TEMPERATURE-DEPENDENT DEVELOPMENT OF EGGS AND LARVAE OF *WINTHEMIA FUMIFERANAE* TOTH. (DIPTERA: TACHINIDAE), A LARVAL–PUPAL PARASITOID OF THE SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

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Abstract

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Relationships between temperature and development rates of eggs and larvae of *Winthemia fumiferanae* Toth. were experimentally determined, using the spruce budworm as host. Hatching of parasitoid eggs was triggered by host pupation. The median time required to complete egg development at different temperatures was estimated from distributions of percentage development success of the parasitoid over time between egg deposition and host pupation. For parasitoid eggs that had sufficient time to hatch, detachment from the host before pupation was the most important cause of mortality at 15°C or higher, but was negligible below this temperature. A curvilinear model describing egg development rate as a function of temperature was used to simulate the development of *W. fumiferanae* eggs in the field. The relationship between larval development rate and temperature also was modelled, and the variability described. Simulations initiated by host pupation-driven egg hatching, and terminated with prepupal drop to the ground, are presented and discussed with respect to the appropriateness of using host pupation as an indicator of parasitoid egg hatching in the field.

Résumé

Les relations entre la température et les taux de développement des oeufs et des larves de *Winthemia fumiferanae* Toth. ont été établies expérimentalement en utilisant la tordeuse des bourgeons de l'épinette comme hôte. L'éclosion des oeufs du parasitoïde était initiée par la pupaison de l'hôte. Le temps médian requis pour compléter le développement de l'oeuf à différentes températures a été évalué à partir de distributions du pourcentage de succès du parasitoïde en fonction du temps écoulé entre l'oviposition et la pupaison de l'hôte. Le décollement de l'oeuf avant la pupaison de l'hôte s'est avéré la cause la plus importante de mortalité des parasitoïdes ayant eu assez de temps pour éclore à 15°C ou plus, mais était négligeable sous cette température. Un modèle curvilinéaire décrivant le taux de développement des oeufs en fonction de la température a permis de simuler le développement des oeufs de *W. fumiferanae* en milieu naturel. La relation entre le taux de développement des larves et la température a été modélisée de façon similaire et la variabilité décrite. Des simulations, initiées par la pupaison de l'hôte comme indice de l'éclosion des oeufs et terminées par la tombée au sol des prépupes, sont présentées et discutées en rapport avec la pertinence d'utiliser la pupaison de l'hôte comme indice de l'éclosion des oeufs du parasitoïde en milieu naturel.

Introduction

Winthemia fumiferanae Toth. (Diptera: Tachinidae) is a common parasitoid of the spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae) (Coppel and Smith 1957). Female *W. fumiferanae* deposit macrotype eggs on late-instar larvae of the spruce budworm (Hébert *et al.* 1989). Coppel and Smith (1957) observed that the first-instar parasitoid larva does not usually leave the egg until the host begins to pupate; thus, larval development of the parasitoid takes place in the host pupa. When larval development is complete, *W. fumiferanae* leaves the host and drops to the ground in search for a pupariation site in the forest litter under conifers.

Phenology models have been developed for the spruce budworm (Régnière 1982, 1987; Hudes and Shoemaker 1988; Lysyk 1989). Temperature-dependent development relationships of some parasitoids are known (Nealis 1988; Nealis and Fraser 1988) but not for *W. fumiferanae*. This information is needed to understand better the seasonal biology of parasitoids, and also may be included in models of spruce budworm population dynamics. Phenology models would improve our understanding of host–parasitoid synchrony and of their ecological interactions, and would help develop pest management strategies. Such models can improve the timing of parasitoid mass releases (Osborne 1982; Lawrence *et al.* 1985) and be useful in the determination of the optimum periods for insecticide application without affecting parasitoids (Herbert and McRae 1983; Drummond *et al.* 1985).

In this paper, we present evidence in support of Coppel and Smith's (1957) observation on host pupation-dependent egg hatch in *W. fumiferanae*. We also studied the relationships between temperature and the development rates of eggs and larvae of this parasitoid. A stochastic model predicting parasitoid prepupal drop to the ground was developed and validated.

Materials and Methods

Hosts and Parasitoids. Overwintered spruce budworm larvae were supplied by the Forest Pest Management Institute (Forestry Canada, Sault Ste. Marie, Ont.). Larvae were reared in glass vials (Thomas 1984) on an artificial diet (McMorran 1965) at 20°C, 16L:8D photoperiod.

Winthemia fumiferanae females were collected with sweep nets in June on conifer trees, at Armagh, Qué. (46°46′N, 70°39′W, 270 m altitude) in 1985 and 1986, and Lac Solitaire, Qué. (47°12′N, 73°00′W, 350 m altitude) in 1987. Females were placed in screened cages and kept at 15°C, 16L:8D photoperiod. They were fed daily on a diet of 10% honey solution and crushed raisins, and the cages were sprayed with water twice per day, as suggested by Coppel and Smith (1957).

Laboratory Experiments. Sixth-instar larvae of the spruce budworm were exposed to a single attack by parasitoid females and then reared individually as described above. Host larvae were reared at 12, 16, and 20°C in 1985; 10, 15, 20, 25, and 30°C in 1986; and 20 and 27.5°C in 1987 (±0.5°C, 16L:8D photoperiod). Each year host larvae were reared at 20°C to verify that results obtained in different years were comparable. Following parasitoid egg deposition, host larvae were checked daily to record host pupation or emergence of a parasitoid larva. Host sex was determined using pupal characters (Miller 1963*a*). Once emerged, mature parasitoid larvae were placed in plastic cups (5 mL) containing moist vermiculite to favor pupariation. Because parasitoid eggs hatch at the time of host pupation, the duration of larval development was defined as the time elapsed between host pupation and parasitoid pupariation.

Many *W. fumiferanae* did not develop successfully in the laboratory. To determine the causes of parasitoid mortality, we collected exuviae of host larvae after pupation in 1987. Five causes of mortality were identified: 1, egg detachment (egg absent from host exuvium); 2, egg destruction (egg visibly damaged); 3, egg infertility (no evidence of embryonic development); 4, aborted egg development (dead embryo or larva inside the egg); 5, inability of first-instar larva to establish within the host (egg hatched, as evidenced by the presence of an exit hole).

Field Data. Egg deposition by *W. fumiferanae* on spruce budworm larvae and the appearance of spruce budworm pupae were monitored twice weekly by collecting 150-g branch tips of balsam fir and white spruce at Lac Solitaire in 1987. Spruce budworm pupation also was monitored by sampling at 2- to 3-day intervals at Armagh in 1985 and 1986, and at Lac à l'Épaule, Qué., in 1985 (balsam fir only). The Armagh and Lac à l'Épaule study sites were described by Lethiecq and Régnière (1988). To monitor *W. fumiferanae* prepupal drop to the ground, 50 funnel traps (Bean 1958), containing a small amount of humus to favor pupariation, were placed under balsam fir and white spruce trees in each study site. The traps were emptied three times per week and the puparia identified using the key of Ross (1952). Automatic weather stations installed in each study site recorded daily minimum and maximum air temperatures and precipitation.

Data Analysis. To model development success (Y) as a function of time (t) since oviposition at a given temperature, a cumulative Weibull distribution function (Weibull 1951) was fitted to the percentage of hosts from which a parasitoid emerged as a function of the time between oviposition and host pupation:

$$Y = \lambda\,(1 - e^{[-(t/\gamma)^{\alpha}]}) \qquad [1]$$

where λ is the maximum development success (%), and γ and α are scale and shape parameters, respectively. Parameters were estimated by non-linear regression (BMDP-AR, Dixon *et al.* 1985). Under the assumption that, at a given temperature, most parasitoid mortality resulted from failure to hatch before host pupation, the median time required before eggs could hatch ($t_{\lambda/2}$) was estimated by rearranging Eq. [1]:

$$t_{\lambda/2} = \gamma\,\sqrt[\alpha]{-\ln 0.5}. \qquad [2]$$

Development success was related to temperature by establishing a linear regression between λ and rearing temperature.

The relationships between estimates of median egg ($r/(T) = t_{\lambda/2}{}^{-1}$) or larval development rates, and temperature were described using Sharpe and DeMichele's (1977) thermodynamic model, as modified by Schoolfield *et al.* (1981):

$$r(T) = \frac{RHO25\,\dfrac{T}{298.15}\,e^{\left[\frac{HA}{R}\left(\frac{1}{298.15}-\frac{1}{T}\right)\right]}}{1+e^{\left[\frac{HL}{R}\left(\frac{1}{TL}-\frac{1}{T}\right)\right]}+e^{\left[\frac{HH}{R}\left(\frac{1}{TH}-\frac{1}{T}\right)\right]}} \qquad [3]$$

where T is temperature (Kelvin), R is the universal gas constant (1.987 cal $\mathrm{deg}^{-1}\ \mathrm{mol}^{-1}$), *RHO25* is development rate at 25°C (298.15K) assuming no enzyme inactivation, *HA* is the enthalpy of activation of the reaction that is catalized by the rate-controlling enzyme, *TL* and *TH* are the temperatures at which the rate-controlling enzyme is 1/2 inactive at low (*TL*) or high (*TH*) temperature, and *HL* and *HH* are changes in enthalpy associated with low (*HL*) or high (*HH*) temperature inactivation of the enzyme. The SAS (SAS Institute 1985) procedure provided by Wagner *et al.* (1984*b*) was used to select the form of the model and calculate estimates of the regression parameters.

To describe the variability in larval development of *W. fumiferanae*, we used the method of Wagner *et al.* (1984*a*), in which a Weibull function is fitted to the cumulative frequency distribution (y) of normalized development times (τ, relative to the median):

$$y = 1 - e^{[-(\tau-\beta/\gamma)^{\alpha}]} \qquad [4]$$

where γ and α are scale and shape parameters, and β is the minimum value of the expected normalized development time in the population.

Simulation of Egg Development and Prepupal Drop. The SAS (SAS Institute 1985) procedure of Wagner *et al.* (1985) was used to simulate the development of eggs and to predict the prepupal drop to the ground of *W. fumiferanae*. Air temperatures at intervals of 3 h were derived from records of daily minima and maxima (Wagner *et al.* 1985) obtained from weather stations. One-day cohorts of egg deposition were generated from a cumulative Weibull distribution (Eq. [1]) fitted to field data on percentage budworm larvae bearing *W. fumiferanae* eggs at Lac Solitaire in 1987. Each cohort was considered ready to hatch when accumulated development reached unity. The percentage of host pupae in the population when parasitoid egg development was complete also was calculated using a cumulative Weibull distribution function, for each cohort of egg deposition. Under the assumption that older host larvae are attacked randomly with respect to age, any difference between percentage host pupae in the population once egg development was complete, and percentage pupae at oviposition time may be used as an estimate of percentage parasitoid egg mortality due to inability to hatch at the time of host pupation.

Budworm pupation curves (cumulative Weibull distributions) were used to generate cohorts of eggs hatching at intervals of 4 days. Simulations of larval development were initiated from the midpoint of each cohort. Development was accumulated under field temperatures and became the independent variable in the variability function to predict the cumulative proportion of a cohort dropping to the ground over time. To predict overall cumulative proportion of prepupal drop to the ground, simulation results for all cohorts were added. Data from balsam fir and white spruce were treated separately because of differences in spruce budworm development and *W. fumiferanae* drop to the ground. At Armagh in 1986, populations of parasitoid and host were too low to obtain separate estimates, and data from both tree species were pooled. Model predictions were compared graphically with observed prepupal drop to the ground for validation.

Results

Egg Development. Ten *W. fumiferanae* eggs were dissected 4 days after being deposited on host larvae reared at 25°C. Five of the hosts from which an egg was collected had not pupated and five had. All five eggs in the first group contained a mature larva, but none in the second did. Two instances of entrance of a parasitoid larva in a pupating host also were observed directly. Parasitoid development lasted 17.0 ± 2.6 (SD) days ($n = 9$, range: 14–21) on male hosts attacked on the same day and reared at 15°C, when considering oviposition as the onset of development. It was much less variable (9.3 ± 0.5 days, range: 9–10) when considering host pupation as the onset. Therefore, it is clear that egg hatching is triggered by host pupation, with a variable period of quiescence between completion of embryonic development and hatching.

The distributions of percentage development success, as a function of the time elapsed between egg deposition and host pupation, are shown for each temperature tested in Figure 1. Eggs developed in less than 1.5 days at 25°C or higher (Table 1). An inverse relationship was observed between maximum percentage development success and temperature (Fig. 2). The causes of mortality were determined for 120 parasitoids for which parasitism failed despite sufficient time for egg hatch. Examination of host exuviae indicated that 66.6% of the eggs fell off before host pupation, 15% hatched but the parasitoid larva failed to establish, 6.7% contained a well-formed dead larva, 6.7% were damaged, and 5% were infertile.

Equation [3] was fitted to the estimated median rates of egg development as a function of temperature (Fig. 3, Table 2). Simulation of the development of *W. fumiferanae* eggs at Lac Solitaire in 1987 is illustrated in Figure 4. Eggs were deposited over a period of 2 weeks and needed close to 3 days to complete development (time lapse 1 in Fig. 4**A**). Mature first-instar larvae remained quiescent for about 7 days within the egg before host pupation (time lapse 2 in Fig. 4**A**). Assuming that older host larvae are attacked randomly with respect to age, the probability of parasitoid mortality because of insufficient time to complete egg development before host pupation (Fig. 4**B**) rose above zero in less than 1 week after the beginning of egg deposition, reaching ca. 15% at 80% completion of oviposition.

Larval Development. *Winthemia fumiferanae* larval development time was slightly longer in female than male host pupae, but differences were not significant (analysis of variance for influence of host sex using temperature as covariate: $F = 0.72$, df $= 1$, $P = 0.39$)

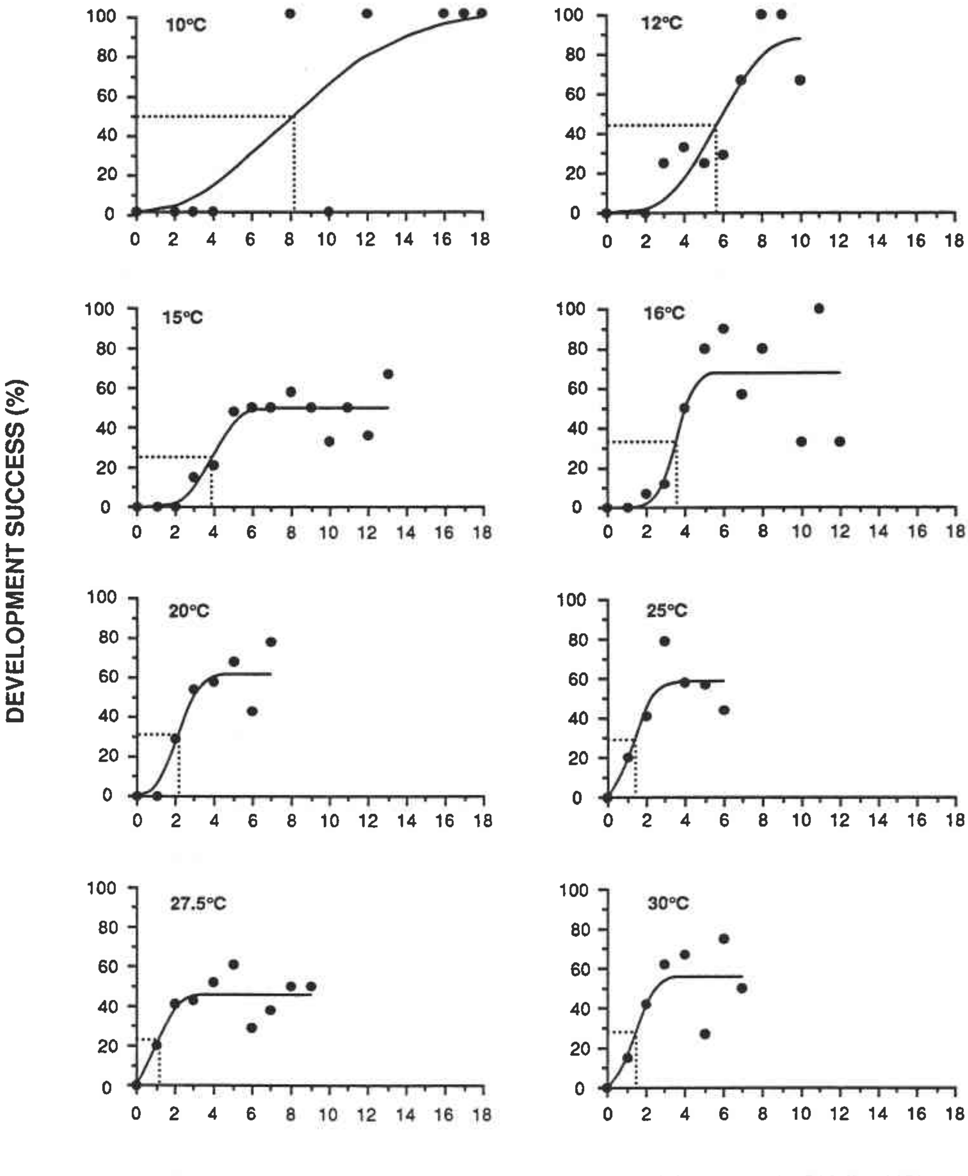

FIG. 1. Development success (%) of *Winthemia fumiferanae* as a function of the time elapsed between oviposition and host pupation at different temperatures. Solid lines: Eq. [1], fitted Weibull distribution function; dotted lines: $t_{\lambda/2}$, estimation of median time required to complete egg development.

(Table 1). The same analysis was realized on development rates, given that development times are usually skewed toward the longer times, and that development rates will be used in the model. The results were similar ($F=0.47$, df$=1$, $P=0.49$); thus, data on host sexes were pooled to produce a single model of larval development (Fig. 5**A**, Table 2). A correction factor of 1.06 was applied to the data obtained at 27.5°C, because of faster development of the parasitoid in 1987. The cumulative distributions of normalized development

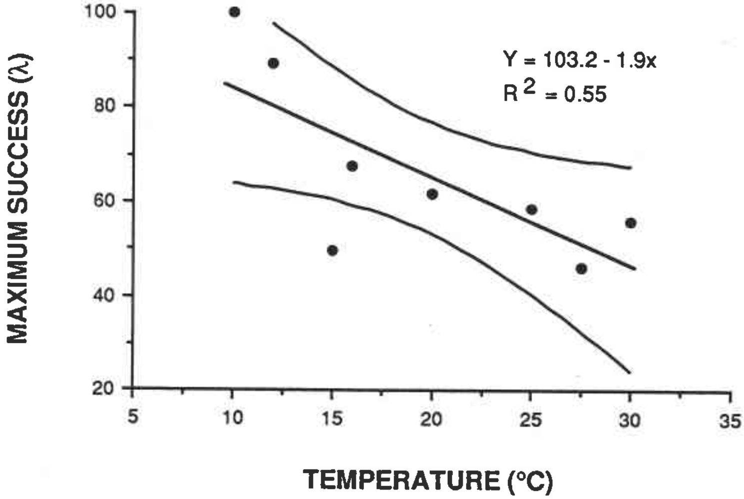

FIG. 2. Relationship between maximum development success (%) of *Winthemia fumiferanae* and temperature, with 95% confidence limits.

times at the eight temperatures overlapped broadly (Fig. 5**B**). The coefficients of variation at the 1 and 100% points of the curves were 9.7 and 22.7%, indicating a high level of consistency in the shapes of the distributions. Equation [4] was fitted to the cumulative distribution of normalized times pooled over temperatures (parameter estimates: $\gamma = 0.374$, $\alpha = 2.507$, $\beta = 0.680$, $R^2 = 0.999$).

Simulation of Prepupal Drop to the Ground. The model predictions compared favorably with observed parasitoid prepupal drop to the ground under both tree species at Armagh and Lac à l'Épaule in 1985 (Fig. 6). The prediction was late at Armagh in 1986, possibly due to poor estimates of host pupation caused by the presence of a large number of moribund sixth-instar budworm larvae parasitized by *Meteorus trachynotus* Vier. Indeed, pupation did not exceed 15%. The predictions were somewhat early in Lac Solitaire in 1987, more so under balsam fir than under white spruce. Heavy rainfalls between days 176 and 180 may have retarded prepupal drop. A similar situation was observed at Armagh in 1985 near the beginning of prepupal drops (days 187–189), when virtually no drop was recorded during 2 rainy days.

Discussion

The observation of Coppel and Smith (1957) that *W. fumiferanae* eggs hatch only when the host is pupating was confirmed in this study. *Winthemia manducae* Sabrosky and DeLoach is another species of the genus in which eggs are known to hatch at the time of host pupation (DeLoach and Rabb 1971). These authors reported that most larvae remained within the egg until 5–120 min before host pupation. They also reported that the larva must penetrate the host within 60 min after exuviation because after this time the host cuticle has already hardened sufficiently to prevent the parasitoid larva from penetrating. However, this hatching behavior is not generalized throughout the genus, other species being known to enter the host well before pupation (Allen 1925; Marsh 1937; Lentz and Pedigo 1974; Danks 1975).

Eggs that detach from larvae before hatching may be one of the major causes of parasitoid mortality. This may partly explain how curves of oviposition and effective parasitism by this parasitoid can be very different (Hébert *et al.* 1989). In the laboratory, egg detachment from the host before pupation was the major cause of mortality of parasitoids

Table 1. Effect of constant temperatures on median and mean (±SD) development times (days) of *Winthemia fumiferanae* eggs and larvae, in male and female pupae of its host, *Choristoneura fumiferana*

Temp. (°C)	Eggs	Larvae in male host pupae			Larvae in female host pupae			Larvae in both sexes of the host		
	Median	*n*	Mean ± SD	Median	*n*	Mean ± SD	Median	*n*	Mean ± SD	Median
10	8.3	9	27.8±3.6	28.8	3	30.7±3.5	31.0	12	28.5±3.2	29.0
12	5.7	3	14.0±1.0	14.0	13	16.6±3.6	16.0	16	16.1±3.4	15.5
15	3.9	31	10.1±1.8	9.9	36	10.8±1.0	10.9	67	10.5±1.5	10.4
16	3.6	7	10.1±1.8	9.7	16	10.6±3.8	9.3	26*	10.1±3.3	9.2
20†	2.1	33	6.6±0.7	6.7	38	7.3±0.6	7.3	71	7.0±0.7	7.0
25	1.4	38	5.1±0.6	5.0	48	5.5±0.9	5.4	86	5.3±0.8	5.2
27.5	1.1	31	4.9±0.8	4.7	19	5.1±0.8	5.0	50	5.0±0.8	4.9
30	1.5	34	5.2±1.2	5.0	29	5.2±0.7	5.1	63	5.2±1.0	5.1

*Three non-sexed hosts were included.
†Data of 1986.

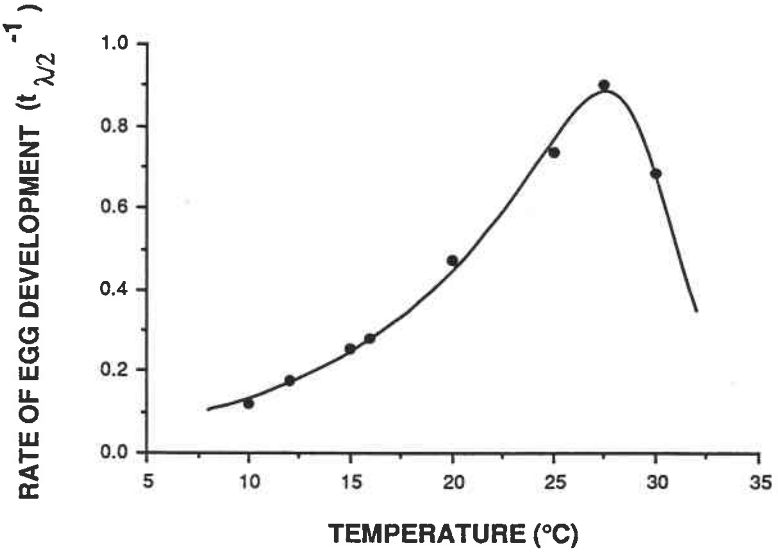

FIG. 3. Development rate of *Winthemia fumiferanae* eggs as a function of temperature. The curve shows Sharpe and DeMichele's (1977) model (Eq. [3]) fitted to estimates of median development rates at different constant temperatures.

which had sufficient time for hatch. The observed relationship between maximum percentage development success of *W. fumiferanae* and temperature was probably caused by lower parasitoid egg losses through detachment from the host at low temperatures, which may have resulted from temperature-dependent differences in larval activity.

At Lac Solitaire in 1987, we estimated that parasitoid larvae remained about 7 days within the egg waiting for host pupation. This waiting period may represent an important risk of mortality for *W. fumiferanae*. This parasitoid has reduced chances of survival when eggs are deposited on larvae attacked by other larval parasitoids, because all other parasitoids attacking late-instar larvae of the spruce budworm can actually develop in sixth-instar larvae, thus being presumably superior competitors. In particular, *W. fumiferanae* eggs probably never hatch when deposited on larvae already parasitized by *M. trachynotus*, a common competitor attacking fifth- or sixth-instar larvae of the spruce budworm, and which emerges nearly always from the sixth instar (McGugan 1955). *Meteorus trachynotus* is known to reach high incidences of parasitism in the last years of outbreaks (McGugan and Blais 1959; Blais 1960, 1965; Miller 1963*b*; Miller and Renault 1976), and may be responsible for the decrease in frequency of *W. fumiferanae* at this time. A 14-fold decrease in population density was observed for *W. fumiferanae* between spring adult emergence (3.14 per square metre) and prepupal drop to the ground (0.22 per square metre) at Armagh in 1986 (Hébert *et al.* 1989), when the incidence of parasitism by *M. trachynotus* reached 35% (Maltais *et al.* 1989).

In the laboratory, *W. fumiferanae* prefers to oviposit on sixth-instar larvae of the spruce budworm (unpublished data). However, a lag of 3–4 days was observed in the field between the appearance of sixth-instar larvae and the beginning of oviposition, indicating that young sixth-instar larvae may be less acceptable or susceptible to attack by *W. fumiferanae* (Hébert *et al.* 1989). As shown in the present study, the period of actual availability of sixth-instar larvae for successful parasitism by *W. fumiferanae* also is shortened, because of the rapidly increasing risk of failure due to insufficient time to complete egg development before host pupation. This probably explains the short period of oviposition (2 weeks), which ended when about 50% of the hosts were no longer suitable because they had already

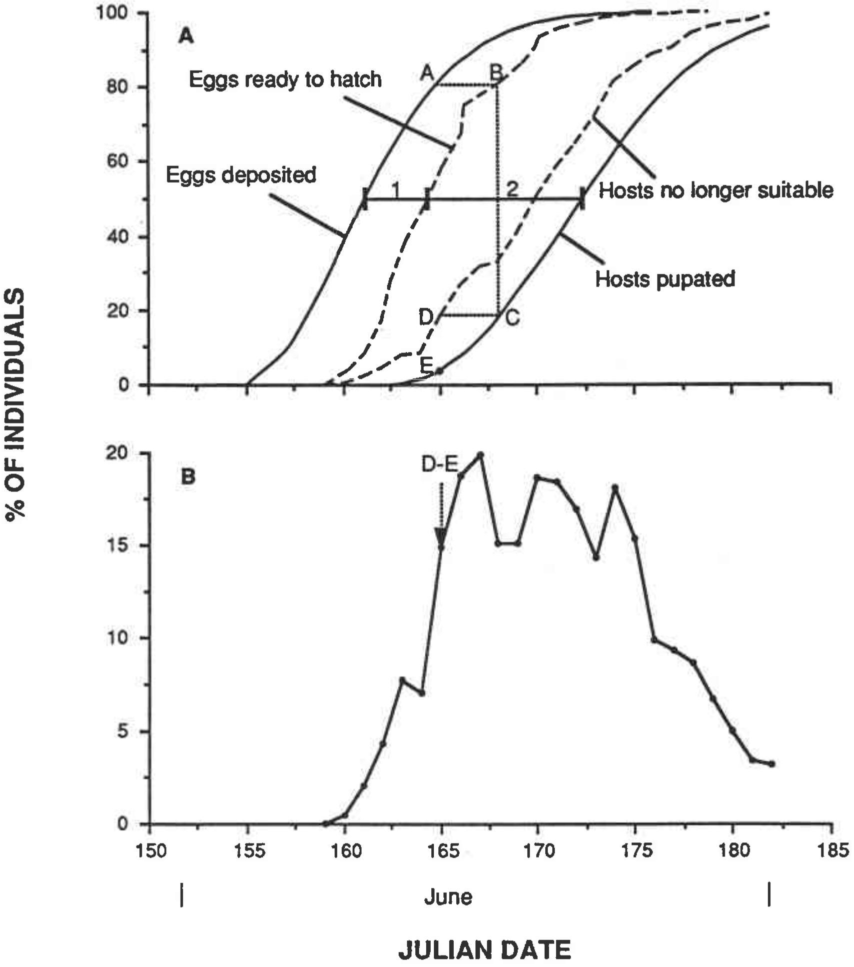

FIG. 4. Seasonal trends in *Winthemia fumiferanae* egg deposition, development, and mortality in relation to host pupation at Lac Solitaire in 1987. (**A**) Trends for parasitoid oviposition and host pupation were generated from field data whereas trends for egg readiness to hatch and hosts no longer suitable for completion of parasitoid egg development were simulated. A–D shows relationships between observed and simulated trends for cohort of eggs deposited on day 165: A–B, B–C, C–D determine projected date of hatching, proportion of hosts pupated on that date, and proportion of host population actually unsuitable for successful parasitism, respectively. Time lapse 1 represents the average time of egg development, and time lapse 2 represents the average waiting time of mature first-instar larvae within the egg. (**B**) Percentage of budworm larvae exposed to parasitoid attack but escaping parasitism due to insufficient time for the parasitoid to complete embryonic development before host pupation. For day 165, calculated as D − E obtained from (**A**).

Table 2. Parameter estimates for Sharpe and DeMichele's (1977) model fitted to the median rates, for egg and larval development of *Winthemia fumiferanae*

Life stage	*RH025*	*HA*	*TL*	*HL*	*TH*	*HH*	R^2
Eggs	0.7899	19265.5	—*	—*	303.2	126155.2	0.999
Larvae	0.2266	12390.3	283.2	−96003.3	305.0	72245.0	0.999

*Four-parameter model without low-temperature inhibition.

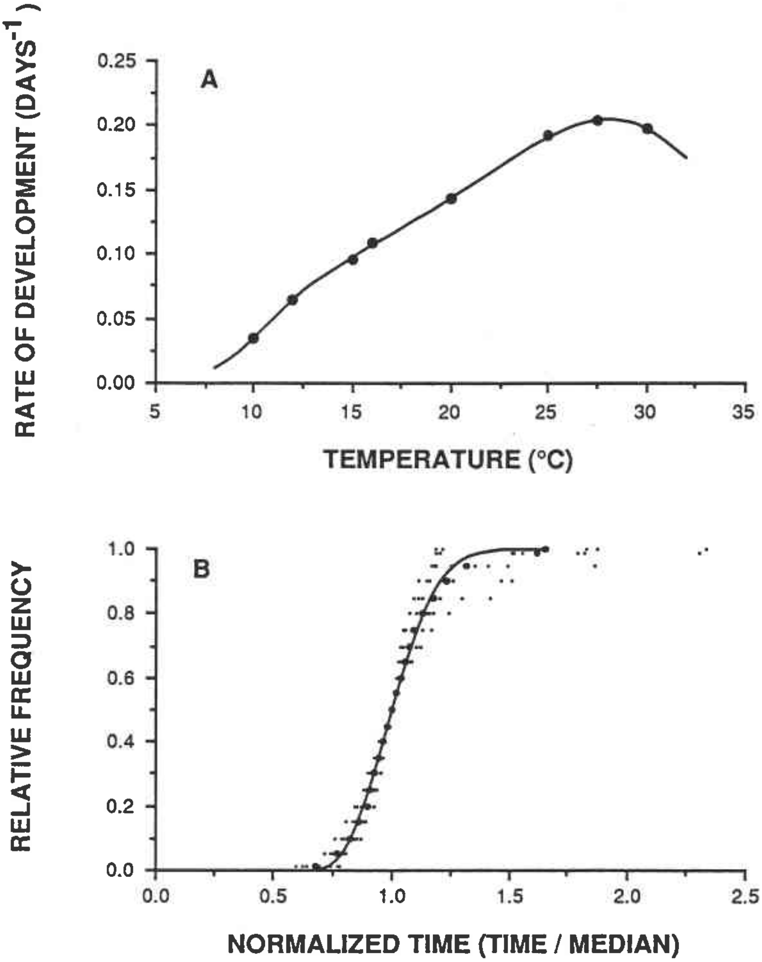

FIG. 5. Development of *Winthemia fumiferanae* larvae. (**A**) Development rate as a function of temperature; the curve shows Sharpe and DeMichele's (1977) model fitted to estimates of median development rates at constant temperatures. (**B**) Description of the variability in development times.

pupated or were still larvae but were too old to allow maturation of first-instar parasitoid larvae.

Host pupation provided a good estimate of parasitoid egg hatch in the field, as shown by the fact that its utilization to generate the cohorts of egg hatching used in the simulations of prepupal drop to the ground provided generally good results, except in the collapsing population of Armagh in 1986. In this case, the slow disappearance of moribund larvae from the samples may have biased forward the host pupation curve (see Fig. 6). However, other environmental factors than just temperature, such as rainfall, should also be considered when simulating *W. fumiferanae* prepupal drop to the ground. The assertion that rainfall had an influence at Lac Solitaire in 1987 seems reasonable because the delay recorded in prepupal drop to the ground during bad weather conditions was rapidly recovered, the end of the drop being well predicted by the model (see Fig. 6).

Although a population of *W. fumiferanae* may suffer important losses due to its hatching behavior, this waiting strategy may be adaptive, given that it is a truly pupal parasitoid,

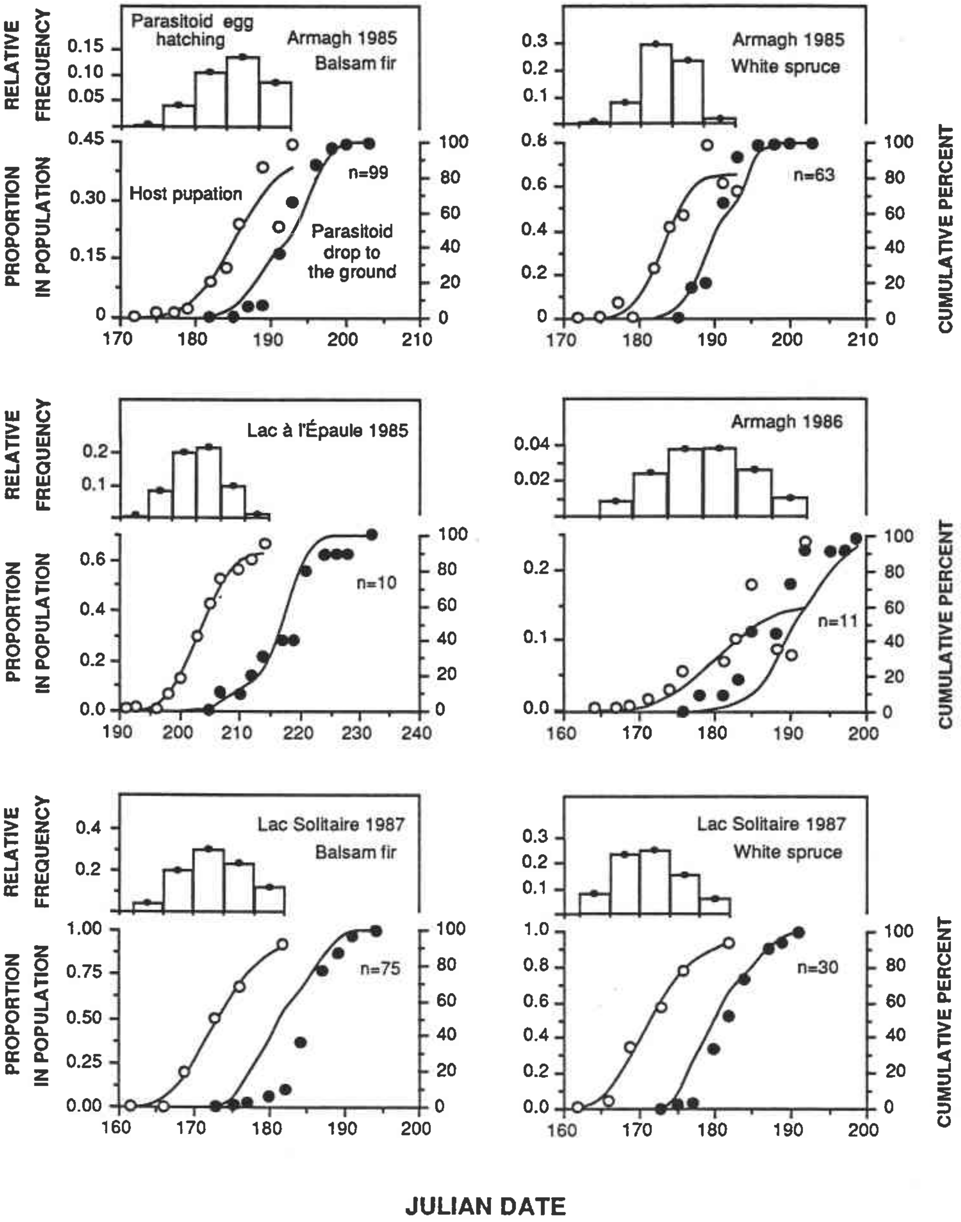

FIG. 6. Model predictions (solid lines) and observed values (closed circles) of cumulative prepupal drop to the ground of *Winthemia fumiferanae* under white spruce and balsam fir at different sites-years. Model predictions are based on multiple simulations initiated at the midpoint of each 4-day class of the frequency distribution of egg hatch (upper portion of each graph). The cohorts of hatching parasitoids were driven from host pupation curves (solid lines) that were generated from data on proportion of pupae in each population (open circles).

by ensuring that first-instar larvae will begin development at the earliest possible time. Thus, it may confer a competitive advantage to this parasitoid over other pupal parasitoids of the spruce budworm.

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