Temporal and Spatial Activity Patterns of an Adult Parasitoid, *Glypta fumiferanae* (Hymenoptera: Ichneumonidae), and Their Influence on Parasitism

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ABSTRACT Temporal and spatial activity patterns of adult *Glypta fumiferanae* (Vierick) were assessed through use of malaise traps placed in tree canopies and on the forest floor. Many parasitoids were trapped in the tree canopies while none was caught on the forest floor. A model that related malaise trap catches to weather was used to draw inferences from these data. It was concluded that cool wet weather inhibited activity of the parasitoid. Historical data on interaction between *G. fumiferanae* and its host were used to illustrate the possibility that reductions in parasite activity due to weather factors led to reductions in rates of parasitism.

NUMEROUS theoretical investigations have explored parasitoid/host interactions by examining host-searching behavior, the host distribution, and the dynamics of parasitoid/host systems. Based on these studies, the characteristics of successful biological control agents have been advanced (Beddington et al. 1978). In most of these studies, the only factors considered to influence parasitoid host searching are host density and distribution, although the temporal and spatial dynamics of the adult parasitoid are also involved. These organisms are small, highly mobile, and often few in number, and thus, they are difficult to sample.

In this paper, we present the results of an investigation of the spatial and temporal dynamics of adults of the parasitoid *Glypta fumiferanae* (Vierick). *G. fumiferanae* is a common, specific, univoltine parasitoid that attacks first- and second-instar spruce budworm, *Choristoneura fumiferana* (Clemens). It overwinters in the budworm larva and emerges from either fifth- or sixth-instar hosts. It then spins a pupal case in the tree and emerges as an adult at approximately the time when budworm eggs are eclosing. The general biology of *G. fumiferanae* is provided by Brown (1946), Wilkes et al. (1948), Dowden et al. (1948), and Miller (1960).

This paper consists of two sections. First, information on the temporal and spatial dynamics of adult *G. fumiferanae* is presented using data obtained through field studies of the parasitoid's activity patterns. Second, the relationship between the temporal dynamics of the adult parasitoid and its searching efficiency is examined using historical data of the interaction between *G. fumiferanae* and its host.

Materials and Methods

Field Studies. Data were collected on the temporal and spatial activity patterns of adult *G. fumiferanae* in the Upper Peninsula of Michigan in one forest stand in 1980 (stand 1), and two different stands in 1981 (stands 2 and 3). Mature balsam fir, *Abies balsamea* (L.) (Miller), composed ca. 60, 100, and 50% of stands 1, 2, and 3, respectively.

Based on previous sampling of adult parasitoids (Julliet 1963, Price 1971, Simmons & Chen 1975, Simmons 1976, Reardon et al. 1977, Ticehurst & Reardon 1977), malaise traps were selected to measure the activity of adult *G. fumiferanae*. The traps were designed and constructed for placement in tree crowns and on the forest floor (Fig. 1).

During early July 1980, 14 of these traps were placed in the middle to upper crowns of 14 balsam firs, and 14 were placed on the forest floor, one within 10 m of each tree containing a trap. Traps in the trees were positioned so that one of the two open sides of the trap was tangent to the tree crown. During late June 1981, 13 traps were located in balsam firs and 13 on the forest floor in both stands 2 and 3. Traps in the trees were oriented so that both open sides of each trap were perpendicular to the crown. Trees in which traps were placed were selected on the basis of good crown condition and ease of access for trap placement. We placed traps on the forest floor because *G. fumiferanae* might use plants that produce nectar and pollen as food, as a number of parasitoids are known to do (Simmons et al. 1975, Syme 1975). Traps were emptied each morning before 0700 hours between

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2 July and 15 August. During the 1981 peak female flight, traps in stand 2 were emptied every 2 h for 3 days.

The pupal density of *G. fumiferanae* was estimated by sampling balsam fir branches at the middle crown. These estimates were made just before the adult parasitoid began to emerge from the pupal stage. The emergence rate of *G. fumiferanae* from the pupal stage was estimated in stand 2 by sampling balsam fir foliage from the middle crown of trees and counting pupae and empty pupal cases. Samples were taken irregularly at 1- to 3-day intervals, depending on the cumulative emergence to date and the weather since the last estimate. Physiological time for the parasitoids was approximated with degree-days (DD) base 8.9°C. This base was chosen because it is close to the base for the parasitoid's host (Miller et al. 1971) and no information on the developmental base for the parasitoid is available. DD were calculated using the method of Baskerville & Emin (1969). Hourly measures of rainfall, relative humidity, temperature, and barometric pressure were collected in stand 2. Stand 3 was ca. 25 km from stand 2 in an area of uniform geography. We, therefore, assumed weather variables measured at stand 2 would be indicative of conditions in stand 3.

Data were analyzed by constructing a model with which the relationship between weather and trap catch was studied. An adjusted G statistic (G_{adj}) (Sokal & Rohlf 1981) was used to test the independence of trap catch and weather.

Historical Data. From our field studies of *G. fumiferanae*'s activity patterns, we concluded that wet and cool weather reduced the parasitoid's activity. This relationship was explored further by using historical data on the interaction between the parasitoid and its host to determine if reductions in parasitoid activity lead to decreased parasitism rates.

Original data on spruce budworm densities and on the rate of budworm parasitism by *G. fumiferanae* in the years 1950–58 at the Green River field station (Morris 1963) were obtained from the Maritime's Forest Research Center, Fredericton, New Brunswick. We selected data from three plots (G2, G4, G5) because each data series spanned 5 or more years, budworm densities were relatively constant, and no appreciable tree mortality occurred. These data were analyzed by Miller (1960), who also thought that rainfall might influence the attack efficiency of *G. fumiferanae*. In contrast to Miller (1960), we analyzed the Green River data without a particular parasitoid attack model by exploring the relationship between the ratio of the number of hosts to the number of parasitoids, rainfall, and percentage of hosts parasitized.

An index of the density per 10 m^2 foliage of female *G. fumiferanae* was computed by first assuming that both the parasitoid's survival rate from the larval stage located within the budworm to the adult stage and its sex ratio (assumed to be 1:1) did not vary from year to year. The index was then determined by multiplying the density of third- and fourth-instar budworm by one-half the parasitism rate.

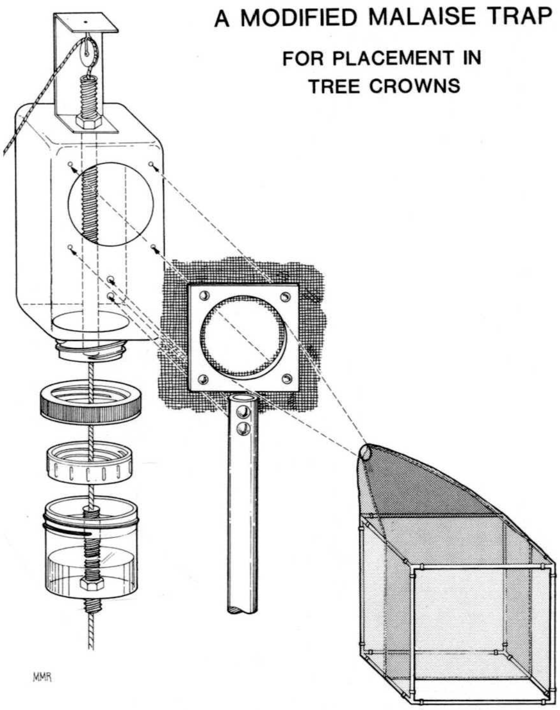

Fig. 1. Details of a malaise trap designed for placement in tree crowns. Trap volume is 1 m^3. Frame is constructed of PVC pipe and screening of saran 20-mesh screening. Intermediate and final collection jars and face plate are plastic. Final collection jar is affixed to a nylon cord that passes through a threaded pipe. The pipe is attached to the intermediate collection jar. Trap catch is inspected by lowering the final collection jar.

The index of host density (second instars) was based on egg counts less egg mortality (Morris 1963) and an assumed constant dispersal loss of first instars. An assumption of a constant first-instar dispersal loss is supported by references contained in and the simulation results obtained by Kemp et al. (1980).

To determine rainfall during the female's flight period, the approximate calendar dates over which parasitoid flight activity occurred were determined by relating DD accumulation to calendar date. We assumed that flight activity with respect to DD was the same in northwestern New Brunswick as it was in Michigan. The period of activity in Michigan was determined from the malaise trap catches of 1980 and 1981. Minimum and maximum DD values for which females were caught for these 2 years were 388 and 663. But the numbers caught during this period varied. Total precipitation for the interval 428–584 degree-days was computed because it was the period during which peak activity occurred.

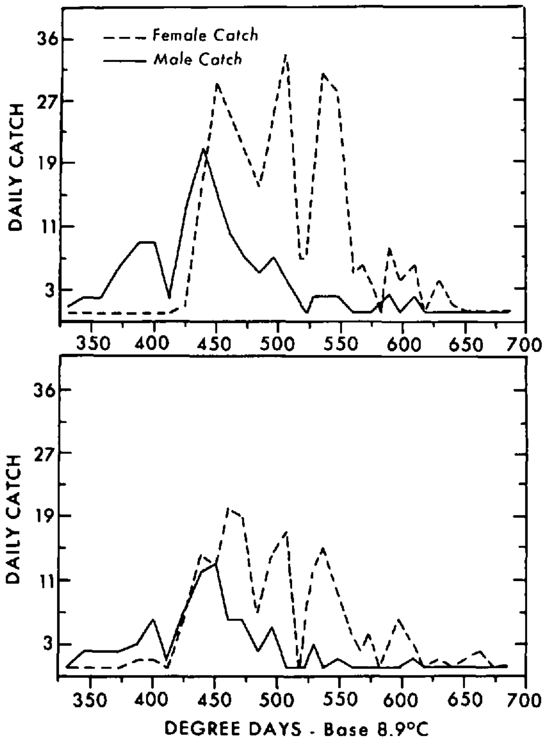

Fig. 2. Daily catches of male and female adult *G. fumiferanae* from 13 malaise traps located in balsam fir trees in stands 2 and 3 during 1981.

The data were used to generate a parasitism surface using a least squares cubic spline (Ahlberg et al. 1967) with the host/parasitoid ratio and rainfall as independent variables.

Results and Discussion

Field Studies. In 1980, 39 female parasitoids were trapped in the trees and none was caught on the forest floor. In 1981, 125 males and 294 females were trapped in trees in stand 2, and 72 males and 182 females were trapped in stand 3. We feel the low trap catch in 1980 was due to trap orientation since the parasitoid pupal densities in 1980 and 1981 were not significantly different ($t = 1.2$, $P > 0.05$). The pupal density per m^2 foliage in stand 1 (1980) was 7.61 (SD = 10.02, $n = 48$); in stand 2 (1981), 10.45 (SD = 11.20, $n = 40$); and in stand 3 (1981), 9.87 (SD = 9.03, $n = 40$).

The flight activity as measured by trap catch of both male and female parasitoids in stands 2 and 3 during 1981 was remarkably similar (Fig. 2). Because these stands were separated by ca. 25 km, we hypothesized that weather strongly influenced flight activity. To evaluate this hypothesis, we constructed a model with which to examine the relationship between weather and the time series of trap catches. A model was used because, in the absence of any other influencing factors, trap catch would be proportional to the density of adult parasitoids. However, this density was unknown. With a model and the assumptions outlined below, a density index could be derived from the trap catch data.

Predicted trap catch ($T\hat{C}$) of *G. fumiferanae* was expressed as a function of adult density (Ad) and adult activity (Aa). In addition, the Aa was related to a set of weather variables (W). Thus,

$$T\hat{C} = f(\mathrm{Ad}, \mathrm{Aa}) \qquad (1)$$

and

$$\mathrm{Aa} = f(W). \qquad (2)$$

The time-specific adult density, Ad(t), was not known. However, it is a function of adult parasitoid emergence from the pupal stage and dispersal and death rates until time t. We assumed that immigration and emigration were balanced and that mortality of the adult parasitoid population was negligible before old age attrition. Thus, Ad(t) was a function of the emergence rate and physiological time (DD > 8.9°C) between emergence and death. With these assumptions, we 1) specified a function for the change in Ad through physiological time, 2) specified a function relating trap catch to Ad and W, 3) fitted parameters to a model based on these functions through the use of a nonlinear optimization algorithm using the data collected from stand 2, and 4) evaluated the model fit by determining the amount of variation in the trap catch data accounted for by the model and by comparing predicted trap catch to a data set other than the one used to parameterize the model.

Emergence and mortality rates are physiological time delays (PTD) and each was modeled as a distributed delay (Manetsch & Park 1977). For a parasitoid population, PTD are random variables. The distributed delay is based on the probability density function of a PTD. If $f(t)$ is the probability density function of the PTD between emergence and death, and $e(t)$ and $m(t)$ are the emergence and mortality rates, then

$$m(t) = \int_0^t e(v) f(t - v)\, dv, \qquad (3)$$

where t = physiological time, and v is a dummy variable of integration. The adult density is given by:

$$\mathrm{Ad}(t) = \int_0^t e(v) - m(v)\, dv. \qquad (4)$$

Note that the mortality rate ($m[v]$) is simply the rate at which individuals leave the population due to death from old age.

Parameters for the emergence rate were estimated from data on the cumulative emergence of *G. fumiferanae* collected in stand 2 (Fig. 3). Parameters for mortality were estimated jointly with other model parameters from the trap catch data. The γ density function with an integer shape parameter (k) was used for $f(t)$. The shape parameter was determined by initially selecting a value based on the shape of $p(t)$ and $\mathrm{Ad}(t)$ and then adjusting it before determining the other model parameters until a good fit was obtained. The value for k was estimated independently of the optimization because it must be an integer and the optimization algorithm used requires continuous decision variables. The mean of PTD ($\overline{PTD}$) and k are sufficient statistics for $f(t)$.

Variables in the set W included rainfall, RH, temperature, and barometric pressure. Hourly measures of these variables were averaged over 0800–2200 hours, the period in which we found *G. fumiferanae* to be most active (Table 1). The values of W and TC (actual trap catch) used in the model are constant during a given day while those for Ad changed continuously during the day according to the DD accumulated. Therefore, we used the value for Ad midway through the day in equation 1.

To estimate model parameters, a linear form of equation 1 was adopted. Predicted trap catch is, thus, given by

$$\hat{TC}_n = (a + \underline{b}'\underline{W}) \cdot \left(\int_0^{t_n} e(v) - \int_0^{t_n} f(t_n - z)e(z)\,dz\,dv \right), \tag{5}$$

where n is a daily index, t_n are DD accumulated on day n, and underlined variables denote vectors. The parameters a, b, and $\overline{PTD}$ of the mortality rate were estimated using Box's nonlinear optimization algorithm (Kuester & Mize 1973). The objective function for the optimization is given by

$$\text{minimize } F = \sum_{n=1}^{m} (TC_n - \hat{TC}_n)^2, \tag{6}$$

where m is the number of days parasitoids were trapped. This objective function chooses parameter values that minimized a sum of squares about the observed trap catch.

The model was parameterized for female trap catch only. To begin parameter estimation, the initial input (i.e., total number of pupal female parasitoids) was arbitrarily selected for two reasons. First, the absolute number of pupal *G. fumiferanae* in the trapping area was not known. Second, we were interested in the qualitative aspects of the model; knowing this value, therefore, was unnecessary. As a result, model parameters except $\overline{PTD}$ are scaled by the initial input.

The rate of adult female emergence was separated from the male emergence rate by assuming that the initial trap catch of females indicated the onset of female emergence and that the shape of the female emergence curve was similar to the joint male and female emergence curve. The first assumption is based on the fact that *G. fumiferanae* was not collected in any habitat other than the forest canopy. Hence, it is unlikely that females emerged at the same time as males and used a habitat other than the trees containing budworm to find food or alternative hosts. If this were the case, they might not be trapped. Parameters for the distributed delay used to describe female emergence were selected so that predicted emergence resembled the combined male and female curve, but was appropriately delayed in time (Fig. 3).

Results of the parameter estimation are given in Table 2. Only models that had some ability to predict trap catch are presented. Since the objective function for the optimization process can be thought of as a residual sum of squares, an R^2 was computed for each model. However, a test of significance cannot be made due to correlation among variables within the model and because the distri-

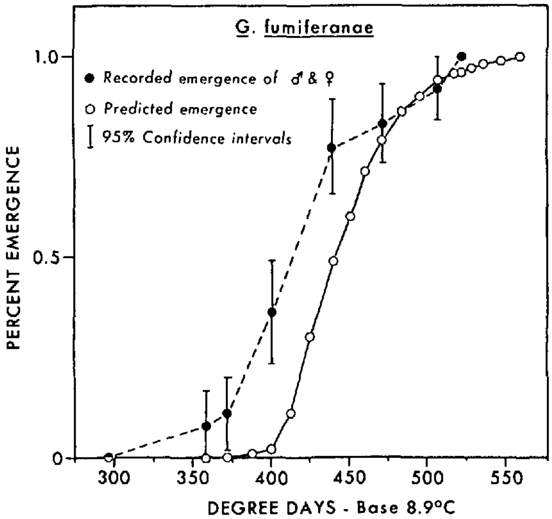

Fig. 3. Observed cumulative emergence of adult *G. fumiferanae* (male and female combined) in stand 2, and predicted emergence of females as a function of DD base 8.9°C.

Table 1. Bi-hourly proportion of total trap catch of female *G. fumiferanae* from 13 malaise traps located in balsam fir trees

h	Replicate (day) Proportion of total trap catch 1	2	3
0	0	0	0
2	0	0	0
4	0	0	0
6	0	0	0
8	0	0	0
10	0.05	0.25	0.10
12	0.10	0.25	0.15
14	0.18	0.31	0.35
16	0.38	0.19	0.30
18	0.19	0	0.05
20	0.05	0	0
22	0	0	0
24	0	0	0
Total trapped	21	16	20

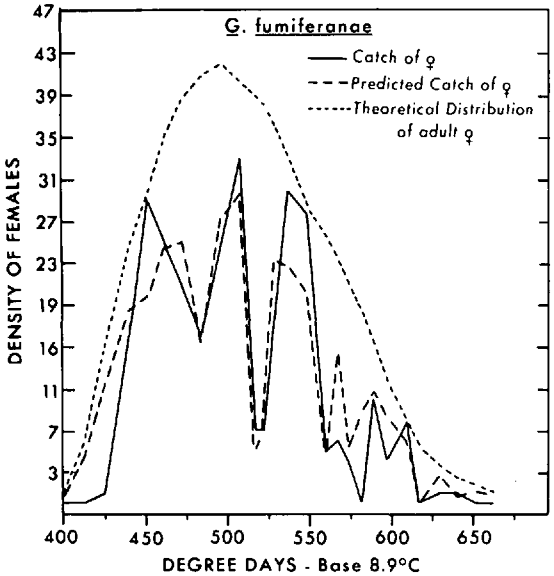

Fig. 4. Predicted and actual malaise trap catch of adult female *G. fumiferanae* in stand 2 and the theoretical, relative temporal distribution of adult females. Malaise traps were located singly in 13 balsam fir trees.

Table 2. Models used to predict the temporal distribution of malaise trap catch of female *G. fumiferanae*

Model	$\bar{P}\bar{T}\bar{D}_m$	Residual sum of squares	R^2
1 $TC = 0.605\mathrm{Ad}$	81	1,300	0.51
2 $TC = (0.12 + 0.852\ T)\mathrm{Ad}$	84	1,117	0.58
3 $TC = (1.24 - 0.892\ \mathrm{RH})\mathrm{Ad}$	76	1,046	0.61
4 $TC = (154.6 - 1.89\ R)\mathrm{Ad}$	86	708	0.74
5 $TC = (0.662 - 0.714\ \mathrm{RH}$			
$+ 0.559\ T)\mathrm{Ad}$	87	982	0.63
6 $TC = (0.29 - 1.232\ R$			
$+ 0.9553\ T)\mathrm{Ad}$	87	546	0.80

TC, predicted trap catch; *T*, average temperature between 0800 and 2200 hours; RH, average relative humidity between 0800 and 2200 hours; *R*, rainfall in cm between 0800 and 2200 hours; Ad, a measure of adult female density; PTM_m, expected adult female life span in DD.

In all models, the emergence rate is given by a distributed delay with $\bar{P}\bar{T}\bar{D} = 55.5$, $k_p = 4$ and $t_o = 388$ DD base 8.9°C. The value of k_m was 8.

bution of the various sum of squares is unknown. The best prediction of trap catch was achieved with precipitation and temperature as independent variables. Wet and cool weather was associated with declines in trap catch. Reasonably large changes in the residual sum of squares associated with the stepwise inclusion of each variable in this model ensured that the model was not over-parameterized. The predicted trap catch and predicted temporal distribution of adult females using this model and actual trap catch for stand 2 are shown in Fig. 4. The predicted temporal distribution of adults is an index of adult density.

It was not possible to evaluate the statistical significance of the relationship between wet and cool weather and diminished trap catch. Nonetheless, we conclude that the relationship is not spurious for two reasons. First, the model closely predicts the actual trap catch in stand 3 (Fig. 5). In this case, the initial input of pupal parasitoids was set equal to the input from stand 2 scaled by the ratio of estimated pupal densities in stands 3 and 2. The close fit of the model is not surprising considering the similarity in the trap catch from stands 2 and 3.

The second reason for doubting a purely spurious relationship is that the likelihood of obtaining the relationship by chance is very small. For 21 days spanning 460–630 DD, the deviation in daily trap catch from an average of the previous 3 days' catch was determined. A 3-day average was used so that the deviation in trap catch would measure a departure from a short-term trend. A contingency table was constructed by relating each deviation to rainfall. There was no instance when a positive deviation in trap catch occurred with rainfall; there were 11 days with positive deviations and no rainfall; there were 8 days with negative deviations and rainfall; and there were 2 days with negative deviations and no rainfall. A test of the null hypothesis that there is no difference in the number of positive or negative deviations associated with wet or dry days versus the alternative hypothesis that a greater number of negative deviations occurred during wet days results in rejection of the null hypothesis ($G_{adj} = 8.29$, $P \leq 0.001$).

It should be noted that the 2 days with negative deviations in trap catch and dry weather occurred during two unique times. The first occurred between 2 days with heavy rain. Other factors (i.e., cloudy and damp conditions) associated with the weather system that realized the two rainy days may have influenced trap catch. The 2nd day occurred near the end of the trapping period when adult parasitoid numbers were rapidly declining. We conclude that the trap catch from structurally different and spatially separated forest stands was strongly influenced by the same weather patterns.

The estimated mean and variance of the lifespan of adult *G. fumiferanae* are given by the mean and variance of the γ density function used to describe the PTD between emergence and death of the adult parasitoid. The mean is $\bar{P}\bar{T}\bar{D} = 87$ DD and the variance is $(\bar{P}\bar{T}\bar{D})^2/k = 946$ DD. The mean corresponds to ca. 10.5 days in 1981. A similar lifespan was evident in 1980.

In the laboratory, we found that adult female *G. fumiferanae* died within 3 days if they were not fed carbohydrates. This implies that in the natural environment, adult *G. fumiferanae* do indeed feed. Our data suggest that they may not use the vegetation on the forest floor as a food source. This is based on two observations. First, although many parasitoids were caught in malaise traps on the forest floor, no *G. fumiferanae* were trapped. Sec-

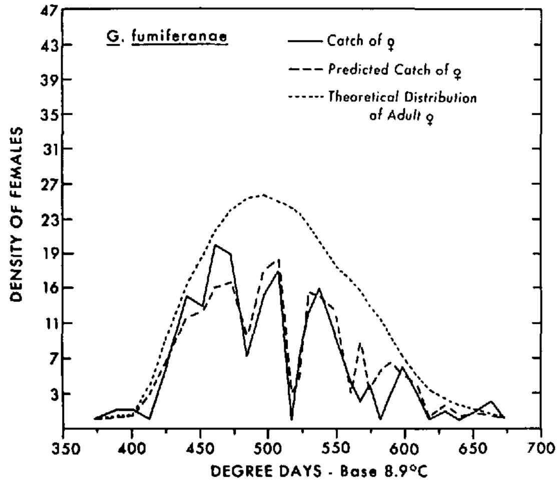

Fig. 5. Predicted and actual malaise trap catch of adult female *G. fumiferanae* in stand 3 and the theoretical, relative temporal distribution of adult females. Malaise traps were located singly in 13 balsam fir trees.

ond, extensive sweep netting of the ground vegetation failed to reveal the presence of *G. fumiferanae*.

Historical Data. The Julian dates during which *G. fumiferanae* was assumed to be most active in New Brunswick (428–584 DD) and total precipitation during these periods are listed in Table 3. The parasitism surface generated with the data is shown in Fig. 6. The pronounced influence of rainfall on the parasitism rate is apparent at both high and low host/parasitoid ratios. There are, however, two unexplainable irregularities in the parasitism surface. With moderate rainfall and high host/parasitoid ratios, a distinct valley exists. There is also a lack of response in the parasitism rate to a decline in the host/parasitoid ratio when associated with a moderate to high rainfall. It must be remembered that the data used in the analysis are subject to a great deal of potential bias and variation.

In the spring, bias may arise because parasitized larvae disperse less than unparasitized ones (Lewis 1960) and dispersal at that time may vary from year to year (Kemp et al. 1980). As a result, the measured parasitism rate may vary due to changes in dispersal loss. A large amount of sampling variability must also be present, although information on this variability is unavailable. Finally, temperature has not been included as an independent variable although it has been shown to influence the activity of the female parasitoid. Nonetheless, a discernible relationship between rainfall and parasitism was produced. When this relationship is combined with the observation that rainfall impedes the activity of the parasitoid, a conclusion can be drawn that excessive rainfall greatly diminishes the attack efficiency of the parasitoid, resulting in declines in parasitism rates.

Table 3. Julian dates for the DD interval 428–584 (base 8.9°C) and precipitation during this period from 1950 to 1957 at the Green River field station, New Brunswick

Year	Julian dates	Precipitation (cm)
1950	215–244	7.29
1951	216–240	7.80
1952	203–221	6.53
1953	204–232	5.08
1954	214–241	14.91
1955	203–225	7.09
1956	221–248	7.62
1957	217–245	1.78

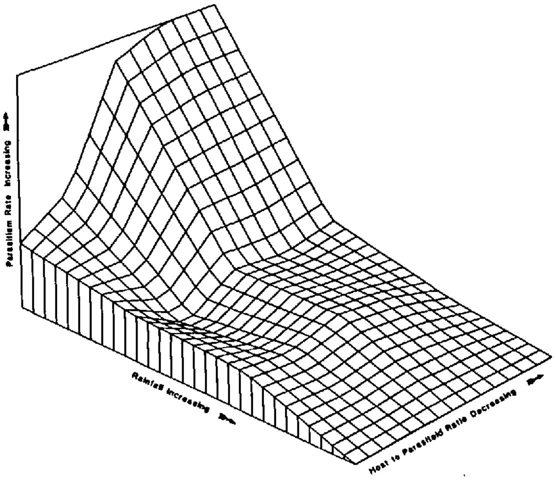

Fig. 6. Parasitism of spruce budworm by *G. fumiferanae* as a function of the host/parasitoid ratio and rainfall during the period of adult parasitoid activity.

Factors other than the host that influence the number and distribution of hosts attacked by a parasitoid may be classified into those that management cannot influence and those it can. Rainfall and temperature are two factors that appear to affect *G. fumiferanae*. Similar phenomena have been observed for other parasitoids. Klomp (1959) found that the attack efficiency of the tachinid parasitoid *Carcelia obesa* (Zett.) was correlated with the amount of sunlight during the period of parasitoid egg deposition. Burnett (1951, 1954, 1956) demonstrated that as the temperature declined, the number of sawfly pupae attacked by a chalcid parasitoid decreased. This decrease was attributable to a decline in the capacity of the parasitoid for oviposition and also to a reduction in the number of hosts contacted by the insect. In field experiments, he noted that parasitism was inhibited by rain and heavy dew. Messenger (1968) found that temperature extremes affected the aphid parasitoid *Praon exsoletum* (Nees) by inducing a shift in the proportion of ovipositional activities relative to other activities engaged in by the females and by reducing the proportion of successful attacks.

The changes induced by abiotic factors in a parasitoid's ability to locate and parasitize hosts may influence the dynamics of parasitoid/host systems because the number of hosts killed by the parasitoid is altered. *G. fumiferanae* and other parasitoids do not, by themselves, contribute to observed population oscillations of spruce budworm (Royama 1984). However, mortality due to a disease complex and unknown causes in combination with parasitism seems to be the most plausible force driving spruce budworm dynamics (Royama 1984). Weather-induced changes in parasitism may contribute to variations in the oscillations. In other parasitoid/host systems where the parasitoid(s) plays a more vital role in determining system dynamics, variation in parasitism rates due to abiotic factors may be more important.

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