percentage of population infected by *Nosema fumiferanae* (b) for a population of *Choristoneura fumiferana* near Black Sturgeon Lake, Ontario, Canada, as well as (c) current-year defoliation (%).

moths from black spruce was similar to that of insects collected from the other host species in the same year.

The effect of infection by *N. fumiferanae* was much weaker than the effect of either defoliation or host species, but it was significant ( $F_{N_f} = 5.50$ ,  $P = 0.028$ ) as long as the interaction with defoliation was kept in the model ( $F_{D \times N_f} = 2.76$ ,  $P = 0.11$ ). This weak influence of infection by *N. fumiferanae* agrees with the findings of Thomson (1958) and Wilson (1980), who reported differences in mean fecundity of only about 10% between infected and uninfected females collected in the field. Bauer and Nordin (1989) reported larger differences in fecundity in laboratory experiments where very high spore loads were induced experimentally. Although the effect of the  $S \times N_f$  interaction term was not significant, its influence in the model suggests that the impact of

**Table 1. Fecundity of the female spruce budworm (*Choristoneura fumiferana*), current-year defoliation of three host tree species (bF, balsam fir (*Abies balsamea*); wS, white spruce (*Picea glauca*); bS, black spruce (*Picea mariana*)), mean number of eggs per egg mass, and percentage of population infected by the microsporidian *Nosema fumiferana* (Nf).**

Plot and year	Fecundity			Pooled	No. of eggs/mass	Defoliation (%)			Nf (%)
	bF	wS	bS			bF	wS	bS	
Gargantua									
1982	153.3	190.6				36	23		52
1983	197.6	198.6			20.4	20	22		59
1984	217.9	197.8							60
Armagh									
1985	141.5	121.8				46	33		90
Épaule									
1985	220.2					18			25
Black Sturgeon Lake									
1983	177.4					72	22	3	17
1984	93.3	96.8			13.4	100	90	3	21
1985	167.6	150.9			17.4	52	27	0	32
1987	93.6	93.1			15.9	80	81	17	
1988				129.7*	17.4	75	66	10	55
1989	85.1	132.1			14.2	99	98	47	63
1990	53.9	87			14.8	100	98	39	36
1991	142.5	119.7			18.5	78	92	22	50
1992	134.8	121.8			14.0	83	81	8	54
1993	92.4	117.4			13.7	97	85	66	27
1994	156.3	140.1			18.6	26	58	3	60
1995	80.0	167.6			17.8	7	53	9	
1996		211.1				2	9	1	
1997				230.7		0	8	0	33

\*Estimated from wing surface area.



*N. fumiferanae* on fecundity is affected by starvation, as might be expected from the observed decrease in several measures of nutritional physiology associated with infected larvae (Bauer and Nordin 1988).

A strong negative relationship was detected between mean fecundity and current-year defoliation at the stand level (Fig. 2). Note the relatively high fecundity from Gargantua and Épaule in collapsing outbreaks in these areas. Note also the general agreement of the relationship between fecundity and current-year defoliation with observations made during the Green River study and reported in Table 2 of Royama (1984).

### Recruitment rates

The log yearly rate of change in spruce budworm density at Black Sturgeon Lake reflected a sustained increase in population density during the late 1970s and early 1980s (Sanders 1988; Fig. 3a, ⊙). After 1983, when defoliation became evident (Fig. 1c), the log yearly rate of change in the density of spruce budworm oscillated about 0 (no change) until the last few years, when egg density declined sharply (Fig. 3a, ●). This pattern in yearly rate of change in egg density,  $R_t$ , was more highly correlated ( $r = 0.638$ ,  $P = 0.014$ ) with log generational survival,  $G_t$ , (Fig. 3a, ◇) than with fluctuations in the egg recruitment rate,  $F_t$  ( $r = 0.330$ ,  $P = 0.248$ ). Thus, the available data for the outbreak and decline phases of the population cycle indicate that the overall trend in the yearly rate of change in egg density was associated more with generational survival than with egg recruitment. This pattern is similar to that reported from the outbreak in the 1950s at Green River (Royama 1984).

Egg recruitment does, however, appear to have the potential to moderate abrupt changes in generational survival to produce a more stable density of spruce budworm from generation to generation. Note that drops in survival rates in 1984, 1988, 1990, and 1996 (Fig. 3a) did not result in commensurate decreases in the rate of change in density because of relatively higher  $E/M$  ratios in those years (Fig. 3b). The correlation between  $G_t$  and  $F_t$  was negative and nearly significant ( $r = -0.516$ ,  $P = 0.059$ ). The most striking incident occurred in 1990 when, in the midst of the outbreak, generational survival declined sharply (Fig. 3a). Recruitment to the 1991 generation, however, was very high (Fig. 3b), likely because of moth immigration from surrounding forests (see below). As a result, population density in 1991 was maintained at outbreak levels. Nonetheless, once generational survival began to decrease steadily after 1994, increases in the recruitment rate (Fig. 3b) were not sufficient to reverse the decrease in population density associated with declining survival as the outbreak came to an end.

Comparison of fecundity and recruitment rates ( $E/M$  ratios) among years of the outbreak at Black Sturgeon Lake revealed that in most years, the  $E/M$  ratio was much lower than would be expected from fecundity estimates (Fig. 3b). Even when fecundity was reduced by a factor of 0.6 to account for moth mortality (Royama 1984; Leather 1988), estimates of the  $E/M$  ratio were lower than expected. It is possible that we underestimated apparent fecundity; however, our results are similar to those of others. We may have overestimated local moth density because survival in the field is likely less than that in the laboratory. Such an overestimate of the denominator would lead to an underestimate of the  $E/M$  ratio. However, the average difference between log  $E/M$  ratios and log fecundities in our data (excluding 1990) was  $-0.797$ , which represents a 6-fold difference. It is difficult to imagine that moth density could have been so grossly overestimated (Fig. 3b). We therefore conclude that in most years there was a net emigration of reproducing female moths from Black Sturgeon Lake.



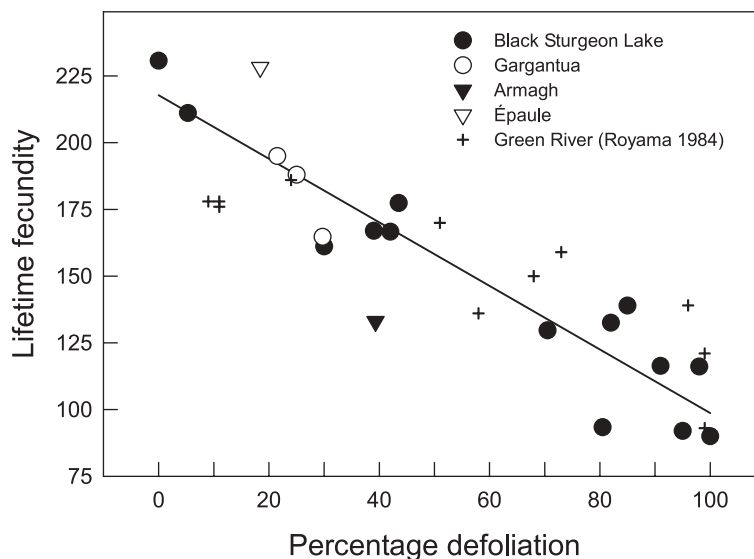


FIGURE 2. Relationship between fecundity of *Choristoneura fumiferana* and current-year defoliation at five study sites in eastern Canada. Regression line:  $y = 216.8 - 1.17x$  ( $F_{1,19} = 91.0$ ,  $P < 0.01$ ,  $r^2 = 83.3$ ). Data from Green River are not included in the regression.

## Discussion

Mean fecundity of spruce budworm observed in our study locations fell within the range reported by others, but the mean number of eggs per egg mass was slightly less than the value of 20 reported in the Green River study (Miller 1963; Royama 1984). It is not possible to ascertain from the publications of Miller (1957, 1963) how his estimate of mean egg mass size was derived. The only statistical description of egg mass size is given in Table IV of Miller (1957) and indicates mean egg mass sizes of 15.7 eggs per mass in a “severe infestation” and 18.5 eggs per mass in a “light infestation”. These values are essentially the same as those reported here, so actual differences may be insignificant.

The clearest influence on spruce budworm fecundity is that of the availability of food for the larvae, as measured by the degree of current-year defoliation (Fig. 2). The influence of either host tree species or infection by the microsporidian *N. fumiferanae* is much smaller. The inverse relationship between defoliation and fecundity means that fecundity is inversely related to the density of feeding spruce budworm larvae. This first-order negative feedback between larval density and fecundity reduces budworm population growth rates during the high-density phase of the outbreak when rates of change in population density show little trend.

Our results support the conclusion of Royama (1984) that variation in fecundity of spruce budworm is small compared with annual fluctuations in the *E/M* ratio (Fig. 3*b*). *E/M* ratios or recruitment rates are subject not only to variation in local fecundity but also to movement of egg-carrying moths at the regional level. Movement is perhaps the most enigmatic process in population dynamics. It is rarely measured directly and must be inferred from other population measures. Our population measurements at Black Sturgeon Lake indicate that in most years the per capita rate of egg recruitment, expressed as the *E/M* ratio, was much lower than would be expected from independent measures of fecundity. Although unmeasured sources of variability, such as moth

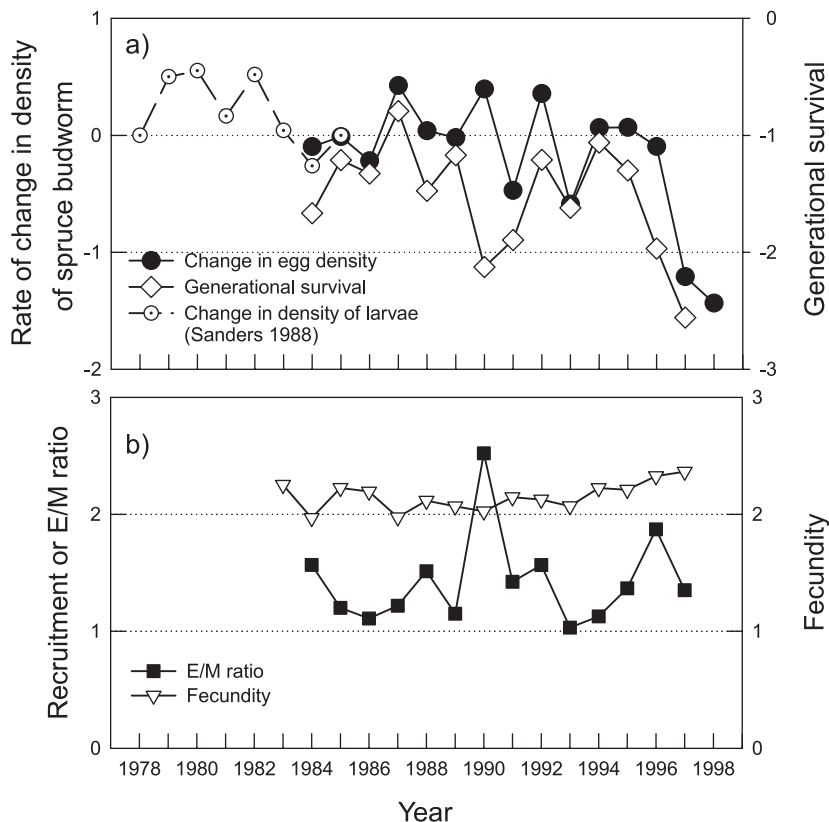


FIGURE 3. (a) Yearly rate of change in *Choristoneura fumiferana* larval density, egg density, and generational survival and (b) annual egg density to moth density ( $E/M$ ) ratio and mean fecundity of moths at Black Sturgeon Lake from 1978 to 1997. All response variables are plotted on a log scale.

survival, may account for some of this difference, its magnitude is such that we follow the arguments of Greenbank (1963) and Royama (1984) and suggest that the observed difference between recruitment and fecundity was the result of frequent net emigration from Black Sturgeon Lake during the outbreak. This conclusion must be interpreted in the context of the outbreak situation in the surrounding region.

During the 1980s, the area of defoliation around Black Sturgeon Lake was isolated from other defoliated areas further west (Evans and Melbourne 1990), so recruitment of eggs to the next generation at Black Sturgeon Lake during this period was influenced largely by local survival and fecundity, although some net emigration of moths from an area of high relative budworm density would be expected (Greenbank 1963). However, a series of annual increases in the area of defoliation occurred in northwestern Ontario from 1989 to 1991, and the Black Sturgeon Lake study site was engulfed in an area-wide outbreak that lasted much of the 1990s (Biggs et al. 1994). In 1990, there was a sharp reduction in survival of larvae at Black Sturgeon Lake (Fig. 3a) (Nealis and Régnière 2004). We believe that this event was fairly localized because the rate of egg recruitment ( $E/M$  ratio) was very high in the following generation, which is an indication that the surrounding area provided numerous immigrating moths (Fig. 3b). Independent evidence of moth immigration to Black Sturgeon Lake in 1990 comes from daily catches of male and female moths in passive traps suspended in the forest canopy

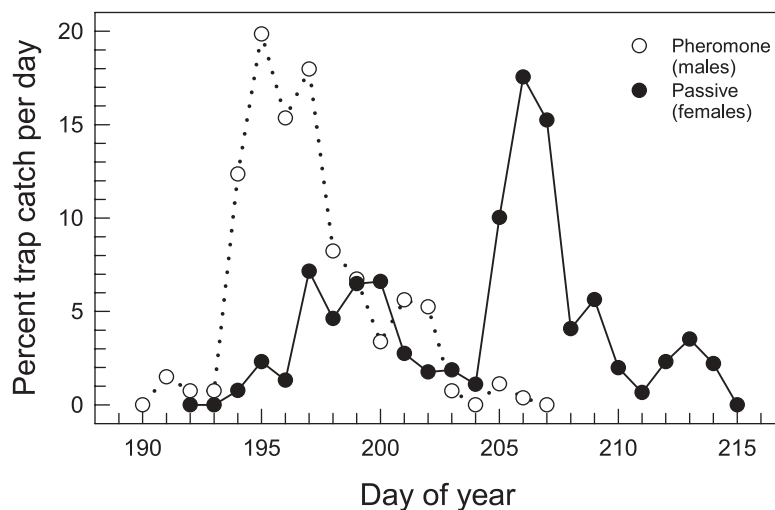


FIGURE 4. Percentage of total *Choristoneura fumiferana* moths caught in traps each day at Black Sturgeon Lake in 1990. ○, male moths caught in pheromone traps; ●, female moths caught in passive traps suspended in the forest canopy. Data from CJ Sanders (Canadian Forest Service, Sault Ste. Marie, Ontario).

and comparison with captures of male moths in standard pheromone traps (personal communication, CJ Sanders, Canadian Forest Service, Sault Ste-Marie, Ontario). In most years, moth catches were unimodal. The catches from 1990, however, show two distinct peaks separated by a full week (Fig. 4). The first peak corresponds to the expected seasonality of local female moths based upon frequent branch sampling (Nealis and Régnière 2004). This first peak in captures of female moths occurred about 4 days later than the corresponding single peak in the daily catches of male moths in pheromone traps, a delay that can be expected as a result of protandry (Fig. 4). The second, larger peak in female moth catches indicates immigration of egg-bearing moths. This corroborates the inferences from Figure 3*b* regarding moth movement and the comparison between local fecundity and the apparent *E/M* ratio.

After 1990, the local situation changed rapidly. Cumulative defoliation at Black Sturgeon Lake resulted in severely thinned crowns, and significant tree mortality was beginning to occur (Nealis and Régnière 2004). Surviving dominant trees, however, were still producing ample current-year shoots (Nealis and Régnière 2004) such that larvae were well-fed and mean annual fecundity was actually increasing (Fig. 1*b*). Moths, however, were faced with a habitat increasingly inadequate for oviposition as a result of successive years of severe (>75%) defoliation between 1989 and 1993 (Fig. 1*c*). The result was the annual exodus of moths between 1992 and 1996, evident in the large differences between local fecundity and the *E/M* ratio in those years (Fig. 3*b*).

That the population at Black Sturgeon Lake should act as a net source rather than a sink for dispersing moths throughout most of the outbreak is interesting. The available analysis of Green River data (Royama 1984) shows that the situation at severely defoliated K-series sites was similar, whereas moderately defoliated G-series sites were net recipients of egg-carrying moths. Areas under prolonged and severe defoliation should tend to produce emigrants for at least two reasons associated with the behaviour of female moths. First, as we show here, severe current-year defoliation results in moths with fewer eggs. These less fecund moths are also smaller (Miller 1957) and therefore more likely to be able to fly as soon as they eclose (Blais 1953; Sanders and Lucuik 1975). Well-fed, fully gravid moths are unable to take flight until they lay at least a few

of their eggs locally (Wellington and Henson 1947). Second, prolonged defoliation reduces the number of preferred oviposition sites (needles <5 years old) for moths (Morris 1955), which should also promote emigration from the damaged area.

An analysis of historical defoliation records for Ontario shows that the cumulative frequency of moderate and severe defoliation was greater in the area immediately around Black Sturgeon Lake than in the larger regional zone centred on Lake Nipigon in northcentral Ontario (Candau et al. 1998). Given our evidence that the Black Sturgeon Lake area acted as a source of gravid moths for most years between 1985 and 1995, what is the role of this dispersal in both the local dynamics and the spatial patterns of the regional outbreak? Our inferences are limited because despite the uncommonly long time series accumulated, the period of observation was restricted to the outbreak and the beginning of the decline phase of the population cycle. Pheromone trap and larval density data for the Black Sturgeon Lake area in the period leading up to the outbreak of the 1980s reveal a more or less steady increase in density of both life stages after 1970 (Sanders 1988). There is little evidence of the sudden outbreak that one might expect from an influx of moths, nor is there a high-density population outside the study area that could serve as a source of such moths (Howse et al. 1983; Candau et al. 1998). Similarly, although spruce budworm populations in areas surrounding Black Sturgeon Lake reached outbreak levels after the mid-1980s (Evans and Melbourne 1990; Biggs et al. 1994), it is impossible to determine the influence of emigration from Black Sturgeon Lake or area-wide dynamics without data on rates of change in population density in these surrounding areas.

In conclusion, we show that fecundity in field populations of the spruce budworm is determined largely by the supply of current-year foliage. The lowest fecundities were measured in areas with the greatest levels of current defoliation, irrespective of the stage of the outbreak. Throughout the course of an outbreak, variation in fecundity contributes less to fluctuations in rates of change in population density than does variation in generational survival. However, our data indicate that fecundity can, at times, compensate for annual changes in generational survival and thus maintain population densities at outbreak levels. This compensation occurs because of the inverse relationship between fecundity and severity of defoliation: as budworm density and defoliation increase, fecundity decreases, and vice versa. In the same manner, we have shown that immigration of fecund moths can also compensate for sharp drops in generational survival rates during an outbreak and thus help maintain spruce budworm populations at outbreak levels.

### Acknowledgements

CJ Sanders generously provided measurements of defoliation and observations of moth activity at Black Sturgeon Lake. TJ Lysyk made the estimate of fecundity from wing areas in 1988. Technical assistance was provided by R Fletcher, P Duval, D Oliver, D Ortiz, and P Roden.

### References

- Bauer LS, Nordin GL. 1988. Nutritional physiology of the eastern spruce budworm, *Choristoneura fumiferana*, infected with *Nosema fumiferanae*, and interactions with dietary nitrogen. *Oecologia* **77**: 44–50
- 1989. Effect of *Nosema fumiferanae* (Microsporidia) on fecundity, fertility, and progeny performance of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Environmental Entomology* **18**: 261–5
- Biggs WD, Constable DC, Keizer AJ, Bolan PM. 1994. Results of the forest insect and disease survey in the northwestern region of Ontario, 1993. *Canadian Forest Service Information Report* **O-X-435**

- Blais JR. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). *Canadian Journal of Zoology* **30**: 1–29
- . 1953. Effects of the destruction of the current year's foliage of balsam fir on the fecundity and habits of flight of the spruce budworm. *The Canadian Entomologist* **85**: 446–8
- Campbell IM. 1962. Reproductive capacity in the genus *Choristoneura* Led. (Lepidoptera: Tortricidae). I. Quantitative inheritance and genes as controllers of rates. *Canadian Journal of Genetics and Cytology* **4**: 272–88
- Candau J-N, Fleming RA, Hopkin A. 1998. Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Canadian Journal of Forest Research* **28**: 1733–41
- Delisle J, Simard J. 2002. Factors involved in the post-copulatory neural inhibition of pheromone production in *Choristoneura fumiferana* and *C. rosaceana* females. *Journal of Insect Physiology* **48**: 181–8
- Evans HJ, Melbourne S. 1990. Results of the forest insect and disease surveys in the north central region of Ontario, 1989. *Canadian Forest Service Miscellaneous Report* **92**
- Fettes JJ 1950. *Investigations of sampling techniques for population studies of the spruce budworm on balsam fir in Ontario*. Annual progress report. Sault Ste. Marie, Ontario: Canadian Forest Service
- Greenbank DO. 1963. The analysis of moth survival and dispersal in the unsprayed area. pp 87–99 in RF Morris (Ed), *The dynamics of epidemic spruce budworm populations*. *Memoirs of the Entomological Society of Canada* **31**
- Hardy Y, Auger M, Caron M. 1976. *Étude du développement de la tordeuse des bourgeons de l'épinette*. Bulletin Technique 2. Québec: Service d'Entomologie et de Pathologie, Ministère des Terres et Forêts du Québec
- Howse GM, Syme PD, Gross HL, Myren DT, Meating JH, Applejohn MJ, Smith KL. 1983. Forest insect and disease conditions in Ontario, 1982. *Canadian Forest Service Information Report* **O-X-350**
- Leather SR. 1988. Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. *Oikos* **51**: 386–9
- Lethiecq J-L, Régnière J. 1988. Comparative descriptions of the physical characteristics and vegetation of six sites used by the Canadian Forestry Service in the study of spruce budworm population dynamics. *Canadian Forest Service Information Report* **LAU-X-83**
- Miller CA. 1957. A technique for estimating the fecundity of natural populations of the spruce budworm. *Canadian Journal of Zoology* **35**: 1–13
- . 1963. The analysis of fecundity proportion in the unsprayed area. pp 75–87 in RF Morris (Ed), *The dynamics of epidemic spruce budworm populations*. *Memoirs of the Entomological Society of Canada* **31**
- Morris RF. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. *Canadian Journal of Zoology* **33**: 225–94
- . 1963. The dynamics of epidemic spruce budworm populations. *Memoirs of the Entomological Society of Canada* **31**
- Nealis VG, Régnière J. 2004. Insect–plant relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. *Canadian Journal of Forest Research*. In press.
- Nealis VG, Smith SM. 1986. Interaction of *Apanteles fumiferanae* (Hymenoptera: Braconidae) and *Nosema fumiferanae* (Microsporidia) parasitizing spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Canadian Journal of Zoology* **65**: 2047–50
- Perry DF, Régnière J. 1986. The role of fungal pathogens in spruce budworm population dynamics. pp 167–70 in RA Samson, JM Vlak, D Peters (Eds), *Fundamental and applied aspects of invertebrate pathology*. Wageningen, Netherlands: Foundation of the 4th International Colloquium of Invertebrate Pathology
- Régnière J, Lysyk TJ, Auger M. 1989. Population density estimation of spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) on balsam fir and white spruce from 45-cm mid-crown branch tips. *The Canadian Entomologist* **121**: 267–81
- Royama T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs* **54**: 429–62
- Sanders CJ. 1988. Monitoring spruce budworm population density with sex pheromone traps. *The Canadian Entomologist* **120**: 175–83
- . 1991. Biology of North American spruce budworms. pp 579–620 in LPS van der Geest, HH Evenhuis (Eds), *Tortricid pests, their biology, natural enemies and control*. Amsterdam, Netherlands: Elsevier Science Publishers
- Sanders CJ, Lucuik GS. 1975. Effects of photoperiod and size on flight activity and oviposition in the eastern spruce budworm (Lepidoptera: Tortricidae). *The Canadian Entomologist* **107**: 1289–99
- SAS Institute Inc. 1999. *SAS/STAT® user's guide*. Version 8. Cary, North Carolina: SAS Institute Inc
- Thomson HM. 1958. The effect of a microsporidian parasite on the development, reproduction, and mortality of the spruce budworm, *Choristoneura fumiferana* (Clem.). *Canadian Journal of Zoology* **36**: 499–511

- Wellington WG, Henson WR. 1947. Notes on the effects of physical factors on the spruce budworm, *Choristoneura fumiferana* (Clem.). *The Canadian Entomologist* **79**: 168–70
- Wilson GG. 1980. Effects of *Nosema fumiferanae* (Microsporida) on rearing stock of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Proceedings of the Entomological Society of Ontario* **111**: 115–6
- . 1987. Observations on the level of infection and intensity of *Nosema fumiferanae* (Microsporida) in two different field populations of the spruce budworm, *Choristoneura fumiferana*. *Canadian Forestry Service Forest Pest Management Institute Report* **FPM-X-79**

(Received: 25 September 2003; accepted: 2 February 2004)