

both the prey and the predator. At a temperature of 72°F. and a relative humidity of 80 per cent, development of the male and of the female was completed in nine and ten days respectively on a diet of prey larvae; these periods lasted eleven and fifteen days respectively when the mites fed upon eggs of the prey. Only the mated females laid eggs, and oviposition began from three to five days after mating. Usually eggs were laid singly at intervals of two or three days, and longevity of the females averaged about seven weeks. The predator cannot develop or reproduce in the absence of prey but will probably survive for a longer period if mould is available than in the absence of any food.

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The Interaction of the Spruce Budworm, *Choristoneura fumiferana* (Clem.), and the Parasite *Glypta fumiferanae* (Vier.)¹

By C. A. MILLER²

This is the second of a series of papers (Miller, 1959) describing the interaction of primary parasites and the spruce budworm, *Choristoneura fumiferana* (Clem.), based on data collected during an outbreak of the budworm in northern New Brunswick during the period 1947-1958. The first paper showed that the interaction between the spruce budworm and *Apanteles fumiferanae* Vier. is adequately described by the general mathematical model developed by Watt (1959). The data on the parasite *Glypta fumiferanae* (Vier.) to be presented in this paper are also analysed by means of Watt's model and consequently the method is essentially the same. There is, however, one important difference. In the case of *A. fumiferanae*, the estimated number of adult parasites was only an index based on the potential number emerging from the previous host generation. The observed density of *G. fumiferanae* is a more realistic estimate. It is based on the actual number of cocoons found on the foliage during the adult emergence period.

The study of the role of parasites in a spruce budworm outbreak is part of a long-term project, called the Green River Project, which was set up in 1945 to

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investigate the population dynamics of the budworm (see Morris *et al.*, 1958). The study area is located on the Green River Watershed in northwestern New Brunswick. A description of the permanent study plots and the annual population density of first-instar larvae on each has been presented (Miller, 1959, Table I). The *G. fumiferanae* analysis is based on data collected on these plots with the exception of Plot K1-S and N1 for which detailed cumulative defoliation records pertinent to the present analysis are lacking.

Life-History of *Glypta fumiferanae* (Vier.)

G. fumiferanae is a common parasite of the spruce budworm in eastern and western North America (Wilkes *et al.*, 1948; Dowden *et al.*, 1948). A description of the adult and immature stages is given by Brown (1946). In the Green River area it may be considered a specific univoltine parasite since it has not been recorded from other hosts. Its synchronization with the life-history of the budworm is as follows:

Time	Budworm	<i>G. fumiferanae</i>
Late July to early August	Egg	Adult
Early August	First instar	
Mid-August	First and second instar in hibernaculum	Egg
Late August to mid-May	Second instar in hibernaculum	First instar
Early June	Third instar	First instar
Late June to early July	Sixth instar	Maturing larva
Mid-July to late July	Pupa and adult	Cocoon

Observations on caged adults indicate that *G. fumiferanae* attacks first- and second-instar larvae in hibernacula. Female longevity is approximately 30 days in cages. The parasite overwinters as a first-instar larva and emerges from either fifth- or sixth-instar hosts. Oviposition experiments using both small glass containers and caged trees in the field were not successful in indicating reproductive potential. The maximum number of attacks per female was 143, but this figure is not considered a reliable estimate since the failure of a number of females to oviposit suggests that nutrition or the environment was sub-optimal. In both series of experiments the adults were fed on an aqueous honey solution.

Estimation of Number of Hosts Attacked and Parasite Density

Number of Hosts Attacked.—The number of hosts attacked is the product of second-instar host density and the proportion of hosts parasitized. The second-instar host density is an estimate based on egg counts (less egg mortality) assuming that the fall dispersal loss of larvae from eclosion to the spinning of hibernacula is approximately 64 per cent. This estimated population figure is used because actual counts of second-instar larvae in hibernacula are lacking for many plots, although a reliable sampling technique has been subsequently devised for this stage (Miller, 1958). In any case, the analysis of fall dispersal loss on a number of plots in different years (Miller, 1958) indicates that it is relatively constant (in contrast to spring dispersal loss) and the use of a mean estimate of 64 per cent therefore does not introduce a significant variable in assessing the number of hosts attacked.

Estimates of per cent parasitism by *G. fumiferanae* were obtained by two methods owing to the protracted period during which the parasite is present in the host, and also to the particular methods used in studying the parasite complex of the budworm. Thus, in most instances early-stage larvae were dissected and

TABLE I
Variation in Per Cent Parasitism Based
on Two Sampling Methods and Also on Periodic Collections, 1954

Plot	No. of larvae		Per cent parasitism		Seasonal variation in parasitism (Diss.) ¹			
	Reared	Dissected	Rearings	Dissections	Early June	Mid-June	Late June	Early July
G2	181	295	5.0	9.2		-4.2	+3.2	-0.7
G4	291	315	16.8	14.0		+2.7	-0.1	-4.0
G5	191	350	8.4	11.4	-3.4	+0.7		+1.9
G6	111	300	9.9	8.7	+0.5	-0.9		+0.1
G8	340	300	12.6	10.3		-2.3		+2.4
K2	304	510	8.9	6.5	-1.3		+0.5	+3.5

¹Deviations from mean per cent parasitism calculated from the total number of larvae dissected.

ultimate-instar larvae were reared. Both techniques yield reliable estimates of parasitism as shown in Table I and, in practice, both results are combined to give a single estimate. Tables I and II also show that no consistent deviations exist in per cent parasitism based on periodic collections ranging from second- to sixth-instar larvae. Deviations in estimates of parasitism based on second- and third-instar collections that may have resulted from the dispersal of second-instar larvae (Miller, 1958) did not occur because *G. fumiferanae*, unlike *A. fumiferanae*, shows no differential degree of attack within tree crowns. Dissection of second-instar larvae collected from five trees showed means of 10 per cent parasitism in the top half and 11 per cent in the bottom half of the crowns.

Adult Parasite Density.—The density of *G. fumiferanae* is based on cocoon counts obtained from the same foliage samples that are used for estimating the population of spruce budworm pupae. This ensured a representative sample per plot (Morris, 1955). At low host densities, however, cocoons are scarce and

TABLE II
Comparison of Per Cent Parasitism Based
on Second- and Third-Instar Host Collections

Plot	Instar	Larvae examined	Per Cent parasitism
K2	II	109	0
	III	331	0.6
K1	II	156	0.6
	III	177	2.3
K2	II	170	2.4
	III	332	2.1
G12	II	610	2.5
	III	147	4.1
K2	II	620	3.2
	III	200	0.5
K3	II	540	3.7
	III	200	4.0

zero counts may occur in the sample. The following technique was devised to correct for zero counts. The correction is based on the hypothesis that cocoon counts (P_c) are a function of the estimated number of cocoons (P_e) that should occur in a population where host density and proportion of hosts parasitized are known. An analysis of 44 sets of data showed that P_c is a linear function of P_e and that the mean ratio of $P_e/P_c = 2.82 \pm .28$. In the following analysis this ratio was used to obtain calculated P_c values in five cases where zero counts were obtained from foliage samples, and in two cases where no foliage samples were collected on the plot. The standard error of P_e/P_c also indicates that in an analysis of host-parasite interaction, an index of adult parasite density based on host density and the proportion of hosts parasitized in the previous generation may often be reliable when practical difficulties exclude cocoon or actual adult counts.

No precise estimates of cocoon mortality were obtained during this study. One hyperparasite, *Mesochorus sylvarum* Curtis, was recorded on a few occasions.

Analysis

The development of the mathematical model used in the following analysis is discussed in detail by Watt (1959), and its application to field data by Miller (1959). The reader is referred to these papers for a more detailed account of the development of the model and its application.

Definition of symbols:

- N_A = number of hosts attacked
- N_o = number of hosts vulnerable to attack
- P = number of parasites searching
- A = coefficient of attack, or the number of hosts attacked per parasite and considered an instantaneous rate
- K = maximum number of attacks that can be made per parasite when the hosts are vulnerable
- C = cumulative defoliation
- a and b = positive constants

The number of hosts attacked expressed in terms of the number of parasites searching and host density is given by the following equation:

$$N_A = PK(1 - e^{-aN_oP^{1-b}}) \dots \dots \dots (1)$$

Relationship of N_A to N_o .—Fig. 1 shows the relationship of the number of hosts attacked to host density for three mean parasite densities. The curves are similar to those plotted for *A. fumiferanae* (Miller, 1959) and show that N_A increases at a diminishing rate with an increasing N_o . Holling (1959) also shows similar functional response curves for a wide variety of host-parasite data.

Estimation of K .—The maximum number of attacks capable per parasite (K) is obtained from the following transformation of equation (1):

$$\ln \left(\frac{PK}{PK - N_A} \right) = AN_o \dots \dots \dots (2)$$

where P , and consequently aP^{1-b} , are held constant. Approximate estimates of K were first obtained graphically and subsequently refined by choosing that value of K which maximizes the correlation coefficient. Table III shows correlation coefficients for the accepted values at three mean parasite densities. K was assumed to equal 70 from these data. This represents, in theory, a reproductive

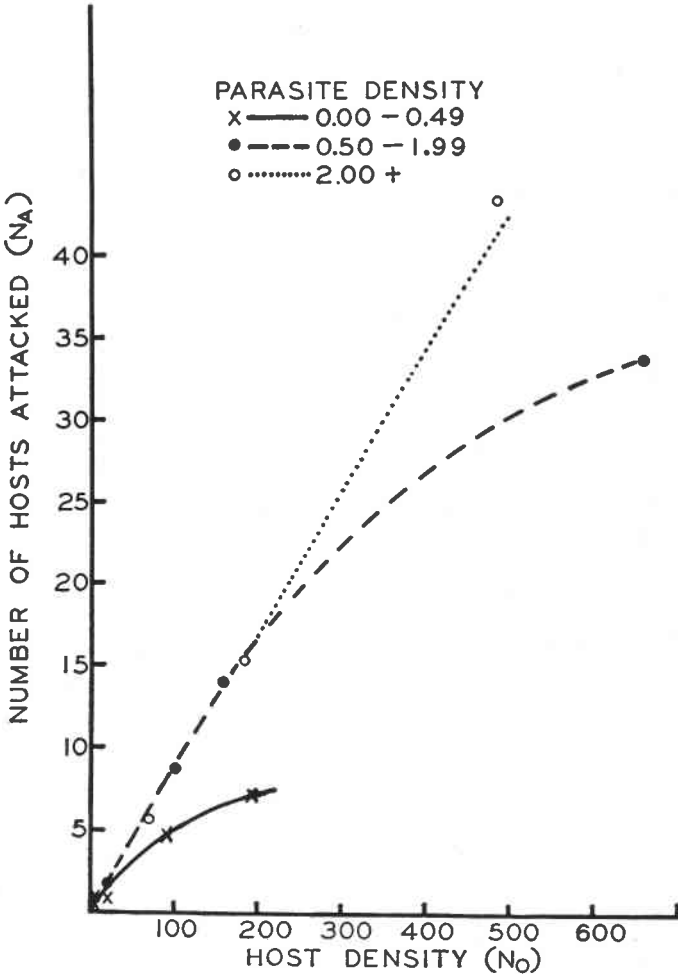


Fig. 1. The relationship of hosts attacked to host density for three densities of *G. fumiferanae*. Plotted points represent group means.

rate of 140 eggs per female (sex ratio 1:1) and approximates the apparent reproductive rate found in oviposition experiments.

Estimation of the Constants a and b.—These constants are obtained from the following transformation of equation (1):

$$\ln \left[\frac{\ln \left(\frac{PK}{PK - N_A} \right)}{N_0 P} \right] = \ln a - b \ln P \dots \dots \dots (3)$$

with $K = 70$, this regression analysis yielded a correlation coefficient of $-.978$ (Fig. 2) and the following values for a and b :

$$a = .00094$$

$$b = 1.8095$$

Substitution of the above values for K , a , and b , in equation (1) gives the appropriate equation for estimating the number of host attacked.

$$N_{Ac} = 70P(1 - e^{-.00094N_0P^{-1.8095}}) \dots \dots \dots (4)$$

TABLE III
Estimated K Values at Three Parasite Densities

Mean parasite density	0.16	1.06	4.30
N	19	17	15
K	60	70	70
r	.64	.76	.88

The Effect of Other Factors on N_A

A preliminary plotting of the calculated over the observed values of N_A indicated that N_{A_c} was overestimated on these plots where severe defoliation either caused a marked thinning of the foliage on living trees or ultimately resulted in tree mortality. It was first determined that the deviations in N_{A_c} could not be explained by the relationship of either N_o or P to defoliation and then deduced that the attack efficiency of the parasite is apparently lowered in severely defoliated stands, either because defoliated trees are less attractive to the parasite, or defoliation increases crown exposure to light, which, in turn, affects parasite behaviour. The fact that *G. fumiferanae*, unlike other budworm parasites (Miller, 1953, 1959), does not attack a greater proportion of hosts in the top half of tree crowns may indicate a preference for the more shaded portions of the crown and adds weight to the latter assumption.

Although the causal relationships are not clearly understood, *a* was assumed to be a function of defoliation. The term defoliation as used herein does not refer to current defoliation, but is defined as the yearly accumulation of current defoliation estimates. It is, therefore, an index of the total defoliation history of the stand.

$$a = f(C) \dots \dots \dots (5)$$

substituting (5) in (1) gives

$$\frac{\ln\left(\frac{PK}{PK - N_A}\right)}{N_o P^{1-b}} = f(C) \dots \dots \dots (6)$$

This regression was first tested graphically using cumulative defoliation and the natural logarithm of cumulative defoliation. The latter gave the line of best fit (Fig. 3).

The equation of this line, with a correlation coefficient of — .94 based on class means, is

$$\frac{\ln\left(\frac{70P}{70P - N_A}\right)}{N_o P^{-.8095}} \times 10^4 = 31.28 - 4.374 \ln C \dots \dots \dots (7)$$

$$\text{or } a = .0031 - .00044 \ln C \dots \dots \dots (8)$$

Substitution of (8) in (4) gives the modified equation for estimating the number of hosts attacked.

$$N_{A_c} = 70P[1 - e^{-(.0031 - .00044 \ln C) N_o P^{-.8095}}] \dots \dots \dots (9)$$

The calculated number of hosts attacked by *G. fumiferanae* was obtained from equation (9). A comparison of observed and calculated values by means

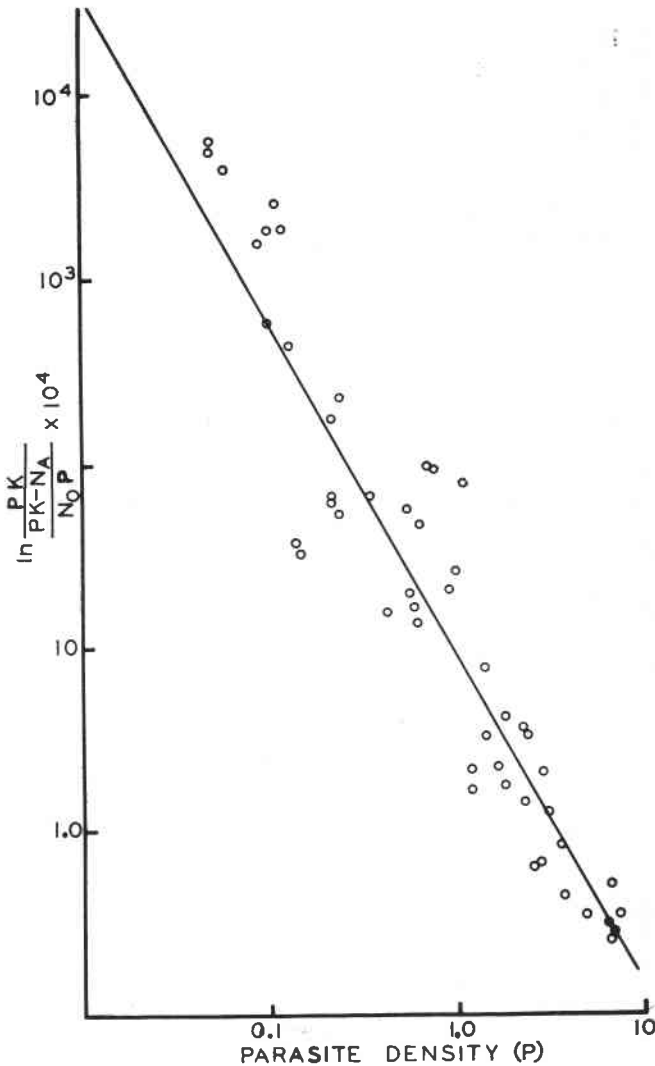


Fig. 2. Test of equation 3 to evaluate searching by *G. fumiferanae* for second-instar budworm. See text for definition of symbols.

of a regression analysis showed that the equation explained 78 per cent of the variation in N_A , which is an increase of 5 per cent over that explained by equation (4). This compares favourably with the results for *A. fumiferanae* where the model explained 71 per cent of the variation in N_A .

Attempts to find other factors that may have had a significant effect on the number of hosts attacked were carried out graphically by plotting the ratio of N_{A_0}/N_{A_c} over values of these factors. Particular attention was paid to weather including cloud cover, precipitation, and temperature. Mean annual estimates of these factors for the period when *G. fumiferanae* were active showed no significant relationship. An analysis of precipitation did indicate that in years of heavy precipitation, particularly 1954, the calculated number of hosts attacked was higher than observed values, suggesting that heavy precipitation hinders parasite attack. However, since only eight values for rainfall were available, and seven of these had a narrow range, it was not possible to show significant effects.

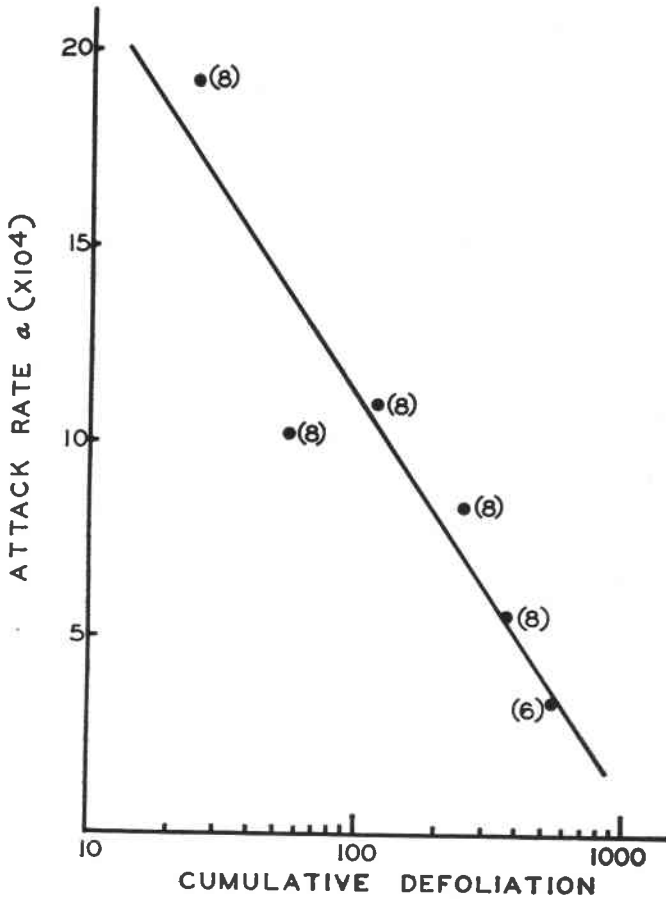


Fig. 3. Graph showing the effect of cumulative defoliation on the attack rate of *G. fumiferanae*.

Stand factors including the number of trees per acre, average diameter at breast height, and density were also investigated but none showed a relationship to N_A .

Discussion

The presentation of two equations that mimic the interactions of the spruce budworm and the parasites, *A. fumiferanae* (Miller, 1959) and *G. fumiferanae*, provides an opportunity to evaluate the practical aspects of the results obtained from this type of mathematical analysis. An important contribution is that the numerical values of the parameters in the equation will provide hypotheses for further research into the precise meaning of these parameters in terms of parasite behaviour. A more immediate result, although somewhat unexpected, is that both equations show a decrease in parasite efficiency in a severe infestation. Two dissimilar trends in budworm density occurred on the permanent study plots in the area. In one group, a severe infestation resulted in varying degrees of tree mortality, while on the remaining plots, which were partially isolated by cutting operations, the infestation only reached an intermediate level with little or no effect on the host tree. Both infestations declined to the endemic level at about the same time. Data from these two groups of plots showed that the number of hosts attacked by both *A. fumiferanae* and *G. fumiferanae* was less than expected on plots within the severe infestation area.

No direct cause and effect relationship was found to explain the decrease in parasite efficiency. In the case of *A. fumiferanae*, the decrease was related indirectly to parasite survival (Miller, 1959), while the present analysis shows that defoliation is related to the attack rate of *G. fumiferanae*. In order to show how the latter could affect the trend in host density, a hypothetical example showing the interaction between the spruce budworm and *G. fumiferanae* has been calculated from equation (1).

$$N_A = PK(1 - e^{-aN_0P^{1-b}})$$

Estimates of N_0 and P for successive generations were obtained by substitution of the following values:

$$\left. \begin{array}{l} N_0 = 10 \\ P = .35 \\ K = 70 \end{array} \right\} \text{ (First generation values taken from field data.)}$$

$$a = .0031 \text{ (Value of } a \text{ in the absence of defoliation from equation (8).)}$$

$$b = 1.8095$$

F = rate of increase of the budworm = 3. (This represents the effective rate of increase from year to year in the absence of moth invasion.)

D = rate of increase of the parasite. It was assumed that no mortality factor acted on the parasite. Thus, the number of hosts attacked in one generation (N_A) equals the parasite density P of the following generation. In practice, field data indicate an average survival of *G. fumiferanae* from egg to cocoon of 16 per cent.

The calculations showed a sharp increase in N_0 followed by a similar trend in P . A peak density was reached in the ninth generation and, at a level of approximately 65 per cent parasitism, N_0 began to oscillate about a mean density as shown in Fig. 4B. The effect of defoliation on the attack rate of *G. fumiferanae* may be seen by comparing Figs. 4A and 4B, where both trends in N_0 start from an initial population of 516. In Fig. 4A, where it is assumed that 100 per cent current defoliation occurs in successive years, N_0 increases 15-fold over the next three generations, while Fig. 4B shows N_0 oscillating about a mean density of 545 in the absence of defoliation. This example is clearly exaggerated because of a very high parasite density but it does serve to illustrate how *G. fumiferanae* would fail to regulate a rapidly rising budworm population which reaches a level causing severe defoliation.

Fig. 4B is of further interest since it shows that Watt's (1959) general model can generate a predator-prey interaction with regular oscillations rather than oscillations of increasing amplitude as predicted by Nicholson's theory (1933). Varley and Gradwell (1958) and Voûte (1958), in a discussion of host-parasite relationships on the basis of the Nicholson theory, show the necessity for a density-related factor to damp oscillations in order to "eliminate the contradiction between the Nicholson theory and observations in nature" (Voûte, 1958). However, as pointed out by Watt (1959), the Nicholson and Bailey model does not provide for a limited attack rate, which is evident in most functional response curves for parasites (Holling, 1959). This question, although of fundamental importance in many studies of population regulation, still awaits a critical analysis. Recent experimental evidence on the nature and form of oscillations in a host-parasite interaction (Utida, 1957; Burnett, 1958) shows conflicting results that are confounded by the time and spatial arrangements of the experimental universe and by changes in the "properties" of host and parasite themselves that arise from methods of propagation (Burnett, 1958).

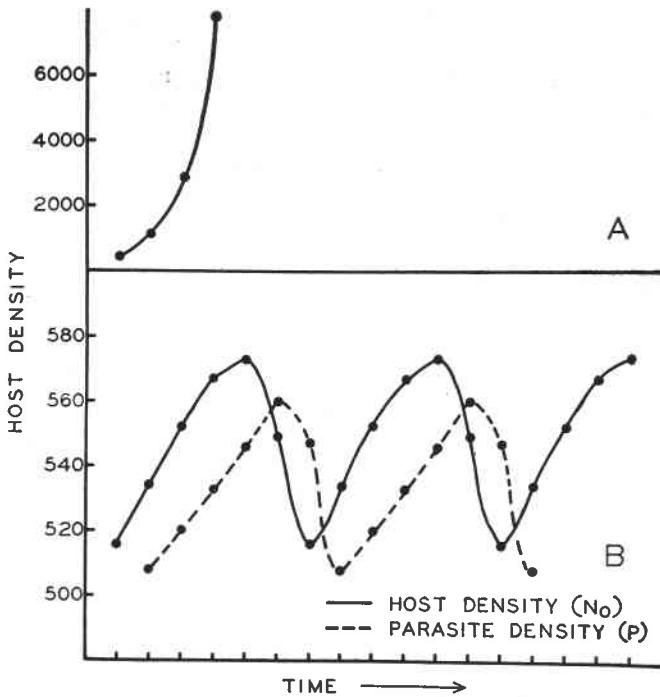


Fig. 4. Two hypothetical budworm population trends, as derived from equations (1) and (9). See text. A. Rapidly rising host population when defoliation causes a reduction in the attack rate of *G. fumiferanae*. B. Regular oscillations of host and parasite in the absence of a defoliation effect on the attack rate of *G. fumiferanae*.

The presentation of Watt's general model (1959) has been followed by an equation describing predator-prey interaction published by Holling (1959). The two models were developed in quite different ways and with basically different objectives. Watt's model is based on a set of reasonable biological assumptions regarding the action of predator and prey at varying densities and has been tested with both experimental and field data. Holling's equation is based on those parts of the functional response, searching, and 'handling' of hosts that are present whenever a predator attacks. These parameters were independently measured in a series of artificial experiments and incorporated into a basic functional response equation. Holling (1959) contrasts the applicability of the two models by comparing the variance explained by each for a series of published data on host-parasite interaction. His equation gave a better fit for nine of 13 comparisons. However, both authors³ agree that the two models may be considered incorrect in the sense that they are incomplete. Holling's equation probably overestimates N_A as N_A approaches PK. This can be noted in his analysis (1959, Table III, and Figs. 4-6) which invariably shows that his equation gives a better fit where the last point (observed number of hosts attacked) is above the line, and Watt's equation works best where the last point falls below the line. It is evident therefore that a combination of the two models might be needed to give a good fit over a wide range of values.

Table IV shows an analysis of the field data for *G. fumiferanae* based on mean values of N_0 and N_A in order to compare the two models. The data were

³Holling (1959): Dr. Watt, personal communication.

TABLE IV
Comparison of Descriptive Values of
Holling and Watt Models, Based on Mean Values of N_0 and N_A for *G. fumiferanae*

P	N_A	Holling	Watt ¹	Sums of squares of deviations		Holling's equation
		N_{Ac}	N_{Ac}	(1)	(2)	
		(1)	(2)			
0.16	.07	.18	.18	2.51	3.34	$N_A = .0457 N_0$
	.58	.37	.37			
	.77	.78	.78			
	4.84	4.16	3.52			
	7.41	8.82	6.17			
1.06	1.71	1.96	1.45	7.42	24.1	$N_A = \frac{.0912 N_0}{1 + .00103 N_0}$
	8.87	8.35	6.13			
	14.0	12.5	9.96			
	33.6	35.8	33.2			
4.32	5.6	5.5	5.9	38.2	17.0	$N_A = .0770 N_0$
	15.4	14.4	15.7			
	43.4	37.3	39.3			

¹Equation (4).

also sub-divided on the basis of P since Holling's equation does not provide for a variable P. The Table shows that Holling's equation gives a better fit to the data at two of the three parasite densities. However, at P values of 0.16 and 4.32 the 'handling' time, or b , is not significantly different from zero and the equation is reduced to a straight line which states that the number of hosts attacked increases linearly with N_0 :

$$N_A = T_t a N_0$$

where, T_t = total time that hosts are vulnerable to attack

a = a constant termed the instantaneous rate of discovery.

A further example of a host-parasite interaction where the 'handling' time is not significantly different from zero is contained in data cited by Burnett (1958), where 20 *Encarsia formosa* Gahan searched for a varying number of hosts equally distributed over a 25-square-inch plane during an 18-hour period. Burnett states that "the percentage of hosts parasitized . . . was approximately equal". Under these conditions Holling's equation becomes a straight line. Although a straight line fully describes the experimental results for *E. formosa* and part of the field data for *G. fumiferanae*, it fails to predict the expected trend in either host-parasite interaction. In both cases N_A would approach an upper asymptote rather than increase linearly with N_0 . For example, Burnett (1958) states that the fecundity of *E. formosa* probably lies between four and eight eggs per female and, with $P = 20$, N_A would approach an upper asymptote at values ranging between 80 and 160.

Watt's model, as well as giving a good fit to the *E. formosa* data, also predicts that N would approach an upper asymptote. The transformation equation (2) gives a PK value of 120. Thus, since $P = 20$, $K = 6$. The computed value of K therefore approximates the biological value and, in this instance, does not warrant the criticisms cited by Holling (1959).

Conclusions

The analysis of field data obtained during an outbreak of the spruce budworm in northwestern New Brunswick shows that the effect of the primary parasite, *G. fumiferanae*, is described by Watt's (1959) model of predator-prey interaction and adds further support to its general application in describing field data (Miller, 1959). The refined model for *G. fumiferanae* contains a modification to express the effect of defoliation on the attack coefficient. The analysis also suggests that extremes in weather conditions may lessen the attack efficiency of the parasite.

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