POST-DIAPAUSE ACTIVITY AND SURVIVAL OF SPRUCE BUDWORM LARVAE IN RELATION TO THE SEQUENCE OF SPRING EMERGENCE

by

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INTRODUCTION

Various behavioral characteristics of an insect may indicate its capacity to survive and reproduce. While rearing colonies of the spruce budworm, *Choristoneura fumiferana* (Clem.), in the laboratory, I have noted that emergence of second-instar budworm larvae from hibernacula in the spring generally spans a period of about 1 week, even when the breaking of diapause is stimulated by high temperature regimes. The emerging population can be readily classified into early and late emergents. Miller (1958) and Lewis (1960) found that the late emergents were more heavily parasitized than the early emergents, and D. C. Eidt (personal communication) has noted that the sex of the first emergents was biased toward males. I have always suspected that early emergents differ in a number of respects from late emergents and this report gives the results of a series of experiments to test this notion.

METHODS

Samples of an overwintering population of spruce budworm were collected in March from a heavily infested stand near Fredericton, N.B. The foliage samples were tied up in small bundles, wrapped in paper toweling, hung in a greenhouse, and watered copiously each day to prevent excessive drying. Emergence began on the fifth day and continued until the thirteenth day: larvae emerging during this period were grouped into five emergence categories according to their sequence of emergence. To avoid placing individuals in the wrong category, the foliage bundles were taken down at the end of each day, unwrapped, shaken vigorously to dislodge crawling larvae, then rewrapped in new paper toweling.

Larvae were collected three times each day. The first lot was used to measure the crawling speed of second instars, the second lot for head-width measurements, and the third was reared to the adult stage to determine: Larval and pupal survival; length of larval and pupal stadia; sex ratio and pupal coloration; and pupal weight, fecundity, and mean egg weight.

The larvae were reared in groups of five on a thin layer of artificial diet (McMorran 1965) in ½-pint plastic containers. Mold-inhibitors in the medium did not prevent fungal growth after 12 to 15 days, and the larvae were transferred to a new container of diet to complete development. Unfortunately, the supply of new diet was sufficient only for the first four emergence categories and an additional quantity (possibly of differing nutritional quality) had to be prepared for category 5. This is referred to again in the Discussion.

RESULTS AND DISCUSSION

The numbers of larvae collected, tested, measured, and reared in the five emergence categories are summarized in Table 1.

Table 1. Summary of numbers of larvae collected, tested, measured, and reared in five emergence categories

Emergence		Number of larvae			
Category	Date	Collected	Crawling tests	Measured	Reared
1	28-29 March	348	100	55	193
2	31 March	274	70	20	184
3	1 April	271	75	20	176
4	2 April	134	25	0	109
5	3-5 April	102	20	0	82

Crawling Rate

This experiment was carried out to test the hypothesis that the last larvae to break diapause and emerge from hibernacula might be less active than the first emergents. The crawling rate was simply determined as the time required to cover a distance of 24 inches on an activity board while moving toward a point source of light. Larvae were tested in groups of five. To standardize the measurements, the first larvae to be picked from the foliage each day were selected as test material but only those larvae that travelled the 24 inches in 1000 seconds or less were considered in the analysis. This constraint was used because of the apparently atypical behavior of slower individuals. In almost all cases, larvae requiring more than 1000 seconds stopped repeatedly or were unable to proceed more or less directly to the light source. In general, these larvae were slow to orientate and proceeded in a stop-go sequence. In many instances, resumption of forward progress was the result of an artificial stimulus such as the observer's movements or close proximity with other more active larvae. About 15% of the larvae acted in this manner but the proportion was not related to the time of emergence (Table 2). No explanation can be given but, as noted later, it could not be attributed to parasitism or sex. The travel time was surprisingly constant regardless of emergence category. (I have used travel time over 24 inches as well as speed as an index of activity.)

Table 2. Proportion of larvae by emergence categories that covered a 24-inch distance in less than 1000 seconds, and the mean and range in travel time for these larvae

Emergence category	Number larvae tested[a]	% travelling 24 inches in <1000 seconds	Travel time		Mean speed (cm/hr)
			Mean	Range	
1	45	89	702	626-782	313
1	55	78	718	583-846	307
2	70	91	769	628-903	286
3	75	83	764	668-850	287
4	25	80	724	643-775	303
5	20	80	726	694-746	302

a. In lots of 5.

Haynes and Sisojevic (1966) found that larvae reached their maximum crawling speed (295 cm/hr) a few hours after emergence from hibernacula. I observed the same crawling speed (Table 2) and also observed, when testing five larvae in two successive trials about 2 hours apart, that the travel time of all five was lower in the second trial:

	Travel time of individual larvae (seconds)				
First trial	587	598	705	945	978
Second trial	562	566	671	876	866

This indicates that larvae do not reach their maximum crawling activity for several hours after emergence from hibernacula.

Figure 1 shows the frequency distribution of travel time for all trials by ½-minute time classes, independent of emergence category. It shows a range in travel time of about 10 minutes. The distribution is skewed to the right and could possibly be bi-modal. To check the assumption that the skewness might be related to parasitism, the crawling speeds of 111 larvae emerging on the same day was determined and these larvae were later reared to identify parasitized and healthy individuals. The mean crawling speed was 299 cm/hr for healthy and 274 cm/hr for parasitized individuals. This difference could be attributed to a few individuals taking a very long time to travel 24 inches. A more rigorous test than a 24-inch crawling distance would be required to confirm the suspicion that parasitized individuals are less active than healthy ones.

The skewness and possible bimodality in Fig. 1 were not related to sex, since travel times of healthy male and female larvae did not differ (Table 3).

Table 3. Travel time of male and female larvae

Parameter	Male	Female
Number tested	37	30
Mean travel time (seconds)	730	740
Coefficient of variation (%)	17	15

Width of Second Instar Head Capsule

The mean head capsule widths did not differ significantly between larvae in categories 1 to 3 (Table 4).

Table 4. Head capsule widths of newly-emerged second-instar larvae

Emergence category	Number measured	Head capsule mean width (mm)	Range in capsule widths
1	26	0.31	0.27 - 0.35
1	29	.31	.29 - .34
2	20	.31	.29 - .34
3	20	.30	.27 - .32

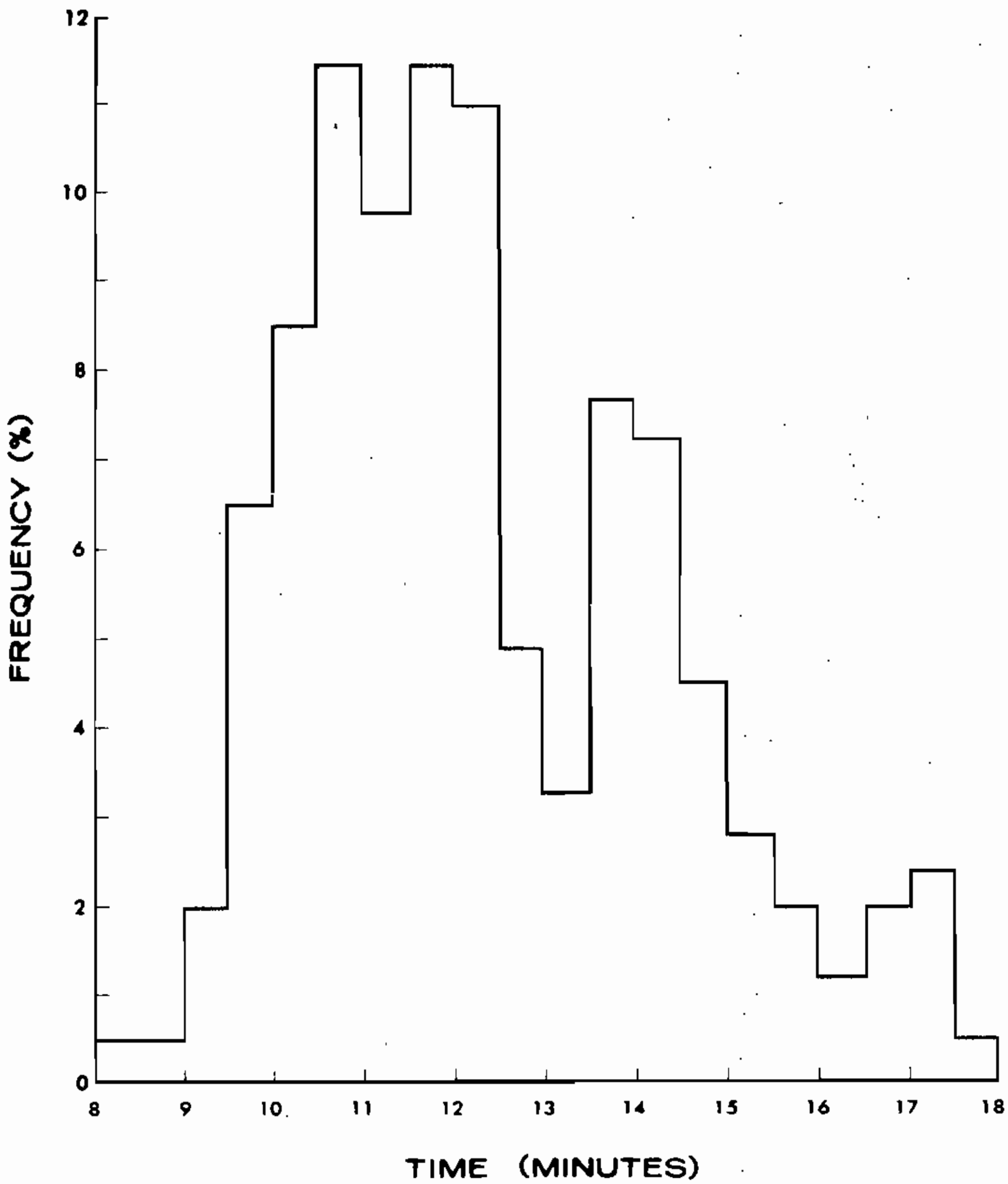

Fig. 1. Proportions of individual larvae covering a test distance of 24 inches in ½-minute time intervals. Results combined for five emergence categories.

Larval and Pupal Survival

Miller (1958) and Lewis (1960) have shown late-emerging larvae to be parasitized by *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) in greater proportion than early emergents. My study confirmed their results with 25% parasitism among early emergents and 48% within the late group (Table 5). Larval mortality from causes other than parasitism was found to be negligible, as was pupal mortality.

Table 5. Summary of mortality in reared group (% of number reared)

Emergence category	Number reared	Died as larvae from --			Died as pupae
		Apantales fumiferanae	*Glypta fumiferanae*	Undetermined	
1	193	20	5	2	1
2	184	30	6	2	5
3	176	31	6	4	2
4	109	35	4	2	0
5	82	42	6	0	5

Larval and Pupal Development Periods

The length of the larval developmental period of males and females in relation to emergence categories is shown in Figure 2A. There is some indication that the first emergents developed faster than the last emergents (26.5 versus 29.0 days for females and 24.7 versus 27.2 for males) but the short developmental time within emergence category 3 confounds this relationship. The confounding results of emergence category 3 also appears in pupal developmental times (Fig. 2B). A surprising result of this study was the shorter developmental period for female pupae.

Sex Ratios, Pupal Coloration, and Survival

Field populations of spruce budworm tend to have equal proportions of males and females. Of all pupae reared in this experiment, 47% were females; however, the first group of larvae collected from the foliage was only 38% females (Table 6). D. C. Eidt (personal communication) has observed a similar phenomenon.

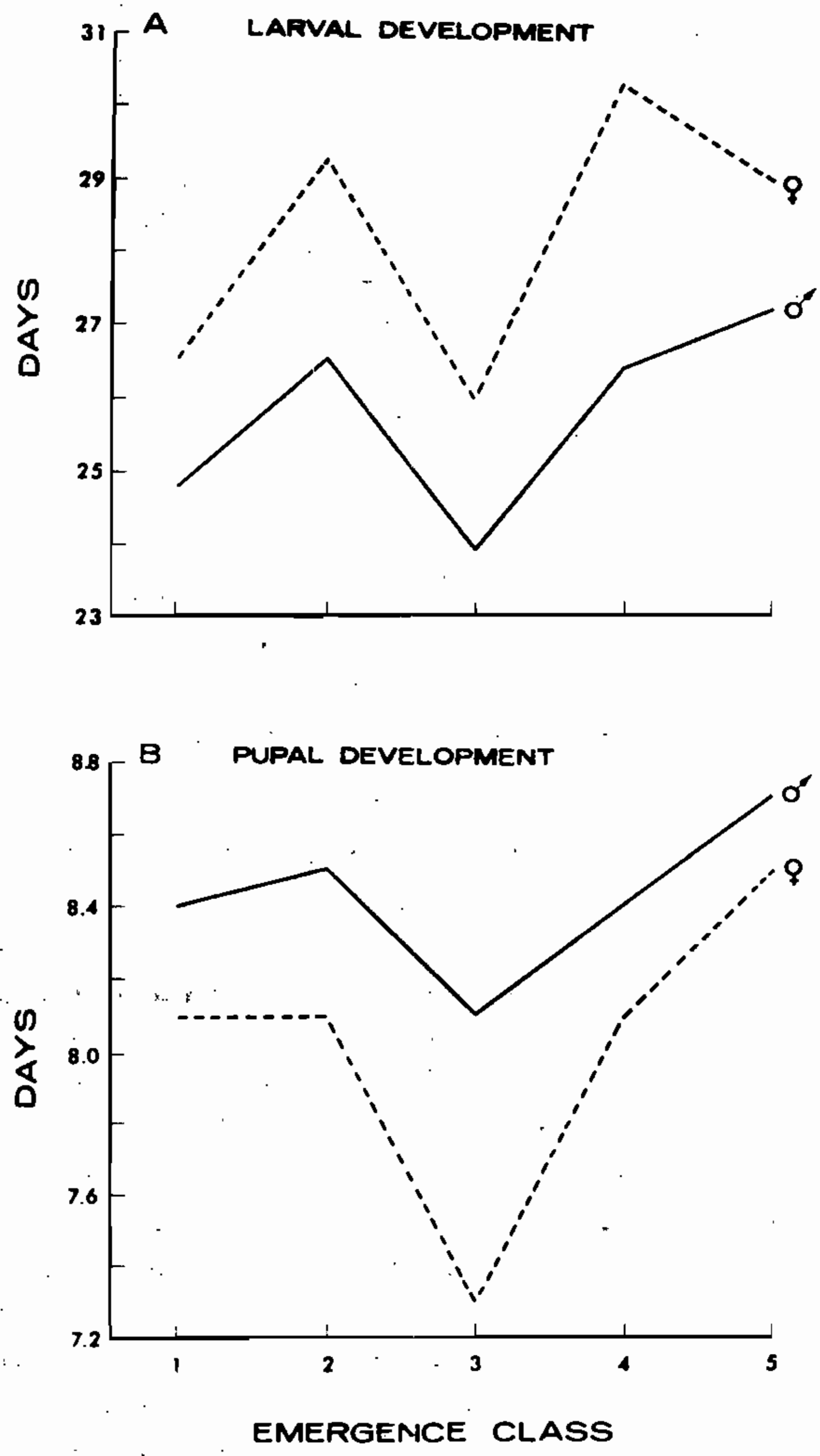

Fig. 2. Relationship of time spent in two developmental stages to emergence categories, for males and females separately. A. Length of active larval stage. B. Length of pupal stage.

NOTE: Change in position of sexes in the two sets of lines.

Table 6. Pupal sex ratios, pupal survival, and pupal coloration by emergence categories

Emergence category	Number pupae	Proportion females (%)	Pupal survival (%)	Pupae displaying green coloration (%)	
				Females	Males
1	137	38	99	74	67
2	109	52	95	84	67
3	97	50	98	77	59
4	59	50	100	80	49
5	56	45	95	75	66

Newly formed pupae are either green or yellow and, in the eastern spruce budworm, about 70% of the females and 55% of the males are expected to be green (Stehr 1959). Emergence categories appeared to have no effect on these color characteristics (Table 6).

Pupal Weight, Fecundity, and Mean Egg Weight

Female pupal weight, egg weight, and fecundity were determined for individuals in emergence categories 1, 2, 4, and 5 (Table 7).

Neither pupal weight nor fecundity was related to emergence category (Fig. 3). In fact, the heaviest pupae were found in categories 3 and 5 (120 and 117 mg) while the smallest (100 mg) were found in category 4 (Table 7). That category 5 was reared on a different batch of diet than the others, leads me to question the pupal weight and fecundity results in this category. There is some possibility that if the diet had not been changed category 5 *might* have shown a low weight and fecundity, similar to category 4, in which case category 3 (the population mean in terms of emergence) with the largest pupal weight would have been the most fecund. Genetic studies (D.D. Shaw, personal communication) suggest that those individuals near the population mean are better adapted in terms of reproductive fitness than either extreme.

Crawling Speed as a Measure of Vigor

Failure to show a relationship between emergence time and a number of indices of 'vigor' raised the obvious question of whether the

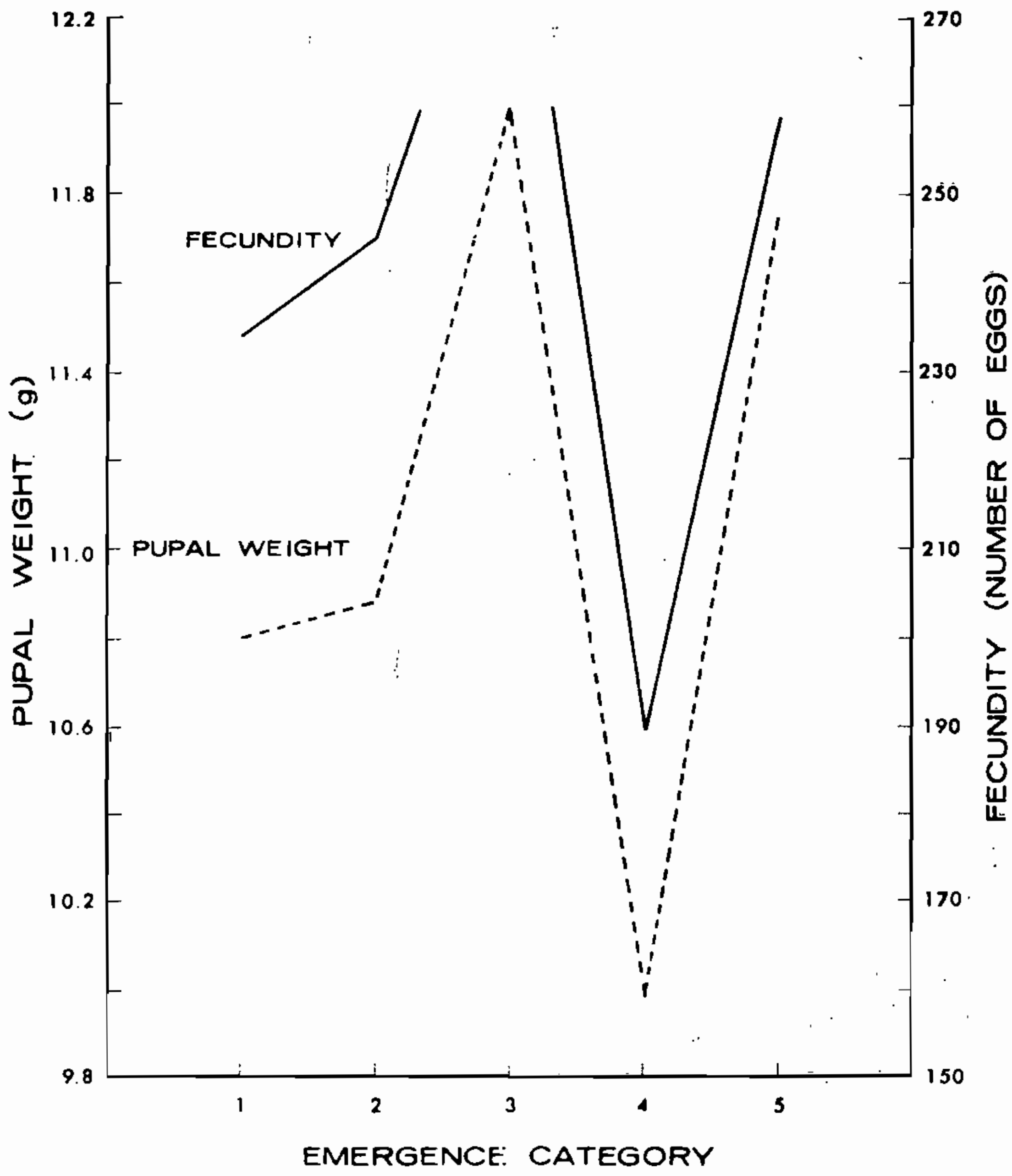

Fig. 3. Relationship of pupal weight and fecundity to emergence category. Note that no value was obtained for fecundity in emergence category 3.

Table 7. Summary of female pupal weights and oviposition results for five emergence categories

Emergence category	Oviposition experiments: Total number	Successful: Number	Successful: Per cent	Mean fecundity (eggs)	Mean egg weight (mg)	Mean pupal weight (mg)	Fecundity/pupal weight: Correlation coefficient r	Intercept a	Slope b
1	54	34	63	234	0.153	108	0.851	-84.425	0.295
2	53	25	47	245	.152	109	.782	-26.352	.250
3[a]	-	-	-	-	-	120	-	-	-
4	30	18	60	190	.157	100	.799	-160.61	.352
5	21	17	81	258	.160	117	.908	-140.96	.340

a. A total of 41 female pupae weighed, but no oviposition assays were conducted.

crawling speed of second-instar larvae was, in fact, an index of their capability to survive and reproduce. To answer this, 51 larvae were individually tested on an activity board and then grouped into speed categories of 'fast' (under 700 seconds) or 'slow' (over 700 seconds). These larvae were reared and all but one survived to the pupal stage. The relationship between crawling speed and a number of vigor parameters are shown in Table 8 which also includes the statistical analyses of the fecundity - pupal weight relationships. The 'fast' females tended to have shorter larval and pupal development times, and to have higher pupal weights and fecundities. Although only a small number of individuals were tested, the trend appears to be worth exploring with larger samples.

Table 8. Relationship of the crawling performance of second-instar larvae in categories of 'fast' (under 700 seconds) and 'slow' (over 700 seconds) to length of larval and pupal stadia, pupal weight, fecundity, and mean egg weight

Group		Number tested	Mean development time (days)		Mean pupal weight (mg)	Mean fecundity (eggs)	Mean egg weight (mg)
			Larval	Pupal			
Females							
	Fast	9	24.9	8.8	113	239	0.164
	Slow	12	26.6	9.5	109	230	.154
Males							
	Fast	14	23.0	8.8	-	-	-
	Slow	15	22.7	9.2	-	-	-

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