ENVIRONMENTAL AND GENETIC EFFECTS ON MEAN EGG WEIGHT IN SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

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Abstract

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Laboratory studies of the mean weights of initial eggs (E_i) of the spruce budworm, *Choristoneura fumiferana* (Clem.), show that this value is determined by the genetic constitution of the female moth and is relatively independent of environmental control. Dietary differences experienced by the female during larval development, and originating from different hosts or from reduced nutrient levels in artificial diets, did not affect E_i values; however, depletion of nutrients sufficient to reduce fertility greatly did reduce E_i. Temperature conditions during the ultimate larval and pupal stages influence E_i values which vary inversely. Mean egg weights are strongly heritable and are readily selected for, thereby demonstrating the presence of strong genetic control.

Résumé

L'étude en laboratoire de la masse moyenne des oeufs initiaux (E_i) de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.), montre que sa valeur est déterminée par le bagage génétique de la femelle et qu'elle est relativement indépendante du milieu. Le régime alimentaire de la femelle au cours de sa période larvaire, qui peut différer selon l'hôte ou selon les carences introduites artificiellement, n'a pas modifié E_i; toutefois, des carences suffisantes pour réduire la fertilité ont grandement réduit E_i. La température au cours du dernier stade larvaire et du stade de la chrysalide ont influé sur E_i de façon inversement proportionnelle. La masse moyenne des oeufs est fortement héritable et fait d'emblée l'objet d'une sélection, ce qui montre l'effet d'un puissant déterminisme génétique.

Introduction

Harvey (1977) described the temporal pattern of change in egg weights during the oviposition period of spruce budworm, *Choristoneura fumiferana* (Clem.), thereby confirming a previous report by Campbell (1962). A unit was described which was called the mean weight of the initial eggs (E_i), and was based on the average weight of the eggs in two of the earliest full-size clusters. This value is highly correlated with the mean weight of eggs based on the total egg complement, and provides a valid, but more easily obtained, measure of the latter (Harvey 1977).

Laboratory measurements of E_i values have revealed the presence of significant differences among populations of spruce budworm. In fact, a cline in mean egg weights occurs across the range of this species from southeast to northwest (Harvey 1983). E_i data were obtained from field-collected insects that completed their development and mating in the laboratory. It was not known whether such E_i values were valid measures of egg weights produced under field conditions. Hence there was a need to evaluate the effects of host, diet, temperature, and other factors during the parental generation on the weights of the eggs they produced. The results of these studies, conducted from 1965 to 1975, are assembled here.

Methods

Insect stocks usually originated as collections of feeding late-instar larvae of *Choristoneura fumiferana*, generally from epidemic-level populations in Ontario and Manitoba, as described previously (Harvey 1967); larvae of *C. occidentalis* Freeman were used in two experiments. Larvae received by mail were allowed to complete their development in the laboratory on fresh foliage (Stehr 1954) from the same host collected at Sault Ste. Marie. (Balsam fir, *Abies balsamea* (L.) Mill., was used for the *C. occidentalis* larvae.)

In some experiments an artificial diet (McMorran 1965, or a modification of it) was used. Laboratory conditions were controlled at 21°C, 70% R.H., and a 17-h photoperiod centred at 1200 h unless otherwise specified. In most of the experiments, second-instar larvae emerging after storage were assigned randomly among the different treatments for all of their development to the adult stage. Pupae were weighed within 24 h of pupation.

Techniques used for matings were described by Stehr (1954). All matings were single-pair and most were *inter se*; identity of progenies was maintained throughout the rearing, matings, and further generations as necessary. Every day moisture was added and eggs were collected. After counting and weighing, the clusters were set up for later checking for hatch and success in moulting to the second instar (Stehr 1954). Fecundity measurements were based on the total number of eggs laid. Where a fecundity value was substantially below that expected from the pupal weight/fecundity regression for that collection or stock, data from that female were rejected from further analysis. Eggs laid by mated adults developing from field-collected larvae constituted the beginning of the first laboratory generation (G_1); subsequent laboratory generations were designated G_2, G_3, etc.

Mean initial egg weights (E_i) were determined as described previously (Harvey 1977). E_i values are based on wet weights, as they can be obtained without appreciable effect on the viability of eggs or emerging larvae and they are directly proportional to the dry weights of those eggs (Harvey 1977). Some attempted laboratory matings result in infertile eggs, even though cluster appearance is normal. E_i values from such matings do not differ from those of fertile matings. The mean E_i in a group of Ontario stocks was 0.159 ± 0.0022 from 135 fertile matings and 0.160 ± 0.0020 in 91 sterile crosses. Although such infertile eggs provide useable E_i values, nevertheless, only data from fertile matings were used in egg weight analyses, except where otherwise specified.

Results of rearing experiments were analyzed by t tests or one-way analysis of variance. Where F values among treatments were significant, differences were further tested by the Tukey Multiple Comparison Test. Significance of linear regressions was evaluated by an F test.

Results

Effects of host on E_i. The possibility that egg weights differ with the host on which parents fed was tested by using insects collected in 1967 from balsam fir, and white spruce, *Picea glauca* (Moench) Voss, in mixed stands in Ontario. Most of these sixth-instar larvae came from light pre-outbreak populations but almost half came from locations experiencing the first or second year of severe defoliation. These insects completed the final part of their development in the laboratory on foliage from the same host. Pupal weights, fecundities, and E_i values showed no significant host-related differences (Table I). Results of multiple regression analysis confirmed this conclusion and showed that E_i values were not influenced by infestation intensity at the collection site. Similar results were obtained in the analysis of 162 mated insects collected the same season in Quebec and New Brunswick.

Table I. Pupal weight, fecundity, and E_i in field collections from balsam fir and white spruce

	Totals[a]	Balsam fir	White spruce	t^b
No. (collections)[c]	230(17)	57(5)	173(12)	
Pupal wt. (mg)	91.51 ± 1.39	93.85 ± 2.07	90.740 ± 1.73	1.156
Fecundity	195.34 ± 4.58	196.84 ± 7.47	194.84 ± 5.57	0.023
E_i	$0.1625 \pm .001$	$0.1633 \pm .001$	$0.1623 \pm .001$	0.568

[a]Data from Ontario, 1967. Values are means ± S.E.
[b]t tests for Bf vs. Sw. No t value significant at $P = 0.05$.
[c]Number of mated females (number of collections represented).

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Effects of diet on E_i. Early studies of spruce budworm nutrition using frozen balsam fir buds and artificial diets indicated that, although development time, mature size and fecundity were commonly affected by these dietary differences, E_i values were not. Results of one such experiment are presented in Table II. Insect stocks in this case were G_i *C. occidentalis* originating from Montana in 1963, but similar results have been obtained for *C. fumiferana*. Emerging second-instar larvae were reared on frozen balsam fir buds (Stehr 1954) or artificial diet at the 'standard' nutrient concentration (Harvey 1974). E_i and other data were obtained from both foliage- and diet-reared insects. Pupal weights and fecundities of mated females (Table II) were typical of all females in the treatment and were significantly lower on foliage than on the diet, as reported for *C. fumiferana* (McMorran 1965; Harvey 1974). Even though pupal weights on buds were 32% below those on diet, E_i values were not significantly different between the two diets (Table II).

Changes in nutrient content in balanced diets produced negligible effects on E_i values (Table III). Families of *C. fumiferana* originating from northwestern Ontario were distributed at pick-off among four diets with nutrient levels ranging from $2\times$ to $0.25\times$ the standard level (Harvey 1974). These diet differences caused differences in percentage of larvae feeding and in yield of adults (Table III) as well as in the weights and development times of females used in matings. Males also showed significant effects of nutrient level differences. However, although the pupal weights of females on the S/4 diet were significantly below those of females on the other diets, E_i values on that diet were not significantly different.

More severe dietary changes did, however, produce significant changes in E_i values. G_2 insects from a Cranberry Portage, Manitoba (1966) collection were used to explore the effects of reduced dietary protein levels. Second-instar larvae from 17 families were assigned equally among three diets: 'standard' and 'control' nutrient level diets (Harvey 1974); and a 'low protein' diet (Table IV). Reduction of protein and sugar to 50% of the standard level ('control' diet) caused some decreases in development rate, pupal weights and fecundities, similar to those on the S/2 diet (Table III), but did not affect E_i significantly. Further reduction of dietary protein to 12.5% of the standard ('low protein' diet) caused substantial reduction in all measures of performance, which were similar to those on the S/4 diet. However, unlike the S/4 diet, the 'low protein' diet caused a significant reduction in the E_i values (Table IV). (The higher E_i values in this experiment in comparison with those in Table III reflect the different origin of the insects (Harvey 1983).)

Regression analysis showed most of the differences in E_i in this experiment to be directly related to diet, although a small portion of the difference was due to diet-caused effects on pupal weights. Although the low protein diet caused a 38% reduction in pupal weights in comparison with the standard diet, and a 40% reduction in fecundities, the change in E_i was only 9%. In the previous experiment (Table III) the diet-caused reduction in pupal weight (S vs. S/4) was 43%, but there was no reduction in E_i. (A reduction of 9% to 0.144 would have been detected.) The S/4 and 'low protein' diets differed in that sucrose and casein levels in S/4 were both 25% of standard whereas in the 'low protein' diet these levels were 50 and 12.5%, respectively, of the standard diet. Thus, the reduction in E_i in Table IV may be a specific effect of diet imbalance.

Effects of temperature during mating and oviposition on E_i. Adults used for laboratory matings may have developed in constant laboratory temperatures or in the fluctuating temperatures of field locations and frequently they are held temporarily at lower temperatures until used for matings. To explore the sensitivity of E_i to differences in adult treatment freshly eclosed adults from laboratory stocks reared on standard diet were subjected to one of four treatments (Table V). For treatments A, B, and C mating pairs were transferred daily from mass mating cages to separate mating jars (Stehr 1954) and distributed

Table II. Effects of frozen foliage vs. artificial diet on pupal weight, fecundity, and E_i of mated females

	Frozen foliage	Artificial diet	t
No. mated females	18	26	
Pupal wt.[a] (mg)	118.12 ± 4.67	173.46 ± 5.69	7.52[b]
Fecundity	162.28 ± 10.77	321.81 ± 16.67	8.04[b]
E_i (mg)	0.175 ± 0.0031	0.183 ± 0.0033	1.78

[a]Mean values ± S.E.
[b]$P < 0.01$.

Table III. Effects of nutrient level of artificial diets on survival and mature size and E_i of mated females

			Mated females				
Diet[a]	Feeding[b] (%)	Adults (%)	n	Pupal wt (mg)[c]	Dev. time (days)[c]	E_i[c]	F:S[d] matings
Standard	77.3	57.2	14	107.1a ± 6.5	23.8a ± 0.5	0.1604a ± 0.004	4:10
S/2	73.3	61.1	22	102.3a ± 5.0	27.8b ± 0.9	0.162a ± 0.003	12:10
S/4	25.4	22.9	4	60.9b ± 6.5	37.9c ± 1.7	0.159a ± 0.006	0:4
2S	77.4	53.8	8	113.9a ± 8.3	26.9ab ± 4.4	0.160a ± 0.007	6:2
P[e]				<.01	<.01	<.05	

[a]Diet constituents as in Harvey 1974 (Standard); S/2, S/4 and 2S contained the same levels of water, alphacel and agar, but had 1/2, 1/4 and 2×, respectively, of all other nutrients (sucrose, casein, vitamins, etc.).
[b]Larvae started: 154 per treatment.
[c]Mean values ± S.E. Means followed by different letters differ significantly at $P = 0.05$ by Tukey test.
[d]Ratio of fertile:sterile matings. No fertile in diet S/4.
[e]Probability in one-way ANOVA.

to provide 15–20 pairs per treatment. For the 15°C treatment (D), individual pairs were set up upon eclosion in a 15° cabinet. Fertile matings were obtained in all treatments.

The general pattern of oviposition in all treatments was similar to that described earlier (Harvey 1977); however, there were minor differences in treatments B and D. Females held at 15° (D) laid significantly fewer eggs per day of oviposition (Table V), as also reported by Sanders *et al.* (1978). However, these females continued ovipositing for 3 days longer than in any other treatment; consequently they equalled other treatments in total clusters and fecundity. They also laid the largest clusters, although this difference was not significant. Delay of mating for 3 days (B) produced the most eggs per day but did not affect cluster size or fecundity. In spite of these differences in oviposition pattern there were no significant effects of the treatments on mean fecundity, cluster size, or E_i values (Table V).

Hatch of eggs and subsequent larval development was normal in all treatments except 15°. Percentage hatch of eggs at 15°C was apparently normal but time to hatch (22.43 days) was very long. Furthermore, development of first-instar larvae was very poor at this temperature; by 6 weeks after hatch only 2.9% of the larvae had completed a hibernaculum and moulted to the second instar. This poor post-hatching survival does not agree with earlier results (Harvey 1957) and is probably not attributable to temperature alone.

From the results, no effect on E_i values is to be expected from such common laboratory practices as holding moths for up to 3 days before mating, either at rearing temperatures or at 5.6°C. Likewise, no effect on E_i is expected in moths held at or ovipositing at temperatures below 21°C to as low as 15°C.

Table IV. Effects of dietary differences on pupal weights, fecundities, and E_i values of spruce budworm in laboratory rearings

	Diets			
	Standard[a]	Control[a]	Low protein[b]	*P*
Survival (%)[c]	25.1	22.2	14.2	
All females				
N	69	65	29	
Pupal wt. (mg)[d]	115.6 ± 2.3a	82.2 ± 2.4b	67.6 ± 2.2c	<.01
Dev. time (days)[d]	25.8 ± 0.3a	29.3 ± 0.6b	34.3 ± 1.3c	<.01
Fertile mated females				
N	34	37	11	
Mean pupal wt. (mg)[d]	119.6 ± 3.4a	86.9 ± 3.1b	73.9 ± 2.9b	<.01
Fecundity[d]	187 ± 11.2a	121 ± 9.2b	112 ± 8.6b	<.01
Mean E_i[e]	0.199 ± .003a	0.192 ± .002ab	.181 ± .001b	<.01

[a]Diet constituents as in Harvey 1974; 'control' diet: sucrose, casein, and salt mixture at 1/2 standard levels.
[b]Dietary casein (0.449/100 g diet) = 1/4 × control and 1/8 × standard. Diet also contained 0.25 g/100 of glutamic acid.
[c]Percentage survival of females per larva established on food. Larvae started = 306 or more per diet.
[d](Values show) mean values ± S.E. See footnote C, Table III.
[e]Probability in one-way ANOVA.

Table V. Effects of several treatments of adult females on oviposition and mean initial egg weights (E_i)

	Treatment[a]					
	A	B	C	D	F^b	P^b
Females	18	12	11	15		
Fecundity[c]	193.8 ± 17.2	229.8 ± 29.1	206.1 ± 32.6	211.7 ± 19.6	0.41	>.05
Eggs/cluster[c]	16.8 ± 1.1	16.9 ± 1.5	17.7 ± 1.9	18.4 ± 1.3	0.34	>.05
Eggs/day	26.8ab ± 2.3	38.6a ± 3.8	29.5ab ± 2.5	16.6b ± 1.3	12.37	<.05
E_i[c]	0.176 ± .004	0.172 ± .004	0.177 ± .005	0.179 ± .003	0.52	>.05

[a]Treatments: A—Mating (within 24 h of eclosion) and oviposition at 21°C.
B—Matings (3 days after eclosion) and oviposition at 21°C.
C—Parents held 3 days at 5.6°C before matings and oviposition at 21°C.
D—Mating (within 24 h of eclosion) and oviposition at 15°C.
[b]*F* and *P* values from one-way ANOVA.
[c]Means ± S.E. See footnote C, Table III.

Effects of temperature during development on E_i. The effects of three temperatures during larval and pupal development on E_i values of eggs produced by adults was tested using two groups of G_2 families: four families ('REF') from French Lake (Quetico Provincial Park, Ontario) and four families ('ROK') of *C. occidentalis* collected in Montana. Following storage (28 weeks at 0°C) equal numbers of larvae from all eight families were set up on diets of freshly thawed balsam fir buds or artificial diet at constant temperatures of 16°, 20°, and 24°C. Rearings and matings were completed in separate temperature cabinets with a 17-h photoperiod; humidity was regulated with salt solutions. Larval survival to maturity was satisfactory at 16° and 20° but was much poorer at 24° (Table VI), partly because of excess moisture inside the rearing containers. Because of low numbers of fertile eggs in the 16° and 20° treatments E_i values from sterile eggs are included in the analysis.

E_i values differed with temperature (Table VI); however, mean E_i values for REF eggs (0.161) were significantly different from those for ROK eggs (0.182). To overcome this difference and the uneven distribution of egg size types among the treatments, differences were calculated between each E_i value and its family mean E_i value (all treatments). The mean differences varied significantly among treatments ($F = 6.63, P < .01$). They also form a regression on temperature ($b = -0.00469$; $F = 20.4$, $P < .01$), demonstrating that there is a significant relationship between E_i and temperature. These results indicate that E_i values vary inversely with developmental temperature.

The genetics of E_i. To investigate the genetic mechanisms regulating E_i collections with widely different E_i values were selected. Data from two of these collections illustrate this difference. The mean E_i from 30 fertile matings of insects from Dawson Bay, Manitoba was 0.182 ± 0.002 mg. The mean E_i from 20 matings of insects from near Atikokan, Ontario in the same season was $0.171 \pm .002$ mg. The difference between these two values is highly significant ($t = 3.89$; $P < 0.01$, d.f. 48). Progenies of 53 families of the G_1 generation of these and other field-collected insects from Ontario and Manitoba (1964) were reared on artificial diet and the adults were mated *inter se*. Mean E_i values (192) from the progenal groups were compared with the E_i of their parents. E_i values of parents and progeny were both distributed normally; hence there was no need for a logarithmic transformation as used by Morris and Fulton (1970). The regression obtained was highly significant ($F = 14.7$; $P < 0.01$):

$$\text{Mean } E_i \text{ (progeny)} = 0.106 \pm 0.376\ E_i \text{ (parent)}.$$

The correlation between the E_i values of parents and progeny ($R = 0.473$) indicates a strong genetic component in this relationship. That there were other sources of variation in the progenal E_i values is indicated by the low R^2 (22.4).

Table VI. Effects of temperature during larval and pupal development on E_i

	16°	20°	24°
Survival[a]	62.9	60.1	31.0
Fertile matings	9	22	19
Treatment mean E_i	0.204	0.187	0.167
± S.E.	±.0042	±.0046	±.0055
Pooled mean E_i[b]	0.187	0.187	0.180
Mean difference	−0.0173	−0.00023	+0.0134

[a]Survival of feeding second-instar larvae to adults, mean %.
[b]Average of family means represented by the treatment group.

Table VII. Differences in E_i in several families and selection of large (L) and small (S) lines

Family number	N[a]	Mean E_i[b]	S.E.	Range	Designation
2	6	0.157a	.0055	.143–.182	S
9	6	0.160a	.0041	.153–.174	
4	5	0.163a	.0041	.154–.177	
7	23	0.163a	.0027	.145–.198	S
8	16	0.166a	.0031	.145–.187	S
15	4	0.167a	.0058	.150–.167	
17	9	0.176ab	.0045	.158–.202	L
11	15	0.189b	.0024	.168–.202	L
S[c]	45	0.163	.0019	.143–.198	
L	24	0.184	.0024	.158–.202	

[a]Number of fertile progenal families contributing to mean E_i value.
[b]Means followed by different letters significant at $P = 0.05$ by Tukey Multiple Comparison Test.
[c]Difference in mean E_i between S and L families highly significant ($t = 6.44$; d.f. = 48; $P < 0.01$).

Table VIII. Stability of mean initial egg weights in lines selected for different egg weights

Generation	Large			Small			t^a	
	n	E_i	s_x	n	E_i	s_x	d.f.	t
G_2	25	0.184	.0024	45	0.163	.0019	68	6.86
G_3	34	0.179	.0043	12	0.155	.002	44	5.06
G_4	18	0.183	.0039	4	0.155	.0055	20	4.15
G_5	26	0.177	.0031	8	0.157	.0039	32	4.01

[a]All t tests significant at $P < 0.01$.

An attempt to select for egg size lines was made using egg masses collected in 1961, also near French Lake. Matings of adults from individually reared egg masses (Harvey and Stehr 1971) produced the first laboratory generation (G_1) and their progenies the G_2 generation. E_i values of G_1 and G_2 showed considerable variation within as well as between families (Table VII). Families were classified as large (L) or small (S) on the basis of the average E_i in the G_2 eggs (Table VIII) and were reared through several generations. Matings were made *inter se* and within lines. E_i data for four successive generations (Table VIII) show that the differential in egg weights between the lines was maintained.

Discussion

Outram (1971) found ovariole development in the spruce budworm to be minimal until the second day of pupal development. At eclosion 6 days later, however, ovariole development was virtually complete and some oocytes were well developed. Thus, almost the entire process of ovariole development and maturation of first oocytes occurs between days 2 and 8 of the pupal stage. Most of the remainder of the oocytes probably complete their development in the first few days of adult life.

The initial eggs laid are the heaviest (Campbell 1962; Harvey 1977). Eggs laid on subsequent days are progressively lighter as a result of progressively greater depletion of physiological reserves for egg production in the moth (Campbell 1962). The mean weight of the initial eggs was reported to be unrelated to the weight of the female producing those eggs (Harvey 1977), but the total number of eggs is strongly correlated with pupal weight (Campbell 1962; Harvey 1983) and pupal size (Miller 1957). More extensive analysis of the relationship between E_i and the weight of the ovipositing female shows that within populations a weak positive relationship does exist, although it accounts for only a small proportion of the variation in E_i (Harvey 1983).

Differences in dietary nutrient level can profoundly affect the mature weight of budworm and the number of eggs they produce, regardless of whether nutrients are supplied as fresh or frozen buds (Table II), from different hosts (Table I) or from artificial diets of different constitution (Tables III, IV). The same dietary differences , however, have little, if any, effect on E_i values. Only a very small proportion of the variation in E_i (Table III) was associated with diet-related differences in pupal weight of the ovipositing female ($R^2 = 8.6\%$, $P < 0.01$). This relationship is also shown in the slightly higher E_i values from diet-fed than from foliage-fed insects (Table II) and reflects the much higher pupal weights in the former. Probably the reduction of egg weight in successive clusters was also increased by the diets that reduced adult weight (Harvey 1977).

A severe reduction in dietary protein content did produce slight but significant reductions in E_i values of fertile eggs (Table IV). The nitrogen level in the 'low-protein' diet was about 23% of that present in late buds of white spruce (Harvey 1974) and substantially below that likely to be encountered in natural foliage. Since survival was low on this diet, the lower E_i values could be due to the selective elimination of moths producing larger eggs. However, comparison with other diets indicates that dietary imbalance

was probably more important in reducing egg weight than low protein. Nevertheless, the possibility exists that under natural conditions in which larvae suffer severe starvation E_i as well as fecundity could be reduced. Miller's (1963) report that moth size/fecundity regressions were different in starved populations could be evidence of such a change under natural conditions. Under most natural conditions, however, the size of budworm eggs is only minimally affected by the size of the females laying those eggs, an indication that the principal control of initial egg size is genetic.

The effects of three temperatures on oviposition were as expected (Sanders *et al.* 1978). The effects of temperature on E_i values are also in agreement with those in earlier reports. Campbell (1962) reported that 'egg growth was to some extent temperature dependent'. In unpublished reports Miller and Renault (1966) and Eidt (personal communication) found weights of eggs developing at lower temperatures to be greater than those at higher temperatures, but in neither case were the differences significant, perhaps because of between-family variation. The egg weights we found at 16° and 24°C were significantly different from 20°C when compared with family means (Table VI). As in the earlier reports, the relationship between E_i and temperature appears to be inverse, lower temperatures producing heavier eggs. Effects of temperature on pupal weight/fecundity regressions would also be expected in view of the effects on E_i values, but the data were insufficient for this analysis.

The insects used in these experiments were exposed to different temperatures during their entire post-diapause development from second instar through to adults, as well as during mating and oviposition. As temperature during adult life did not appear to influence E_i (Table V) the action of temperature must be during larval and/or pupal stages. However, ovariole development is minimal until the latter part of the ultimate instar or even in the first 2 days of the pupal period (Outram 1971). Therefore, the principal direct effect of temperature on egg weight appears to take place during the pupal stage.

Better knowledge of the effects of physical factors on egg weights of spruce budworm provides a basis for evaluation of the variation in E_i values found within and between populations (Table VII; Harvey 1983). The experimental evidence presented and our knowledge of ovariole development indicate that temperature affects E_i mainly during the final days of larval development and during the pupal period. Consequently E_i values determined from larvae that complete these susceptible stages of development under laboratory conditions should be comparable regardless of temperatures at the collection site. And, as diet variables such as host, nutrient levels, etc. usually do not affect initial egg weights, E_i values determined as described must reliably estimate true population values. The strong correlation demonstrated between E_i values from field-collected insects and those of their laboratory-reared progenies lends support to this conclusion.

Most of the variation in E_i values measured as specified appears to be genetic in origin. Egg size shows variation between females that is susceptible to selection. The selection reported in Table VII was made among E_i values represented in a single collection from northwestern Ontario and does not represent the latitude-related cline found among collections in eastern and central Canada (Harvey 1983). Furthermore, the correlation between E_i values of progenies and those of their parents is strong evidence of the heritable nature of E_i. Heritability determined from the regression of progenal E_i on parental E_i (method for offspring and one parent, Falconer 1960) was 0.752 ± 0.098, and this implies that 75.2% of the observed variation in E_i under these conditions was due to additive genetic factors (after Richards and Myers 1980). Mean E_i values differ among the different entities of the coniferophagous *Choristoneura* (Campbell 1958; Harvey unpub.). Further evidence of the genetic nature of the control of egg weight is provided by results of crosses and backcrosses among some of the different entities (Campbell 1958).

The studies described herein provide a basis for the use of E_i measurements in further studies of population quality in the spruce budworm. The cline in E_i of *C. fumiferana* over its range from the largest in the northwest to the smallest in the southeast provides evidence of the ecological significance of egg weight differences (Harvey 1983).

Although the presence of variation among individuals is accepted in studies of spruce budworm population dynamics, eggs are assumed to be more or less equal units of biological material. The evidence of the ecological significance of E_i differences (Harvey 1983) and of the heritable nature of this character points to the need for its recognition as a significant factor in population quality. Studies of E_i in relation to population cycle phase should lead to a better understanding of the part played by insect quality in the population fluctuations of the spruce budworm.

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