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

By C. A. Miller[2]

Introduction

In the late 1940's significant increases in the population of the spruce budworm, *Choristoneura fumiferana* (Clem.), occurred in northern New Brunswick and culminated in a severe outbreak of this major forest pest. The outbreak has been the subject of intensive investigations dealing with emergency chemical control operations (Webb, 1956) and with a long-term study of the population dynamics of the budworm. The latter program, called the Green River Project, is located on the Green River Watershed in northwestern New Brunswick. Its objectives, the co-operating agencies involved, the mortality factors being studied, and methodology have been discussed elsewhere by Morris *et al.* (1956), Morris (1951), Morris and Miller (1954), and Morris (1955).

One of the primary aims in the analysis of the data obtained on natural mortality factors in the Green River area is the development of a mathematical model of budworm survival, which, ideally, will contain a number of structural sub-models mimicking the effect of individual mortality factors on the budworm. This paper deals with the analysis of field data on the interaction of the parasite *Apanteles fumiferanae* and the budworm by means of a structural model. The model was developed and fully described by Watt (1959).

A. fumiferanae is treated here only as a mortality factor and not as a potential regulator of budworm density. Further, the data presented date from 1950 and the budworm was already increasing rapidly in the study area by that time. Results and conclusions are therefore based on outbreak conditions and may require some modification if applied to endemic populations. For example, limited data indicate that, whereas *A. fumiferanae* is a common parasite during an outbreak, it is relatively scarce during the endemic period. A major shift in the parasite complex of the budworm may occur between these two periods since the degree of attack by parasites such as *Horogenes cacoeciae* (Vier.) and *Exochus* sp. that are common during the endemic period is apparently inversely related to major changes in host density. No reference is made to the existing theories of host-parasite interaction since these have already been discussed by Watt (1959).

Description of Study Plots

All but one of the permanent study plots are situated on the Green River Watershed and adjacent parts of the Kedgwick and Iroquois Watersheds. The letters G, K, and I are used respectively to distinguish plots on the Watersheds as shown in Table I. Balsam fir (*Abies balsamea* (L.) Mill.) is the predominant species in the valleys and lower slopes, with white spruce (*Picea glauca* Voss) mixed with the fir in valleys, and white birch (*Betula papyrifera* Marsh.) mixed in varying proportions with the fir on all slopes. However, birch dieback killed most of the birch throughout the area before 1945. The softwood forest is typically mature, interspersed with middle-aged dense stands of balsam fir dating from the spruce budworm outbreak of 1912-1920. Table I lists the study plots

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TABLE I

Description of Study Plots, Including First-Instar Budworm Populations for the Period 1950–57

Plot	Age	Average tree diameter breast high	Total basal area per acre	Per cent of basal area fir and spruce	Number of larvae per 10 square feet of foliage							
					1950	1951	1952	1953	1954	1955	1956	1957
			(sq. ft.)									
G 2	90	6.9	87.7	88	26	16	58	295	52			
G 4	90 130[1]	8.0	94.6	95	343	169	155	472	117	40	340	16
G 5	40	3.7	130.1	96	18	5	32	130	6	34	54	
G 6	60	6.0	166.1	66					328	425	1324	s
G 8	90	9.0	109.4	90		282	511	481	70			
G 9	90	7.8	107.7	91		(2520)[2]	1980	s	258	1470	s	
G 11	40	3.5	164.5	95			(469)	362	29			
G 12	40	3.6	162.2	95			(803)	511	299	520	253	
K 1	90 130	6.8	107.3	90		(2472)	1058	685	185	420	696	43
K 1–S										(1024)	2254	182
K 2	40	3.0	78.8	95		(444)	1022	559	228	643	364	16
K 3	40	3.4	142.5	97				s	(391)	1780	s	
I 1	40	2.5	78.8	76					246	1826		
N 1	30	4.2	20.5	100							1238	486

[1]Two age classes.

s = sprayed with DDT.

[2]Data not used in analysis, since parasite density unknown in that year.

with age and stand density. Plot G2 is an example of a mature softwood stand while plot G5 is a typical balsam middle-aged stand. Two plots in Table I need further description. Plot K1-S refers not to an area, but to the scattered white spruce component on Plot K1. Balsam fir mortality has occurred on this plot and budworm populations are being followed separately on white spruce and the surviving fir. Plot N1 is a white spruce stand on Cape Breton Island, Nova Scotia, and is typical of areas where the budworm persists over a long period of time at a relatively high density (Morris, 1958).

Table I also shows the population density of first-instar larvae (egg counts less egg mortality) on the study plots for the period 1950-57. Data were obtained each year on some plots, whereas other plots were discontinued owing to cutting operations and aerial spraying, or new plots were established as the budworm spread from focal points into new areas. The counts show that on one group of plots (G2, G4, G5, G8) populations remained at a relatively low level while on a second group (especially G12, K1, K2) they were sufficiently high to cause 100 per cent current defoliation for successive years resulting, by 1958, in 78 per cent tree mortality on K1, 68 per cent on K2, and varying degrees of 'top-killing' on G12. These two groups of plots will be referred to as areas of intermediate infestation and severe infestation respectively.

Apanteles fumiferanae Vier.

A. fumiferanae is a small braconid parasite that attacks the spruce budworm throughout the range of this forest pest in Canada and the United States (Wilkes *et al.*, 1948), (Dowden *et al.*, 1948). It also attacks *Dioryctria abietella* (D. & S.) (Muesebeck *et al.*, 1951), and in the Green River area a few specimens have been reared from *Dioryctria reniculella* Grote. This latter species, like the budworm, overwinters as a small larva. Benjamin and Drooz (1954) record it as a parasite of the jack-pine budworm (*Choristoneura pinus* Free.) in Michigan. In general, however, *A. fumiferanae* may be considered a specific and univoltine parasite.

The life histories of the spruce budworm and *A. fumiferanae* in the Green River area and their synchronization are approximately as follows:

Time	*Host stage*	*Parasite stage*
Late July to early August	Egg	
Early August	First instar	Adult
Mid-August	Second instar	
Mid-August to mid-May	Second instar in hibernaculum	Egg
Early June	Third instar	First-instar larva
Mid-June	Fourth instar	Mature larva
Mid-June to early July	Fifth and Sixth instar	
Mid-July to late July	Pupa and adult	Cocoon

Brown (1946) states that "emergence of the adult parasite coincides with the hatching of budworm eggs". The adults probably feed on flowering plants and shrubs in the field since cage experiments indicate that individuals without food die shortly after emergence while those fed on an aqueous solution of honey have a mean longevity of 21 days for males and 36 days for females.

Flanders (1956) states that "the *Apanteles* egg is hydrophic and thus utilizes the embryonic membrane to obtain nourishment from the host's fluids. The

eggs are stored in an enlarged oviduct which is an adaptation permitting restraint in oviposition so essential to host selection".

McGugan (1955) cites data to show that the mature parasite larva emerges from the third-, fourth-, or fifth-instar host, with the majority emerging from the fourth instar. Emergence from the fourth-instar host is most common in the Green River area. Observations in rearing cages indicate that the mature larva migrates to a secluded site and spins a cocoon; in the field cocoons are found among needles and under bark scales. Approximately 10 to 12 days are spent in the cocoon stage.

The fecundity of *A. fumiferanae* was assessed in a series of oviposition experiments using a glass jar of one pint capacity with an open-weave cotton cover as a cage. One male and one female were placed in each cage with 150 to 450 budworm eggs, a number of balsam-fir shoots, and raisins soaked in a honey solution. The shoots provided hibernation sites for the emerging first-instar budworm larvae. Mating was observed and the female parasite was also observed attacking freely moving first-instar larvae, actively searching the shoots, and apparently attacking the first- and second-instar larvae in hibernacula.

When the female parasite died the host larvae on the balsam fir were placed in cold storage to overwinter (Miller, 1958); the larvae were forced from hibernation in the spring, and either dissected for parasite larvae or reared to obtain the parasite adults. Mortality in the rearing program was high owing to the difficulties in handling second-instar larvae. The results of 10 oviposition experiments were analysed on the basis of the number of parasitized second-instar hosts emerging from hibernacula in the spring. The data showed a mean parasite fecundity of 102 eggs, ranging from 38 to 192, assuming that the degree of attack was equal among dead and living hosts.

Table II shows the distribution of parasite larvae among attacked hosts in five oviposition experiments. Superparasitism occurred only in one experiment, indicating that the female shows a degree of discrimination even in a confined environment.

It is impossible to draw conclusions on the searching and oviposition behaviour of *A. fumiferanae* from field studies directed primarily toward population ecology of the host, but tentative conclusions may be drawn from data on host density and the degree of parasite attack. Table III shows rank-correlation coefficients between the degree of *A. fumiferanae* attack and second-

TABLE II

Summary of *A. fumiferanae* Oviposition Experiments

Experiment	Host population provided	Hosts examined for parasites	Frequency of parasites within hosts				
			0	1	2	3	4
1	244	80	56	24			
2	277	219	189	30			
3	217	60	33	27			
4	383	100	70	30			
5	285	190	77	105	5	2	1

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TABLE III

Rank Correlation Coefficients between Degree of *A. fumiferanae* Attack and Host Density on Individual Trees

Plot	Year	No. of trees sampled	Host population range per 10 sq. ft.	tK[1]	P
G12	1956	5	92–227	.80	.04
K2	1956	5	101–473	.60	.12
I2	1956	5	147–260	.00	.60
K3	1956	5	382–869	−.40	.76
13–B	1956	10	206–437	−.42	.95

[1]Kendall's tau statistic.

instar host density on individual fir trees. On only one plot in five (G12) is there a significant correlation. However, it must be noted that only a small number of trees was sampled and also that some of the hosts were probably subject to inter-tree dispersal after attack (Miller, 1958). A similar study was carried out in three plots in 1958 where population densities ranged from one to 20 larvae per 10 square feet of foliage. Results were inconclusive owing to the small number of larvae collected per tree, but again did not suggest a relationship between degree of attack and host density.

Variation in the degree of attack at different heights within tree crowns was also investigated. Five trees were sampled and approximately 1,500 second-instar larvae were collected from hibernacula and separated into two groups on the basis of hibernation site within the crown. Dissections showed 19 per cent parasitism in the top half of the crown, but only seven per cent in the bottom half. This differential attack is not solely related to host density but may also include the effect of a physical factor, such as light intensity (Miller, 1958). Jaynes (1954) obtained similar results from intra-tree studies of parasitism caused by *A. fumiferanae* in Maine.

The effects of the food plant of the host on parasite behaviour have not been investigated thoroughly since budworm population studies have primarily centred on balsam fir, the favoured food plant and the predominant species on most plots. On Plot K1, however, budworm counts have been made on both balsam fir and white spruce. Table IV shows that in the declining years of an infestation, and after severe balsam fir mortality, budworm populations are higher and the degree of parasite attack is greater on white spruce than on the surviving balsam fir. The difference in attack is not only a function of the three-fold difference in host density but is probably also influenced by a preference for white spruce foliage over severely defoliated balsam fir suggested by olfactometer experiments with parasite females.

The low incidence of superparasitism in laboratory and field studies and the higher degree of attack in the upper crown levels suggest that searching by the individual female is not entirely random. Field data suggest that the parasite is guided by certain sensory mechanisms which cause it to: (a) discriminate between parasitized and non-parasitized hosts, (b) go to the upper levels of the crown, and (c) choose foliated spruce over heavily defoliated fir. The spatial relationship between the degree of attack and host density is not well defined except

TABLE IV

Comparison of Degree of *A. fumiferanae* Attack on Balsam fir and White Spruce, Plot Kl, 1955-1957

Year	Tree species	Budworm population per 10 sq. ft.	Tree mortality[1]	Per cent parasitism
1955	Balsam fir (B)	420	15	10
	White spruce (S)	1024	0	20
1956	B	696	44	15
	S	2254	0	19
1957	B	43	70	19
	S	182	0	26

[1]Percentage based on basal area of balsam fir.

where more than one species of host food plant is considered and, in this instance, factors other than host density confound the relationship. A major difficulty arising from this type of parasite behaviour is the accurate assessment of the degree of parasite attack. Consequently, the estimate of per cent parasitism is based on the pooled samples of host larvae collected on a proportionate basis from four crown levels on each of 10 trees per plot.

Estimation of Parasite Density and Number of Hosts Attacked

Indices rather than absolute population data are used in estimating both parasite density and the number of hosts attacked. The reasons for using indices, and the underlying assumptions, are discussed in the following sub-sections.

Number of hosts attacked.—A. fumiferanae attacks either 'freely-moving' first-instar larvae or first- and second-instar larvae in hibernacula, although it is probable that the parasite attacks larvae in hibernacula more frequently. However, during the period from eclosion to formation of hibernacula the host population is subject to severe losses as the result of dispersal and other factors. A comparison of first- and second-instar populations shows reductions ranging from 50 to 80 per cent (Miller, 1958). Thus, the parasite attacks a portion of the population that is constantly changing in time and consequently difficult to measure in the field. Since no relationship exists between host density and first- to second-instar mortality, the data are treated as if *A. fumiferanae* attacked the first-instar population and this density is used in estimating the number of hosts attacked. (The first-instar population is obtained from egg counts less egg mortality.)

The number of hosts attacked is the product of the first-instar host density and the percentage of the hosts parasitized. This percentage is obtained from the dissection or rearing of third- and fourth-instar budworms collected during population sampling of four crown levels of each of 10 trees per plot (Morris, 1955). In the period 1949-1958 approximately 18,000 larvae were examined for the presence of *A. fumiferanae*.

Per cent parasitism based on third- and fourth-instar collections assumes that no differential mortality between parasitized and non-parasitized hosts occurs from the time of attack to the time of collection. Host mortality is high during

TABLE V

Comparison of Estimates of Per Cent Parasitism Based on Second and Third Instar Dissections

Plot	Instar	No. of Larvae dissected	*Apanteles* parasitism	P
G12	II	610	6.7	>.05
	III	147	11.6	
K2.....	II	620	10.2	>.70
	III	200	11.0	
K3.....	II	540	11.7	>.50
	III	200	13.0	
K2.....	II	170	12.4	>.50
	III	139	15.8	

this period as a result of fall and spring dispersal losses and a comparison of second- and third-instar larval dissections show that the assumption is correct. Although Table V shows that estimates of parasitism by *A. fumiferanae* are consistently higher for third-instar dissections than for second-instar dissections, the differences are not significant. However, should it prove that a significant differential mortality between parasitized and non-parasitized larvae does occur during the spring dispersal period, the model could easily be modified to include this effect.

The fact that *A. fumiferanae* attacks a greater proportion of hosts in the top half of the tree also creates difficulties in estimating mean per cent parasitism. This difference is diminished by dispersal of second-instar larvae in the spring but it is not entirely eliminated. Dissections of third-instar larvae from two crown levels (Table VI) also show a higher proportion of parasitized larvae in the top half of the crown. The budworm-sampling technique, however, provides an equal intensity of sampling from each of four crown levels (Morris, 1955) and the probability of obtaining a biased estimate of parasitism is slight when all the larvae in each tree sample are examined for parasites. Examination of all larvae in the tree sample is carried out at low to moderate population levels. The probability of bias could increase at high population levels when only a portion of

TABLE VI

Per Cent Parasitism Based on Third-Instar Collections from Two Crown levels

Year	Plot	Top		Bottom		P
		Total larvae examined	Per cent parasitism	Total larvae examined	Per cent parasitism	
1952	G8	240	18	256	11	<.05
1953	G8	90	19	146	7	<.01
1953	G4	71	32	100	22	>.10

the larvae in the sample are examined, but is, in effect, eliminated because the branch samples are pooled and thoroughly mixed during the collection period.

A further source of error in estimates of parasitism can occur when such estimates are obtained from both mass rearing and dissections. Dissections, as may be expected, give higher estimates of parasitism than rearings. This discrepancy arises partly from the difficulty in assessing the fate of all individuals that die in mass rearings, and partly from the fact that dissections may include species of *Apanteles* that cannot be separated in immature stages from *A. fumiferanae*. Small numbers of the following species have been reared from the spruce budworm but the larval forms have not been recognized in dissections.

A. petrovae Wly.
Apanteles sp. 51, near *tischeriae* Vier.
Apanteles sp. 24[3]
A. polychrosidis Vier.

Two of these species, *A. petrovae* Wly. and *A. polychrosidis* Vier., are recorded by Krombein (1958) as parasites of the budworm.

It may therefore be concluded that discrepancies can arise in estimating per cent parasitism depending on the host stage investigated and the technique used in detecting the parasite. But no systematic errors have been found of a magnitude to warrant corrections of per cent parasitism based on third- and fourth-instar dissections.

Adult parasite density.—The technique of caging foliage samples during the cocoon stage of *A. fumiferanae* and collecting the adults in emergence vials has been investigated as a means of assessing parasite density. The results were encouraging but insufficient data were obtained on the efficiency of the technique to permit firm conclusions. Therefore adult parasite density is calculated as the product of the host density at the time of initial parasite emergence (fourth-instar) and the percentage of the hosts containing parasites. The use of larval population trends in estimating this figure has been described (Miller, 1954). Thus, the potential number of hosts killed by the parasite is used as an index of the number of adult parasites emerging in that generation. Parasite mortality during the emergence period, the cocoon stage, and the adult stage is not known. Further, a parasite-population index and not a female-parasite index is used in the analysis since dissection of larvae prevents the collection of intensive data on sex ratios.

Analysis

The development of the mathematical model used in the following analysis is discussed in detail by Watt (1959). However, some equations are repeated here for ease of reference.

Definition of symbols.—

N_A = number of hosts attacked
N_O = number of hosts vulnerable to attack
N_{O_p} = number of hosts in previous generation
P = number of parasites searching
A = coefficient of attack, or the number of hosts attacked per parasite and considered an instantaneous rate
K = the maximum number of attacks that can be made per parasite when the hosts are vulnerable

If all parasites can generate a total of PK attacks and $\delta N_A/\delta N_o$ diminishes gradually as N_A approaches this maximum, then,

[3]Species identification number.

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$$\frac{\partial N_A}{\partial N_O} = PA(PK - N_A) \quad (1)$$

but, $A = aP^{-b}$ where a and t are positive constants. (2)

Substituting (2) in (1) gives

$$\frac{\partial N_A}{\partial N_O} = PaP^{-b}(PK - N_A) \quad (3)$$

integrating,

$$-\ln(PK - N_A) = -\ln PK + N_O PaP^{-b} \quad (4)$$

$$\text{which gives } N_A = PK(1 - e^{-aN_O P^{1-b}}) \quad (5)$$

Equation (5) expresses the number of hosts attacked in terms of the number of parasites searching and host density. The symbol K refers to the maximum number of attacks made per parasite and in the following analysis it is shown that K = 70 where P, the number of parasites, includes both sexes. However, the biological meaning of K is more evident if considered in terms of a value for females. Thus a K value for females (sex ratio 1:1) would be roughly 70 x 2 = 140. The term aP^{-b} refers to the searching and attack efficiency of the parasite. The constant a is, in effect, a measure of the attack rate per parasite in the absence of competition, and b is, in effect, a measure of intra-species competition and consequent reduction in the attack rate when more than one parasite is searching the environment. The following analysis is an attempt to fit this model to 55 sets of field data and thereby test its basic premises. Each set of data contain values for N_o, P, and N_A and the data were obtained during the period 1950-58 on the plots listed in Table I. The analysis is discussed under a number of sub-sections for purposes of clarity.

Relationship of N_A to N_o.—The 55 sets of data were first ranked on the value of P, and then divided into three equal groups. Fig. 1 shows the relationship of

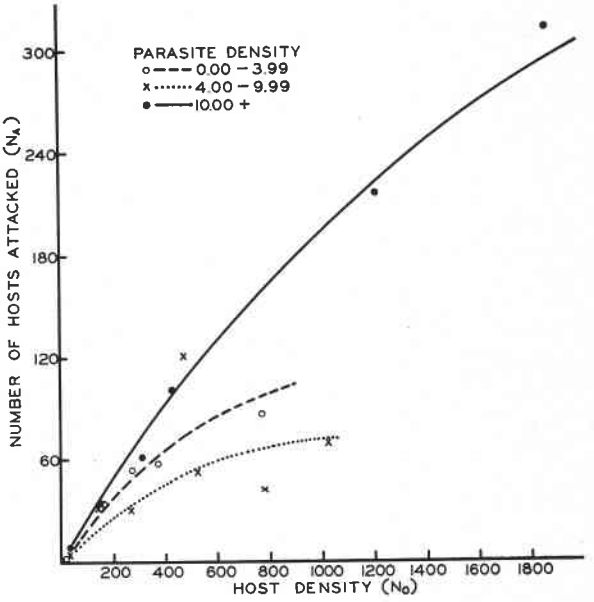

Fig. 1. The relationship of the number of hosts attacked to host density for three ranges of parasite density.

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TABLE VII

The Relationship of the Number of Hosts Attacked per Parasite to Parasite Density

Plot	Year	Parasite density (P)	Host population per 10 sq. ft.	Host attacked per parasite (A)	
				(Observed)	(Calculated)[1]
G4	1956	1.78	340	32.1	38.2
"	1950	2.36	343	29.5	25.2
"	1952	8.35	155	4.00	3.88
"	1951	9.80	169	3.50	3.07
"	1954	15.10	117	1.40	1.47

[1]Where $A = 89\ P^{-1.4774}$

N_A to N_O for each group, that is, for three mean values of P. It indicates that N_A increases at a diminishing rate with an increasing N_o and reaches an asymptote and it is concluded that there is an upper limit to the number of attacks made per parasite. This is denoted by the symbol K in equation (5).

Relationship of A to P.—The concept that the average number of hosts discovered per female parasite decreases with an increase in parasite density has been proved by a number of investigators through laboratory experiments. Data in Table VII show that a similar relationship exists in field populations. Variate values for the number of hosts attacked per parasite (A) and parasite density (P) were subjectively chosen from one plot to minimize the range of host densities and the following equation was fitted to the data:

$$A = 89P^{-1.4774} \tag{6}$$

Table VII shows calculated values of A based on equation (6) consistent with observed values. Apparently the reduction in A with increasing P is a function of the competition for oviposition sites. It should be noted, however, that (6) is given only as an example and that these values are not incorporated into the model.

Estimation of K.—It follows from equation (4) that

$$\ln\left[\frac{PK}{PK - N_A}\right] = N_O P(aP^{-b}) \tag{7}$$

By holding P constant the term $aP^{-b}(=A)$ may be considered constant and a value for K obtained from the regression

$$\ln\left[\frac{PK}{PK - N_A}\right] = AN_O \tag{8}$$

where the value of K chosen is that which maximizes the correlation coefficient. Mean P values were calculated for each of the three groups of data that were ranked on the variate-value P, and Table VIII shows the correlation coefficients within each group for various assumed values of K. At mean parasite densities of 1.65 and 25.31 a K of 70 maximizes the correlation coefficients indicating that the maximum number of attacks made per parasite is 70. At a mean parasite density of 7.45, the data are less homogeneous, with a peak in the correlation coefficients occuring at K = 120. The results in Table VIII, however, do not

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TABLE VIII

Correlation Coefficients for Assumed Values of K at Three Parasite Densities (See Text)

K values	Mean parasite density		
	1.65	7.45	25.31
40	r =	r =	r =
50		.542	.998
60	.964	.554	.998
70	.983[1]	.555	.999[1]
80	.981	.560	.998
90		.552	.997
100	.977	.566	
110		.566	
120		.589[1]	
130		.561	

[1]Peaks in correlation coefficients.

show that K is related to P in a density-dependent manner and it is assumed that 70 is the best estimate of the maximum number of attacks made per parasite.

Estimation of the constants a and b.—It follows from equation (4) that

$$\ln\left[\frac{PK}{PK - N_A}\right] = N_O P a P^{-b} \tag{9}$$

and

$$\frac{\ln\left[\frac{PK}{PK - N_A}\right]}{N_O P} = aP^{-b} \tag{10}$$

which becomes susceptible to linear regression in the form

$$\ln\left[\frac{\ln\left(\frac{PK}{PK - N_A}\right)}{N_O P}\right] = \ln a - b \ln P \tag{11}$$

With K = 70, the 55 sets of field data were analysed using equation (11). Data from one plot illustrate the procedure:
Where P = 0.82, N_o = 26.0, N_A = 3.89, K = 70
then

$$\frac{\ln\left[\frac{PK}{PK - N_A}\right]}{N_O P} \times 10^6 = 3302.1, \text{ and } \ln 3302.1 = 8.1017$$

and ln P = —0.1985. The constant 10^6 is used to give more easily manipulated values.

Fig. 2 shows the regression line for the 55 sets of data and this has a correlation coefficient of — .976 and gives the following values of *a* and *b*.

a = 0.00239
b = —2.0235

Estimation of the number of hosts attacked (N_{A_c}).—Equations (8) and (11) give the following values for *K*, *a*, and *b*.

K = 70
a = 0.00239
b = —2.0235

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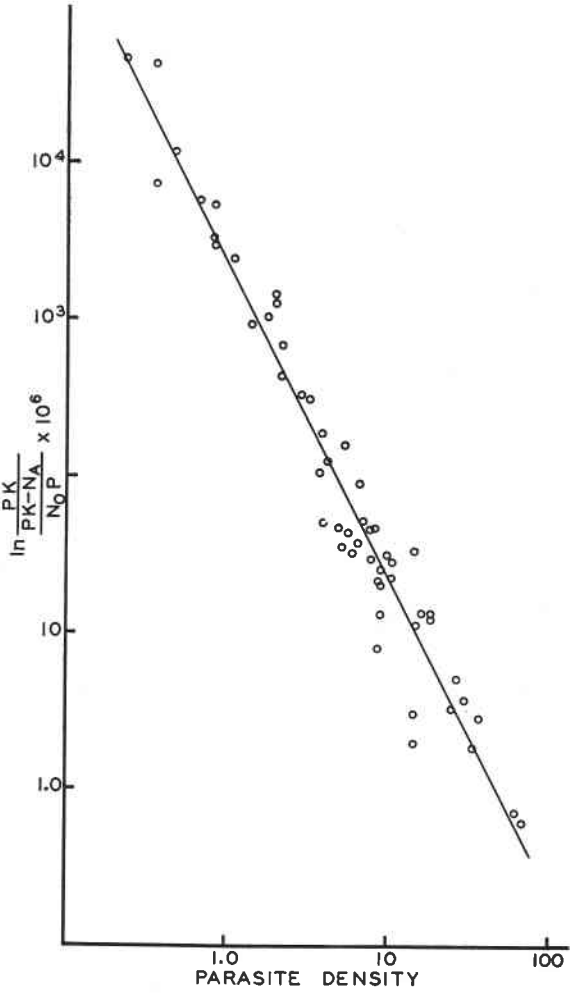

Fig. 2. A test of equation 10 to evaluate searching by *A. fumiferanae* for first-instar budworm. See text for definition of symbols.

and substituting these values in (5)

$$N_{A_c} = 70\ P(1 - e^{-.00239\ N_O P^{-1.0235}}) \qquad (12)$$

The appropriate values of P and N_o were substituted in equation (12) to obtain N_{A_c} values. The example noted in the above sub-section is continued to illustrate procedure.

Where P = 0.82 and K = 70, PK = 57.40
Where b = − 2.0235, $P^{1-b} = P^{-1.0235} = 1.2252$
Where N_O = 26 and a = .00239, $aN_O = .621$
Then $aN_O P^{-b} = .07608$
and $1 - e^{aN_O P^{-b}} = .0732$
and $N_{A_c} = 57.40 \times .0732 = 4.20$ as compared with the N_A observed of 3.89

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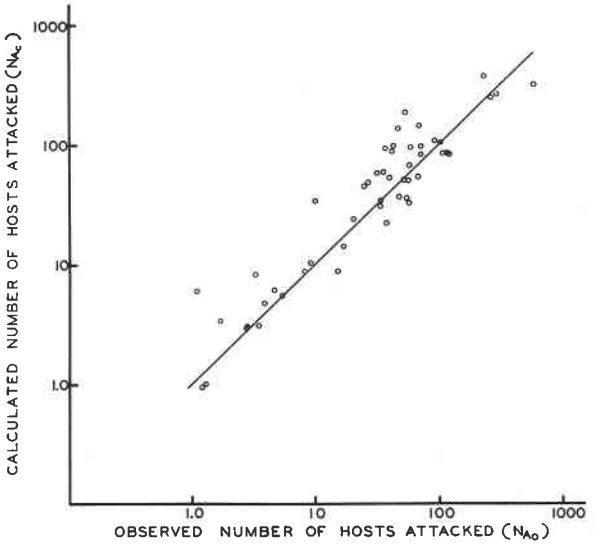

Fig. 3. The relationship of the calculated number of hosts attacked to the observed number of hosts attacked. Calculated data from equation 12 in text.

Fig. 3 shows the calculated values of N_A obtained from (12) plotted over observed values. It can be seen from this graph that N_{A_c} is generally underestimated or that the trend in the data is below the line of best fit, but parallel with it, and further, that a number of points are widely scattered from the line. Consequently, various attempts were made to improve the N_{A_c} values.

The relationship of N_{A_c} to other factors.—If N_{A_c} is related to any other factor, then *a* may be expressed as a function of that factor.
Thus,

$$a = f(x) \tag{13}$$

Substituting (13) in (5) gives

$$\frac{\ln\left[\dfrac{PK}{PK - N_A}\right]}{N_0 P^{1-b}} = f(x) \tag{14}$$

The following factors were examined using this relationship (14):

1. Host density
2. Host density in the previous generation
3. Host survival in the previous generation: (a) first to fourth instar
   (b) fourth to sixth instar
4. Parasite density
5. Number of rainy days: July 26 to August 20
6. Mean daily maximum temperature: July 26 to August 20
7. Stand factors: (a) degree of defoliation of current year's growth
   (b) yearly cumulative defoliation
   (c) number of trees per acre
   (d) average D.B.H.

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The analyses indicated that none of these factors was related to N_{A_c}. However, it was apparent from Fig. 3 that the points widely scattered from the line of best fit denoted plots situated within the severely infested area of the Watershed and applied to a period of time when host density was sufficiently high to cause 100 per cent current defoliation and, in most instances, severe thinning of the older foliage. Therefore, on the assumption that some event or series of events occurred during the peak of the infestation to upset the expected relationship between P and N_A, the data were split into two groups. One group consisted of 42 sets of data and included plots in the area of intermediate infestation and those plots in the severe infestation during the time when current defoliation did not exceed 100 per cent, that is, towards the end of the outbreak period. The other group of 13 sets of data included those plots where complete stripping of the current year's growth occurred for three or more successive generations.

The two groups of data were analysed separately in order to obtain separate parameter values for *a* and *b* and also to determine if any factor could be related on biological grounds to the observed difference in numbers attacked in intermediate and severe infestations. These analyses followed the same sequence outlined above and the methods will therefore be discussed only briefly.

Plots with less than 100 per cent current defoliation.—The 42 sets of data were re-analysed and with K = 70, the transformation (11) gave a correlation coefficient of -.991 and the following values for *a* and *b*:

$$a = .00277$$
$$b = -1.9685$$

Thus, the coefficient of attack

$$A = .00277\ P^{-1.9685} \qquad (15)$$

A comparison of (15) with the parameter values for A (= .00239 $P^{-2.0285}$) in equation (12) shows that the former gives an increased number of hosts attacked per parasite but shows little difference in the rate of change in attack with increasing parasite density. This is to be expected since equation (12) underestimates N_A over a wide range of parasite densities. It is therefore assumed, on the basis of this analysis of 42 sets of data, that equation (15) is the best estimate of the attack coefficient of *A. fumiferanae*.

Plots with successive years of 100 per cent current defoliation.—The 13 sets of data in this group of plots hardly provided a sufficient number of variates from which to estimate a new K value. Table IX shows that when all 13 sets of data were considered the regression coefficients based on equation (8) are bimodal. (The variability in the data is also shown in Table VIII in the initial analysis of K at intermediate parasite densities.) By plotting $\ln(PK-N_A)$ over N_o the data were observed to fall into two distinct groups and values of 70 and 90 were calculated respectively for each group (Table IX). However, since the value of 90 could not be related to any one year, plot, or to parasite density, it was assumed that a K of 70 was still the best estimate of the maximum number of attacks per parasite.

The difference between the observed number of hosts attacked for the 13 sets of data and the calculated values from equation (12) was then examined to see if this difference was related to such factors as host density, parasite density or various stand factors. A relationship was found between the ratio N_{A_o}/N_{A_c} to host density in the previous generation, N_{o_p}. Since parasite density is related to N_{o_p} it was assumed that some mortality factor becomes increasingly effective

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TABLE IX

Correlation Coefficients for Assumed Values of K. Data from 13 Plots in Severe Infestation (See Text).

K values	Mean parasite density		
	All 13 plots 8.22	Group 1 7.50	Group 2 9.06
10	r = .893[1]	r =	r =
20	.840	.926	.464
30	.830		
40	.827	.932	
60			.486
70		.933	.568[1]
80		.935	.517
90		.938[1]	
100		.935	.504
120	.823		
130	.827[1]	.930	
140	.799		

[1]Peaks in correlation coefficients.

at high host densities to reduce the parasite population. Thus P_p, the measured index of parasite density is reduced to P_s. Watt (1959) shows that if this assumption is correct then

$$\frac{dP_s}{dN_{Op}} = - cP_s \tag{16}$$

and

$$P_s = P_p e^{-cN_{Op}} \tag{17}$$

The constant c may be obtained graphically or by regression analysis from the following equation (Watt, 1959, equation 26):

$$\frac{N_{A_o}}{N_{A_c}} = e^{-cN_{Op}} \tag{18}$$

The graphical method was used to find c by plotting the ratio N_{A_o}/N_{A_c} over N_{o_p} on semi-log paper and using that part of the line prior to the curvature caused by the exponential $\exp(-cN_{o_p})$. The following equation was fitted to the line:

$$\frac{N_{A_o}}{N_{A_c}} = e^{-.0006\ N_{Op}} \tag{19}$$

Substituting in (17) gives

$$P_s = P_p e^{-.0006\ N_{Op}} \tag{20}$$

Parameter Values in the Final Equation.—The analysis of the data in two groups provided new parameter values for the coefficient of attack and also showed that parasite populations are reduced by some mortality factor related to host density in the previous generation. These results are combined to give the final equation for estimating the number of hosts attacked by *A. fumiferanae*.

$$N_A = 70\ P_p e^{-.0006\ N_{Op}}(1 - e^{-.00277\ N_O P_s^{-.9685}}) \tag{21}$$

Equation (21) was used to calculate the number of hosts attacked for 50 sets of data and Fig. 4 shows the relationship of calculated to observed values.

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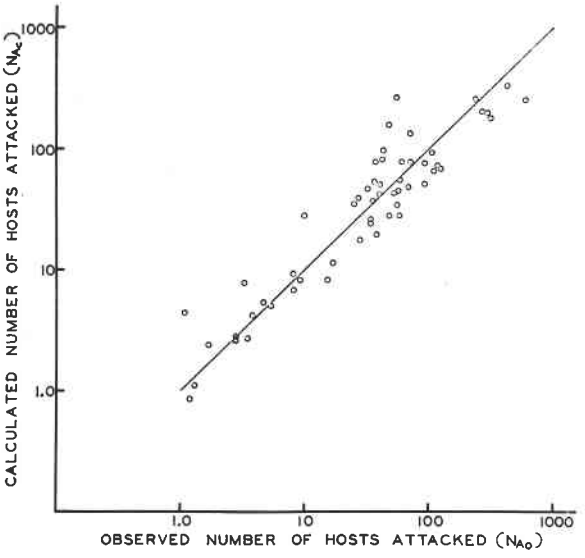

Fig. 4. The relationship of the calculated number of hosts attacked to the observed number of host attacked. Calculated data from equation 21 in text.

(The number of variates was reduced from 55 to 50 because N_{o_p} values were not known for all plots and years.) The correlation coefficient of this regression line is 0.843 indicating that the model explains 71 per cent of the variation in the number of hosts attacked. A comparison with the regression line in Fig. 3 ($r = .751$ for the same 50 sets of data as in Fig. 4) shows the improved fit resulting from changes in the attack coefficient and the inclusion of a parasite mortality factor.

Discussion

The spruce-budworm population data presented herein represent two rather distinct trends in the population behaviour of the spruce budworm in the Green River area in the period 1949 to 1958. Extensive defoliation surveys and limited sampling data show that a gradual increase in numbers occurred from 1945 to 1948. Then, over a large part of the area, populations increased rapidly over the next three years to a level where repeated stripping of the current year's foliage occurred. This resulted in the initial phase of tree mortality in 1954 and approximately 78 per cent mortality of balsam fir, four inches D.B.H. and over, by 1958 in areas of mature balsam fir reserved from aerial spraying. Fig. 5A, which shows yearly counts of first-instar budworm, illustrates this population behaviour. Fig. 5B illustrates the contrasting behaviour on the remaining area which was also reserved from aerial spraying but largely isolated by clear-cutting operations before 1950.

Fig. 5 also shows the contrasting trends in the population of the parasite *A. fumiferanae* in these two areas, particularly in the period 1952 to 1955 in the area of severe infestation (Fig. 5A). Evidence based on small random collections before 1949 in the Green River area, when host populations ranged from 0.05 to 0.10 larvae per 10 square feet of foliage, suggests that less than five per cent of the budworm larvae were attacked by this species. In the area of severe infestation per cent parasitism increased slowly to approximately 10 per cent in 1955, then rapidly to approximately 20 per cent in 1957. In the intermediate in-

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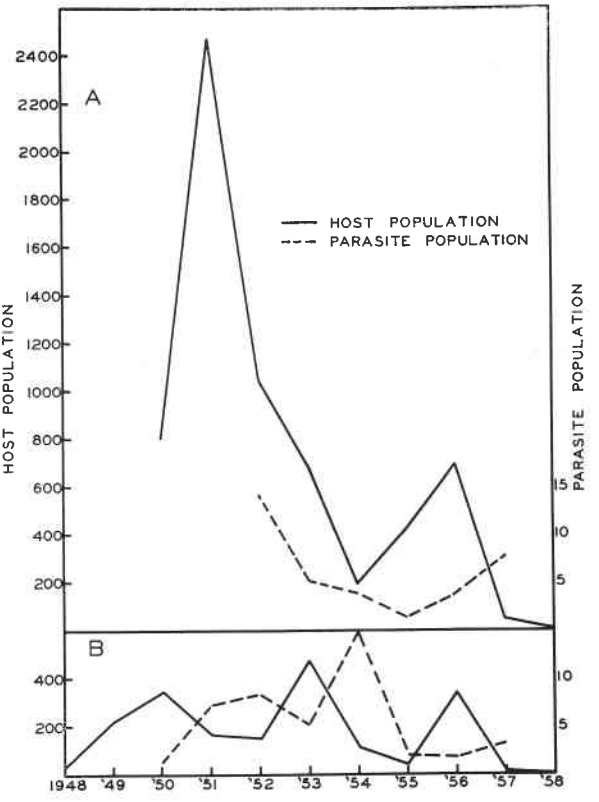

Fig. 5. First-instar budworm counts and the density of the parasite, *A. fumiferanae*, for the period 1948-58. The graph illustrates population trends of host and parasite in a severe infestation (A) and in an intermediate infestation (B). (Not to be confused with Fig. 3, Morris *et al.* (1956) where host density is based on a different stage and time scale.)

festation a sharp increase in parasitism to approximately 20 per cent occurred as early as 1950 and parasitism has fluctuated about this level during the outbreak.

The analysis of field data shows that a general mathematical model (Watt, 1959) will mimic and thereby evaluate the interaction of the spruce budworm and the parasite *A. fumiferanae* in these contrasting population trends with notable success. It also shows that certain discrepancies still exist between expected and observed values. The number of hosts attacked can be predicted with accuracy on plots where the population density remained at a relatively low level. But the model does not accurately evaluate the expected trend in parasite attack on plots and in years when food shortages occurred as a result of complete stripping of the current foliage. It overestimates the number of hosts attacked and this leads to the conclusion that, during the peak of a severe infestation, some factor or factors causes changes in either the number, physiological characteristics, or behaviour of the parasite that are not accounted for in the model. It is the aim of this discussion to enumerate some of the possible factors involved and their potential mode of action, and thereby to point out profitable areas of further research on host-parasite interaction.

Fecundity.—The effect of host starvation on the size of the issuing parasite, and more particularly on the fecundity of the parasite, is difficult to determine since fecundity is probably a function of both adult size and food intake. Linear

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measurements of cocoons show that parasites issuing from starved hosts are smaller than those issuing from non-starved hosts but the effect on fecundity has not been determined. It may be surmised, however, that size is related to vigour and survival.

In the model, K, the maximum number of attacks made per parasite, is an index of fecundity. The analysis did not show that K is related to P, and in fact, a calculated K value of 70 fitted a wide range of parasite density, particularly for those plots where current defoliation did not exceed 100 per cent. The data did show inconsistencies where food shortage occurred, but failed to show a decrease in K, or suggest that the decrease in parasite efficiency in severe infestations is a function of fecundity. However, the estimate of K at intermediate and high values of P are uncertain and the data in Tables VIII and IX (bimodality and slight evidence of maximum correlation coefficients) suggest the necessity of further investigation.

Food supply.—Clausen (1940) states that the great majority of Braconidae feed principally on honey dew and plant exudations, although females of some species subsist on the body fluids of the attacked hosts. In instances where *A. fumiferanae* was observed attacking first-instar budworm the female apparently did not feed on the host, but did feed on an aqueous solution of honey placed in the cage. There is no reason to suspect that food was a factor limiting *A. fumiferanae* attack during the outbreak on any particular plot. Ground-vegetation studies on all plots based on systematic quadrat sampling show a marked similarity in the recurrent groups (Fager, 1957) of flowering plants and shrubs. These recurrent groups always include *Oxalis montana* Far., *Clintonia borealis* (Ait.) Raf., *Cornus canadensis* L., and often include *Maianthemum canadense* Desf. and *Rubus strigosus* Michx. The one major change in ground vegetation has followed the advent of tree mortality in the severe infestation area. Here, increases in the shrub layer (*Rubus strigosus*) has reduced the abundance of some flowering plants but these changes, occurring late in the outbreak, cannot be related to the observed limitations in *A. fumiferanae* attack.

Parasite mortality.—Parasite density is a function of host density in the previous generation, N_{o_p}, and the analysis of the relationship of N_{A_O}/N_{A_C} to N_{o_p} (equation 19) shows that a factor or combination of factors causes a reduction in the survival of parasites particularly when host density in the previous generation is high. Thus, P_p, the measured index of parasite density, is reduced to P_s, the actual number of parasites searching. Among the factors that could contribute to this reduction are: mortality of parasitized hosts, and changes in the sex ratio, since both may be related to N_{o_p}.

Mortality of parasitized larvae.—The index of parasite density P is based on the host density at the initial period of parasite emergence and does not include mortality of parasitized larvae during the two-week emergence period in the latter part of June. In a severe infestation food shortage occurs during this period, and larvae tend to drop from the upper to the lower portions of the crown and to understory trees in search of a new food supply. Thus, a greater mortality may occur, particularly among the less active parasitized hosts, as a result of this intra- and inter-tree movement in a severe infestation, than takes place in an intermediate infestation where food shortage is not a critical factor.

Sex ratio.—Flander (1956) in a discussion on the sex ratio in parasitic Hymenoptera states that "In species with small spermathecal glands such as the bracon type, host density influences the sex ratio of the parasite through its effects on

TABLE X

Sex Ratio[1] of *A. fumiferanae*

Year:	1951	1953	1954	1957	1957[2]	1958
Adults examined	90	32	135	69	26	45
Sex ratio (as per cent females)	46	53	46	59	59	58

[1]Data do not apply to one particular plot.
[2]Field-Collected cocoons.

the rate of oviposition. Activation of the sperm may not keep pace with egg deposition and this results in a preponderance of male progeny". The concept that sex ratio may change in time and place is recognized although only limited data were obtained on this factor in any one year (Table X). A preponderance of males could have occurred at very high host densities on the basis of the theory cited by Flanders. This in effect would act as a mortality factor reducing the parasite population since the population index, P, is based on the total number of individuals and not on the number of females.

However, it must be concluded that parasite mortality does not entirely explain the less effective action of *A. fumiferanae* in severe infestations, although it does apparently increase with increasing host density and a number of factors either singly or in combination could contribute to it.

Cocoon mortality including hyper-parasitism.—No adequate estimates of cocoon mortality resulting from predation and hyper-parasitism were obtained during the study, although the hyper-parasite *Gelis* sp. was reared from random cocoon collections.

Limitations in assessing parasite oviposition behaviour.—It has been assumed in equation (21) that the oviposition behaviour of *A. fumiferanae* is relatively constant throughout a host density range from five to 2,000 per 10 square feet of foliage. This assumption may be questioned since host density can have a modifying effect on the oviposition behaviour of the parasite as shown by Burnett (1958) and Wylie (1958). Oviposition behaviour may be such that, at very high or very low host densities, parasite progeny may tend to be found in 'pockets' within the population. This type of behaviour would be difficult to demonstrate by field sampling techniques where the degree of parasite attack is based on the mean of pooled samples. Thus, the limitations set by sampling methods in accurately assessing parasite attack cannot be ignored, particularly at extreme ranges of host density where the sample is either a very small proportion of the population available to attack, or time and effort limit the number of hosts that can be collected for examination.

Forest composition.—No relationship was found between variations in *A. fumiferanae* attack and forest composition. Table I shows that the study plots are relatively homogeneous except for differences in density associated with age, and the effect that density has on the abundance of ground vegetation. Thus, variations in composition are mainly limited to degree and not to major differences in tree species and ground vegetation complex.

Climate.—A number of weather factors, including mean maximum temperature, hours of rainfall, and amount of cloud, were tested against variation in *A. fumiferanae* attack and showed a surprising lack of relationship. However, the

effect of weather on this parasite may be partly obscured by the length of the attack period since cage experiments indicate a maximum longevity of 36 days.

Conclusions

The analysis of field data on the density of the parasite, *A. fumiferanae*, the density of the host, *C. fumiferana*, and the number of hosts attacked shows that a mathematical model will mimic this host-parasite interaction to the extent that 71 per cent of the variation in the number of hosts attacked is explained by the model. The residual variation emphasizes the need for further research along two general lines: (a) field investigations on methods of assessing adult parasite density, and (b) controlled experiments on parasite behaviour and reproduction to obtain a better understanding of the coefficients contained in the model and of the extent these coefficients are related to the physiology, morphology, or behaviour of the parasite. This should indicate environmental factors that affect parasite efficiency and contribute to our knowledge of the possibility of manipulating the environment through silvicultural methods to improve natural control of the budworm.

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Damage to Cabbage by the Clover Cutworm, *Scotogramma trifolii* (Rott.) (Lepidoptera : Phalaenidae)[1]

By L. M. Cass[2]

The clover cutworm, *Scotogramma trifolii* (Rott.), has been recorded from a wide variety of host plants, but there are few records in the literature associating it with cole crops. Riley (1893) recorded it from cabbage in Maryland. Gibson (1915) recorded it from turnip and cabbage in Canada. Forbes (1954) and Frost (1955) listed cabbage as a host plant in New York and Pennsylvania, respectively. In 10 years' studies on caterpillars on cabbage in the Ottawa Valley, 1949 to 1958, numbers of the clover cutworm on cabbage were almost always negligible. However, in the early summer of 1956 it occurred throughout the area in significant numbers, and in a study field of early cabbage at Merivale, Ontario, caused sufficient damage to affect the market value of the crop.

The feeding injury might easily be mistaken for that of the imported cabbageworm, *Pieris rapae* (L.), except that it is more confined to the developing head, which frequently becomes malformed. On June 22, at Merivale, one larva of the clover cutworm was found per plant; this was more than for the imported cabbageworm, the diamondback moth, *Plutella maculipennis* (Curt.), or the cabbage looper, *Trichoplusia ni* (Hbn.), which commonly attack cole crops in the Ottawa area. This appears to be the first record of the clover cutworm's causing damage of economic importance to cabbage.

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