

A GEOGRAPHICAL CLINE IN EGG WEIGHTS IN *CHORISTONEURA FUMIFERANA* (LEPIDOPTERA: TORTRICIDAE) AND ITS SIGNIFICANCE IN POPULATION DYNAMICS

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Abstract

Can. Ent. 115: 1103–1108 (1983)

The mean weights of the initial eggs (E_i) of the spruce budworm, *Choristoneura fumiferana* (Clem.), vary within and between populations. Measurements of collections from across the range of this species reveal the presence of a cline directly related to latitude and longitude of the collection source. Collection mean E_i values range from 0.219 mg in the northwest to 0.157 mg in the southeast. A similar cline, also related to latitude but negative in slope, is demonstrated for the number of eggs per unit pupal weight. This cline also finds expression in changing slope of fecundity/pupal weight regressions. The cline in egg weight appears to be an adaptation to winter conditions across the range of this insect and should be considered in population dynamics.

Résumé

Le poids moyen des premiers oeufs (E_i) de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.), varie à l'intérieur des populations et d'une population à l'autre. Des mesures effectuées sur des prélèvements provenant de l'ensemble du domaine de l'espèce révèlent la présence d'un cline directement relié à la latitude et à la longitude du point de prélèvement. Les valeurs moyennes de E_i varient de 0.219 mg dans le nord-ouest à 0.157 mg dans le sud-est. On démontre également l'existence d'un cline semblable, également relié à la latitude mais à pente négative, pour le nombre d'oeufs par unité de poids de la chrysalide. Ce cline s'exprime également en changeant la pente des régressions de la fécondité en fonction du poids des chrysalides. Le cline du poids des oeufs semble une adaptation aux différentes conditions hivernales dans le domaine de l'insecte et devrait être pris en considération dans la dynamique de ses populations.

Introduction

The possibility that changes in the intrinsic nature or quality of the insects could be a causative or contributing factor in the population cycles of insects such as the spruce budworm has been suggested by various authors (Campbell 1962; Wellington 1962; Leonard 1970). The mean weights of eggs laid by spruce budworm moths exhibit considerable variation among females (Harvey 1977) and may be an expression of population quality. Further knowledge of the nature and extent of egg weight differences should help us understand their significance in the population dynamics of this important forest pest.

Harvey (1977) described the pattern of egg weight change during the oviposition period of the spruce budworm, *Choristoneura fumiferana* (Clem.), and confirmed a previous report by Campbell (1962). Both the weight of the initial eggs and the pattern of decrease over the oviposition period showed variation among different individuals (Harvey 1977). To study the variation in weight of the initial eggs a unit based on the average weight of the eggs in two of the earliest full-size clusters was described; this unit was called mean weight of initial eggs (E_i). E_i is highly correlated with the mean weight of eggs (based on the total complement) and therefore provides a valid but more easily obtained measure of the latter (Harvey 1977).

Although mean egg weights can be affected by some conditions to which the female parent has been subjected, they are relatively insensitive to environmental variables such as host plant, diet, and temperature (Harvey 1983). Consequently, egg weight data from field-collected larvae which complete their development and oviposition in the laboratory are valid measures of field-laid eggs and are comparable between collections from widely different locations.

Studies of egg weights in several different populations have revealed a cline in mean egg weights across the range of the spruce budworm that is related to latitude and longitude of the collection locations. The existence and possible significance of this cline are reported here.

Methods

Collections of feeding, late-instar larvae were obtained by mail from various locations in eastern and central Canada. Most of these collections originated from outbreak populations described by Stehr (1967). Larvae were allowed to complete their development on fresh shoots of white spruce, *Picea glauca* (Moench) Voss, or balsam fir, *Abies balsamea* (L.) Mill. (Stehr 1954). Laboratory conditions were controlled at 21°C, 70% R.H., and a 17 h photoperiod centred at 1200 h EST. Pupae were weighed within 24 h of pupation.

Techniques used in obtaining matings were described by Stehr (1954) with mature foliage of balsam fir provided for oviposition. Egg cluster counts and weights (in mg) and calculations of mean initial egg weights (E_i) followed procedures described by Harvey (1977). Mean egg weights were based on wet weights; however, mean dry weights are directly proportional to wet weights (Harvey 1977). Fecundity values were based on the total number of eggs laid, as described previously (Harvey 1977). Where a fecundity value was substantially below that expected from the pupal weight/fecundity regression for that collection, data from that female were rejected from further analysis. Only data from egg complements showing a high percentage hatch were used.

Collections of *C. fumiferana* originated across Canada from New Brunswick to Alberta and the MacKenzie River Valley of the Northwest Territories. Data from 1965, 1966, and 1967 collections were pooled by location, and mean values were analyzed for effects related to latitude, longitude, and altitude. Because mean egg weights from New Brunswick and Ontario represented collections of varied size from a large number of widely distributed locations they were grouped by Universal Transverse Mercator grid units (Table I) for analysis. All E_i values in a given unit (approx. 400,000 m east/west \times 100,000 m north/south) were averaged and the mean egg weight was treated as occurring at the centre of the unit.

Collections from the higher latitudes usually consisted of single sizeable collections and the data were used without grouping, other than over years. Mean number of data values per location or grid unit ($N = 25$) was 142 (range 7–754). The location or group mean E_i values were treated as individual values in the regression analysis. For the more detailed analyses of pupal weights and fecundities in relation to E_i , 1967 collections were used since they provided large numbers of mated pairs, an average of 16.9 fertile females from 31 collections.

Results

Variation in E_i , over the range of *C. fumiferana*. Egg weights ranged from 0.132 mg in the southeast to 0.257 in the northwest; mean values for locations ranged from 0.157 to 0.219 (Table I). Multiple regression analysis revealed a positive relationship between mean E_i and the latitude, longitude and altitude of the collection locations, which explained 91.4% of the variation in E_i (line 1, Table II). Only 0.05% of the variation was explained by altitude. Latitude was more important than longitude but, because of limited distribution of the collection locations, effects due to latitude and longitude were interrelated; unfortunately, combinations of latitude and longitude which would resolve the relative importance of the two were not represented in the data. In further analyses, only latitude was studied as it appeared to be the more important of the two but it is assumed to represent the combined effects of both variables for the data available. The relationship between E_i and latitude is shown in Fig. 1, and indicates a cline in size from large eggs in the northwest to smaller eggs in the east.

Table I. Locations and mean egg weights of some of the collections used in egg weight analyses

Code ^a	Location ^b	Latitude	Longitude	N	E_i^c	S.E.
RED	Redstone R., N.W.T.	64.3	124.5	47	.219	.003
FIM	Ft. Simpson, N.W.T.	61.8	121.3	29	.213	.004
BUF	Little Buffalo Falls, N.W.T.	60.0	112.8	20	.202	.005
CHN	Chinchaga R., Alta.	58.7	118.7	15	.198	.005
MCM	Fort McMurray, Alta.	56.7	110.4	19	.212	.004
BES	Besnard L., Sask.	55.5	106.0	49	.191	.003
CRA	Cranberry Ptg., Man.	54.4	101.5	132	.182	.001
15-535	Burchell L., Ont.	48.2	93.0	215	.164	.001
16-535	Manitouwadge, Ont.	48.2	87.0	34	.168	.003
17-535	Chapleau, Ont.	48.2	81.0	335	.165	.001
17-515	Thessalon, Ont.	46.5	81.0	790	.167	.001
17-485	Barrie, Ont.	43.7	81.0	135	.157	.002
18-505	Renfrew, Ont.	45.5	77.0	647	.164	.001
20-515	Bantalor, N.B.	46.5	66.0	295	.163	.001
20-505	Geary, N.B.	45.5	66.0	136	.159	.001

^aName or UTM grid identifier (zone + midpoint of north/south grid location).

^bGeneral location or nearest post office.

^cMean based on 1965, 1966, 1967 collections, weights in mg.

Table II. Regression analyses of egg weight in relation to latitude and other variables

No.	Y	X	Line	R ²	t	% variance due to variable
1 ^a	E_i	1 lat. 2 long. 3 alt.	$Y = 0.0330 + 0.0024X_1 + 0.0003X_2 - 0.0007X_3$	91.4	4.24 ^c 1.34 -0.35	90.7 0.7 0.05
2 ^a	E_i	lat.	$Y = 0.0207 + 0.0031X$	90.7	14.98 ^c	-
3 ^b	E_i	lat.	$Y = 0.0261 + 0.0029X$	80.6	10.97 ^c	-
4 ^b	Pup. wt.	lat.	$Y = 102 - 0.257X$	1.2	-0.60	-
5 ^b	E_i	1 lat. 2 pup. wt.	$Y = -0.0026 + 0.0030X_1 + 0.0003X_2$	84.6	12.32 ^c 2.70 ^d	80.6 4.0
6 ^b	Fec.	1 pup. wt. 2 lat. 3 E_i	$Y = 121.0 + 2.21X_1 - 5.15X_2 + 539.0X_3$	84.2	7.93 ^c -3.52 ^c 1.20	61.5 21.9 0.8
7 ^b	Eggs/mg	lat.	$Y = 3.84 - 0.0428X$	59.9	-6.58 ^c	-
8 ^b	Slope ^e	lat.	$Y = 5.19 - 0.0540X$	23.7	3.00 ^c	-
9 ^b	Mass of eggs ^f	lat.	$Y = 44.0 - 0.316X$	8.5	-1.64	-

^aPooled data 1965, 1966, 1967.

^b1967 data, all weights in mg.

^ct values significant at $P = .01$.

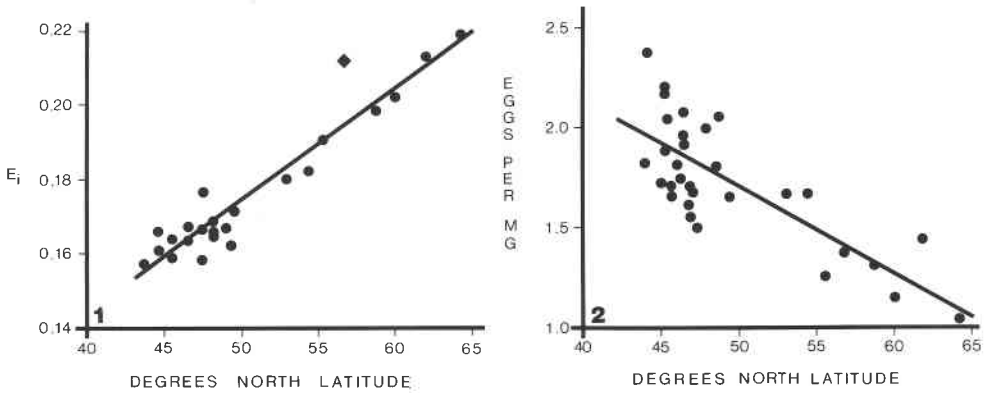
^dt significant at $P = .0168$.

^eSlope of regression of fecundity on pupal weight.

^fMass of eggs = $E_i \times$ fecundity.

Only one value in the regression of E_i on latitude (Fig. 1) deviated widely from the regression. This unexpectedly high E_i value originated from Fort McMurray, Alberta, and by itself deserves no special comment. However, a similar unexpectedly high value was obtained from the first laboratory generation of insects collected from the Cypress Hills, Alberta (lat. 49.6°N; long. 110°W) which had an E_i of $0.198 \pm .015$. The divergence of these two values suggests that, in addition to latitude, some other factors may be operating to control egg weights in this part of the range of *C. fumiferana*, where it is closest to sibling species of *Choristoneura*.

This cline in egg size could possibly be expressed in other stages of the insects besides the eggs. To explore this possibility further, analyses were conducted on the 1967 data



FIGS. 1-2. 1, the relationship between mean weight of initial eggs (E_i) and degrees north latitude. Points represent collection means (solid square: Fort McMurray, Alta. see text). Pooled data from 1965, 1966 and 1967. 2, the relationship between number of eggs per milligram of pupal weight and latitude. Points represent collection means. Data from 1967.

using collection mean values. Variation in mean E_i was found to be strongly related to latitude in these collections (line 3, Table II), as was found with the full data set. Mean female pupal weights showed no significant trend related to latitude (line 4, Table II), so differences in mature body weights cannot explain the trend in E_i , and, indeed, variation in mean E_i was only weakly related to mean pupal weight (line 5, Table II). As pupal weights showed no consistent change related to location, then to compensate for different egg weights there must be differences in mean fecundities, as confirmed in Table II (line 6).

The interrelationship between latitude, fecundity, and pupal weight may be expressed in other ways. The regression on latitude of the ratio of mean fecundity to mean pupal weight (number of eggs per mg pupal weight) was highly significant (line 7, Table II; $R^2 = 60$), higher values of eggs per mg occurring at lower latitudes (Fig. 2). Similarly, the regression on latitude of the slopes of fecundity/pupal weight regressions (calculated at each location from individual values) was significant (line 8, Table II). The slope of this regression was also negative but its low R^2 suggests that much of the variation in slope between collections is attributable to other factors.

In summary, both mean E_i and mean fecundity varied in relation to the latitude of the collection location, but in opposite directions. The product of these two variables, called 'mass of eggs' was no longer affected by latitude (line 9, Table II). Other expressions of insect size, such as pupal weight, showed no change related to latitude. The effects of these differences on egg size and fecundity and their significance are readily demonstrated. For example, a female moth collected from Fort Simpson, N.W.T. whose pupal weight was 100 mg produced 147 eggs with a mean weight of 0.213 mg; a similar moth from Essa Twp., Ontario produced 252 eggs with a mean weight of 0.166 mg. There is no evidence of other changes in insect size over the same range of latitudes and we can conclude that, at high latitudes, egg numbers are reduced to compensate for increased egg size without other obvious changes in larval or adult size.

Variation in E_i within geographic region. In the above analyses only a weak relationship was found between collection mean values for female pupal weights and the E_i of the eggs produced. For further analysis, the data in Fig. 1 were divided into three groups based on region of origin. The largest group which includes all those locations east of the Manitoba

border had low E_i values. Two collections from Manitoba had intermediate E_i values. The remaining six collections from farther north and west had the highest E_i values. Within the eastern group there was a significant positive relationship between mean E_i and mean pupal weight: $E_i = 0.128 + 0.000371 \text{ P.WT.}$ ($R^2 = 54.5\%$; $F = 25.2$, $P < 0.01$). The northwestern group also showed this relationship: $E_i = 0.176 + 0.000325 \text{ P.WT.}$, although the regression was not statistically significant ($R^2 = 55.8\%$, $F = 5.05$ n.s., d.f. 4). These results show that within limited geographic areas there is a direct relationship, albeit a weak one, between mature insect size and mean weight of the initial eggs produced. This same relationship has been found in analyses of pupal weights and E_i values of individuals from first laboratory generations and other laboratory stocks feeding on foliage and on artificial diet (Harvey 1974). In four separate analyses the regressions were significant and the amount of variation in E_i that related to that in pupal weight varied from 4% to 19% as shown by R^2 values. In the study of populations across a broad geographic range this relationship is obscured by the stronger effect of latitude on E_i .

Discussion

Egg weights range from the lightest in the southeast to the heaviest in the northwest. This geographical cline is strongly related to the latitude and longitude of the collection location. These differences in mean egg weight are not attributable to differences in size of the insects producing them as there is no corresponding trend in mature body weight over the same range of locations.

Comparisons of size or weight and fecundities among budworm populations are complicated by large intrapopulation variation. Since fecundity, however, is directly related to pupal size (Miller 1957; Thomas 1978) and to pupal weight (Campbell 1962), the use of slopes of fecundity/pupal size or pupal weight regressions overcomes some of the difficulties in comparisons between populations. Neither Campbell (1962) nor Thomas (1978) found interpopulation differences in fecundity/pupal size regressions but in both cases the latitudinal differences among the populations were small. Differences in slopes of fecundity/pupal size regressions were, however, reported between 'starved' and normal populations (Miller 1963). The present report documents a significant trend in slopes of fecundity/pupal weight regressions from populations across Canada that is related to latitude and is explained by differences in egg weight. The difference between 'starved' and normal populations reported by Miller (1963) may also be explained by differences in mean egg weight, for laboratory studies show that mean egg weights can be reduced by severely impoverished diets (Harvey 1983).

The existence of a relationship between mean egg weight and latitude suggests that insects from heavier eggs have a better chance of survival at higher latitudes, where winters are longer, presumably because they contain greater food reserves. Capinera *et al.* (1977) found that, in the gypsy moth, larger eggs have greater yolk reserves than small eggs. Budworm larvae hatch in late summer, having ingested all the yolk available in the egg (Stairs 1960). This yolk fills the gut of the newly hatched larva but is completely digested by the time of the moult to the second instar that precedes diapause (Harvey 1957). On these food reserves and without any feeding these small larvae must maintain essential body functions through the unfavorable weather until they are able to start feeding the following spring. Although yolk materials *per se* are no longer identifiable in the overwintering spruce budworm larva, larvae from heavier eggs may indeed contain greater metabolic reserves than larvae from smaller eggs, and may owe their better survival to those greater reserves. In the gypsy moth, differences in egg size can be induced by hunger, crowding or cool temperature (Leonard 1970), and result in differences during the development of the progeny, best characterized by differences in instar numbers (Leonard 1970). There is no evidence of similar effects in the spruce budworm; the only demonstrable effect of differences in egg size is related to survival during prolonged storage

(Harvey unpublished). Larvae surviving storage appear to have equal chances of developing to maturity.

The demonstration of different egg weights and different fecundity/pupal weight relationships across the range of spruce budworm has several implications for the population dynamics of this insect. The differences in egg weights undoubtedly point to different limits of time and temperature for survival of overwintering larvae. The cline in eggs per mg pupal weight also points to a greater metabolic cost of oviposition at higher latitudes. The 100 mg moth at Fort Simpson laid 147 eggs, thus utilizing 0.68 mg of body weight per egg produced, while the Ontario moth laid 252 eggs or 0.40 mg per egg. If survival of the resulting larvae in these two locations is similar, then the potential rate of population increase at the high latitude is probably no more than 59% of that at the lower latitude. This increase of the energy commitment to each individual balanced by a reduction in the potential rate of population increase appears to conform to the balanced mortality hypothesis discussed by Price (1974); however, in this example the adaptation is demonstrated over the range of a single species. Such evidence of differential ecology in different parts of the range of the spruce budworm should not be disregarded when one is building general theories of population dynamics.

Acknowledgments

Collections of spruce budworm were provided by members of the Forest Insect and Disease Survey across eastern Canada. I wish to thank them for their assistance and other members of the Centre for critical review of the manuscript. I am indebted to P. M. Roden for technical assistance.

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(Received 8 June 1982; accepted 13 January 1983).