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The mortality of overwintering *Phyllonorycter blancardella* (F.)
(Lep., Gracillariidae) pupae simulated as a loss in a
time-varying distributed delay model

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A time-varying distributed delay model with attrition is used to simulate the development of overwintering *Phyllonorycter blancardella* (FABR.) pupae in orchards. The temperature in the herbal layer was the only driving variable. The following elements were considered in the model: temperature-dependent development and its variance, the influence of diapause on population development, the mortality due to parasitoids and unknown factors as well as the mortality due to leaf burial by earthworms. The model was primarily constructed for illustrative purposes and shows how these effects can be directly built into the basic equation. Nevertheless, it allows us to draw some conclusions with respect to the overwintering phase: the losses due to leaf burial were very high but stable over 4 years at a Swiss location, while great differences were predicted between two years in a Canadian orchard.

INTRODUCTION

Arthropods generally pass through a series of life stages before they reach the reproductive adult life stage. During one growing season we usually observe the occurrence of several different life stages at any point in time but notice that the proportion has often changed if we return to the same field at some later date. The observed frequencies of different life stages can be put into a two-dimensional matrix with the sample dates as lines and the life stages as columns. Various methods have been proposed to analyze such a stage-frequency matrix, however, a discussion of these goes beyond the purpose of this work and the interested reader is referred to MANLY (1989a). Our work is restricted to organisms with temperature-dependent development and differs from many investigations published so far in that the matrix is rigorously deduced from demographic principles. Of these principles, the poikilothermy of arthropod development and the associated variance have already been studied elsewhere (SEVERINI *et al.*, 1990a, 1990b, 1990c). Briefly, the two principles suggest the use of time distributed delay models for the explanation of the stage-frequency matrix. The delay model implies that a group of individuals born at the same time, i. e. a cohort, is the basic population unit which should be considered in parameter estimation procedures.

During passage through the different life stages the cohort may lose or gain individuals because of migration or mortality. VANSICKLE (1977) has used system's theory to show how to incorporate these into the time distributed delay models, and his work has enabled applied ecologists to make the transition from population phenology to population dynamics and agroecosystem analysis (GUTIERREZ & BAUMGÄRTNER, 1984). The mathematical theory is given, for example, by

MANETSCH (1976) and VANSICKLE (1977). A review of the method with reference to ecological applications has been written by SEVERINI *et al.* (1990b), while, among others, WELCH *et al.* (1978), GUTIERREZ & BAUMGÄRTNER (1984) and BAUMGÄRTNER & GUTIERREZ (1989) have demonstrated the use of the model in supervised pest control programs and agroecosystem analyses. SEVERINI *et al.* (1990b) revised elements of the delay theory and parameter estimation procedures in an ecological context, but for the sake of simplicity they refrained from considering multiple entries into a series of delay processes and from incorporating losses (mortalities) which may occur. The first aspect is treated elsewhere (SEVERINI *et al.*, 1990c) while the relationship between losses and the cohort development is currently under study. As an introduction to this investigation we present, in this work, a simple case study which illustrates the relationship between developmental times and variance, the modifying influence of diapause, the combination of different mortalities on transit times and the implications for parameter estimation procedures. The objective can best be met by selecting a simple single-cohort case study with good illustrative qualities. For this purpose the overwintering (diapausing) pupal stage of the lepidopterous leaf miner *Phyllonorycter* (= *Lithocolletis*) *blancardella* (FABR.) appeared to be particularly appropriate, although the data base for both parameter estimation and validation was small. This would have been a serious limitation for the construction of a model for predictive purposes, however, this was not attempted in this work.

Bionomics of *P. blancardella*

The larvae and pupae of the spotted tentiform leaf miner *P. blancardella* inhabit the leaves of *Malus* spp. The females lay the eggs on the under side of the leaves in which the larvae construct conspicuous mines which they don't leave until emerging as adults. In North America and in Europe the mines have been found in such high numbers that they were assumed to affect the growth of apple trees and to decrease the productivity of the orchard. In apple growing areas of both continents the population dynamics was therefore studied to create a basis for rational pest control programs (for example, BAGGIOLINI, 1960; BRIOLINI, 1969; POTTINGER & LE ROUX, 1971; CELLI, 1971–72; JOHNSON *et al.*, 1976, 1979; MAIER, 1983; TRIMBLE, 1983a, 1983b; VAN FRANKENHUYZEN, 1983; LAING *et al.*, 1986; INJAC, 1987).

In 1972 we began to study the population dynamics of *P. blancardella* in several neglected Swiss apple orchards (BAUMGÄRTNER *et al.*, 1981a). We first found that a high number of larvae were unable to reach the overwintering pupal stage at the end of the growing season. The losses to the population appear to be substantial but are not considered in this work. At the time of leaf fall the immature life stages drop, with the leaf they inhabit, on to the orchard floor (POTTINGER & LE ROUX, 1971; LAING *et al.*, 1986). In many studies it has been demonstrated that earthworms are responsible for the burial of the fallen leaves (BIERI & CUENDET, 1989). LAING *et al.* (1986) found that only about 5% of the *P. blancardella* pupae survive if the leaves they inhabit are pulled into the soil by earthworms. Consequently, leaf burial due to earthworms is generally expected to be an important factor for the survival of *P. blancardella* populations during the winter (POTTINGER & LE ROUX, 1971). In Canada LAING *et al.* (1986) found that substantial losses occur in relatively warm springs but many *P. blancardella* adults emerge before all the leaves are buried. A cool spring delays the pupal development so that

the adults do not appear until most leaves have been buried by earthworms. Consequently, the population suffers higher losses under cool spring conditions.

In this work a model is constructed to assess the mortality of pupae overwintering in Swiss apple orchards located near the town of Chur. The model shows how to introduce diapause effects in the developmental process and combines the mortality inflicted by earthworms with the once caused by parasitoids and unknown factors, treating the resultant effect as a loss in a time-varying distributed delay model.

MATERIAL AND METHOD

Mathematical framework

Individuals of *P. blancardella* pass through the egg, sap feeding and tissue feeding larval stages and through the pupal stage before they emerge from the mine as free living adults. This work, however, is restricted to the overwintering pupal stage only and, for the sake of simplicity, assumes that there is only a single cohort entering this life stage on the first day of December. The temperature-dependent development of the cohort is modelled here according to the time-varying delay theory (see SEVERINI *et al.*, 1990b). A number H of identical elementary delays connected in series represents the overwintering pupal stage in which losses, i. e., mortalities, may occur, until the adults emerge distributed in time. For simulation purposes, it is convenient to write the relevant equations in flow rates:

$$\frac{dr_h(t)}{dt} = \frac{H}{DEL(t)} \left[r_{h-1}(t) - \left(1 + \frac{1}{H} \cdot \frac{dDEL(t)}{dt} + B(t) \cdot \frac{DEL(t)}{H} \right) \cdot r_h(t) \right] \quad [1]$$

$h = 1, 2, \dots, H$

where: h = subscript denoting the substage; $r_0(t)$ = flux of individuals entering the overwintering pupal stage (in this case a cohort); $r_h(t)$ = "intermediate fluxes", i.e. fluxes of individuals leaving the h -th elementary delay; H = the number of elementary delays to be determined; $B(t)$ = instantaneous loss rate [as explained below, the model requires a more general definition of losses than given by VANSICKLE's (1977) attrition]; $DEL(t)$ = instantaneous expected transit time to be determined.

There is one cohort only which enters the pupal stage so that $r_0(t) = 1$ at time $t = 0$ and $r_0(t) = 0$ for $t > 0$. The time-distributed outputs $r_H(t)$, cumulated over time, represent the flux of emerging adults, while its integral

$$\int_0^{\infty} r_H(t) dt$$

is called cumulative flight and can be compared with pheromone catches for model validation purposes (WELCH *et al.*, 1978; BAUMGÄRTNER & SEVERINI, 1988). The mortality $B(t)$ considered in our work is an additional element in attempts to predict spring emergence of *Phyllonorycter* adults: TRIMBLE (1983a) and JOHNSON *et al.* (1979) considered the temperature-dependence but not the variance, while DRUMMOND *et al.* (1985) added the variance and used a time distributed delay model for *Phyllonorycter crataegella* (CLEMENS).

There are two versions of the delay model which differ in the way the transit time is defined (SEVERINI *et al.*, 1990b). In the time invariant version a physiological time horizon, conveniently described in units of day-degrees, can be defined on which the cohort development is modelled with constant expected transit time. Though it is difficult to introduce mortalities that operate independently of population development (ZAHNER & BAUMGÄRTNER, 1988; SCHAUB & BAUMGÄRTNER, 1989), this method appears to be more often used than the time-varying version selected here, in which DEL(t) is time-dependent. This quality enables us to incorporate the temperature effects directly into eqn. 1, i.e. as DEL[T(t)] (BAUMGÄRTNER & SEVERINI, 1988; SEVERINI *et al.*, 1990b) and B[T(t)].

In this work DEL[T(t)] and B[T(t)] are expressed in units of days. To simulate the development of the cohort eqn. [1] is discretized for a time step of 1/16 day (1.5 hours), i.e. there are N = 16 simulation time increments a day.

The driving variable T(t)

The temperature is the only driving variable (eqn. 1). In the system under study it should be measured in the herbal layer rather than in the air (TRIMBLE, 1983b). At the Chur location, the daily temperature extremes in both the air (T'_{\min} , T'_{\max}) and in the herbal layer (T_{\min} , T_{\max}) were readily available for 1981 and 1988, so that, for the period from January 1st to June 30, the following relationship could be established:

$$T_{\min} = 1.026T'_{\min} - 2.0211 \quad r^2 = 0.934 \quad [2a]$$

$$T_{\max} = 1.118T'_{\max} + 0.958 \quad r^2 = 0.938 \quad [2b]$$

These linear relationships are used as a first approximation of the herbal layer temperature for both the Chur orchard and the Meaford (Canada) site where JOHNSON *et al.* (1976) were working. Because of these necessary approximations the herbal layer temperature can only be given with a low degree of reliability.

The same method was used to represent the daily temperature extremes under near-field conditions in a shelter in Zurich. The parametrization of the diapause effect required temperature data from December 1979 to May 1980, but thermohygrograph measurements were available from January 19 until February 28 only. During this period the shelter temperatures were related to the corresponding values recorded at the Swiss Meteorological Station in Zurich. In this case, however, the values for r^2 are low which has implications for parameter estimation as discussed below.

Parameter estimation

The instantaneous expected value of transit time DEL[T(t)] under non-diapausing conditions can be derived from BAUMGÄRTNER *et al.* (1981b) who, by neglecting the mortality, used a modified model of LOGAN *et al.* (1976) to relate the daily developmental rates $z(T)$ of *P. blancardella* cohorts to the constant temperatures:

$$z(T) = a \{ e^{b(T-T_b)} - e^{b(T_b-T_m)} - 1/c[(T_m - T_b) - (T - T_b)] \} \quad [3]$$

Observations and preliminary calculations showed that a base of $T_b = 5.6^\circ\text{C}$ and an upper threshold of $T_m = 32^\circ\text{C}$ were appropriate. Subsequently, least square techniques were used to estimate the parameters a, b and c ($a = 0.028$, $b = 0.100$, $c = 2.637$).

We assume that equation [3] can be applied to represent the response of a cohort to fluctuating temperatures $T(t)$ and obtain the instantaneous transit time

$$\text{DEL}[T(t)] = 1/z[T(t)] \quad \text{for } T < T_m \quad [4a]$$

$$\text{DEL}[T(t)] = 1000.0 \quad \text{for } T \geq T_m \quad [4b]$$

The number H of elementary delays can be calculated as follows: If we neglect furthermore the mortality, the same experiment can be used to calculate H according to the method of SEVERINI *et al.* (1990a, 1990b). Briefly, three distributions of adults are obtained by rearing three cohorts in climatic chambers (i.e. 15, 20 and 25°C). These distributions can be plotted with respect to three different time horizons. For example, the expected transit time observed at 25°C is considered as the unit of the time horizon for the adults emerging distributed in time at this temperature. The three distributions can be combined and fitted by an Erlang function.

$$r_H(\omega) = \frac{H^H}{(H-1)!} \cdot e^{-\omega H} \cdot \omega^{H-1} \quad [5]$$

where ω is a new variable which represents the time as a proportion of the expected values at each temperature. The best Erlang function fitted to the data has a $H=54$ (with 2 degrees of freedom and a significance level of 0.124). However, the number of cohorts (3) and consequently, the degrees of freedom (2), are small and should be increased in future attempts to parametrize H .

The diapause effect on the developmental time and the mortality in the absence of earthworms was assessed on a group of $N_i = 79$ individuals which were collected in the field and brought into a shelter on December 1st, 1978. In the absence of reliable information on the age-structure of the population at the time of sampling, we assume that they simultaneously enter the pupal stage on this day. The time the adults left the mine was recorded. On April 30th, i.e. after a time interval of $J = 151$ days, $N_f = 52$ adults had emerged; 3 pupae had died because of parasitoids, but the cause of death could not be determined for the remaining 24 individuals. The stage specific survival was thus $\varepsilon = N_f/N_i = 0.66$ (as a first approximation). The observed mean duration $\Delta \tau'$ in physiological units for the M survivors was computed with the rate summation method (CURRY & FELDMAN, 1987)

$$\Delta \tau' = 0.1 \cdot 1/N_f \sum_{n=1}^{N_i} \sum_{j=1}^{10J} z_{n,j}[T_j] \quad [6]$$

in which j 's is the index for a 0.1 day step, while the index n is used for the surviving individuals. The multiplication with 0.1 is required because $z(T)$ in eqn. 3 is expressed as a proportion per day. $z_{n,j}[T_j]$ is the developmental rate per day on the j '-th time step with the mean temperature T_j . As stated above T_j cannot be represented with a satisfactory degree of reliability. However, as important as accurate temperature recordings may be, observations on clearly defined individual cohorts should be made. At the same time studies under a regime of controlled temperatures and photoperiods should be carried which would permit the formulation of the passage through the diapause in a more realistic way than done here. Without meeting these requirements $\Delta \tau'$ remains a very crude estimation of a retarding effect. This is justified only as we are more interested in illustrating how

it can be built into the model rather than in a precise estimation of its effects.

$\Delta \tau' = 3.76$ represents the observed mean duration under diapause conditions. It is obtained by applying the experimental data to eqn. 6. Under non-diapause conditions, on the other hand, according to eqn. 3 and the rate summation method of CURRY & FELDMAN (1987) pupal development is completed if

$$0.1 \cdot \sum_{j=1}^{10j} z_{n,j}[T_j] = 1 \quad [7]$$

Consequently, $\Delta \tau'$ is 3.76 times longer than the corresponding value for non-diapause conditions. Hence, 3.76 is the factor Ψ which expresses the proportional lengthening of the developmental time in the shelter with respect to the general duration of the pupal life stage.

The solution of a system of delay equations with attrition (eqn. 1) is easier to calculate for a system without mortality. The value of the expected transit time $\Delta \tau'$, calculated for a cohort with mortality, is less than the value $\Delta \tau$ obtained for a cohort which does not suffer from mortality (VANSICKLE, 1977; SCHAUB & BAUMGÄRTNER, 1989)

$$\Delta \tau = \Delta \tau' \cdot \varepsilon^{-1/k} \quad [8]$$

The correction factor $\zeta = \varepsilon^{-1/k} = 1.0078$ is small and consequently causes only a small difference between the expected transit times $\Delta \tau'$ and $\Delta \tau$. Nevertheless, it is important to consider this factor in our model because we can demonstrate from it how to calculate attrition (see eqn. 10). Furthermore, the difference is important if parameter estimation resulted in a low value for H and a high stage-specific mortality which would increase the difference (VANSICKLE, 1977).

The factor Ψ (eqn. 7) and the calibration factor v , discussed subsequently, can be used to represent diapause effects on the instantaneous developmental time as follows

$$\text{DEL}[T_j] = \text{DEL}'[T_j] \cdot \Psi \cdot v \quad [9]$$

The initial simulation carried out at the Chur orchard showed a mean discrepancy of $v = 1.38$, expressed in proportional development, between the observed and predicted mean developmental times. Because of microclimatic influences (see below), the inaccuracy of representing the temperature profile in eqn. [6] and the difficulties of formulating a realistic model on the diapause process, we have refrained from a biological interpretation of v .

The correction factor ζ of eqn. [8] can subsequently be used to define the instantaneous attrition term $B_1[T_j]$ which, as formulated in VANSICKLE'S (1977) equation [18], reduces during the developmental time by a constant proportion the number of pupae

$$B_1[T_j] = H \cdot \left\{ \frac{\zeta}{\text{DEL}[T_j]} - \frac{1}{\text{DEL}'[T_j]} \right\} \quad [10]$$

The stage-specific survival has been estimated with a small number of insects only and is likely to vary widely under different ecological conditions. It serves here merely to illustrate the dependency of transit time on survival, a model with good predictive capabilities should undoubtedly account for such differences.

Mortality due to leaf burial by earthworms was first studied in a neglected and in a commercial orchard (Chur 1978/1979). In the following year (Chur, 1979/

1980) apple leaves from a commercial as well as from a neglected orchard were exposed to earthworms in a neglected orchard only. Briefly, each orchard under study was divided into three blocks with an area underneath the tree crown and between the tree rows. Three cages with leaves were put into each area. At the beginning of the experiment (on December 1st), at the time of the first evaluation (March 7) and at the time of the last assessment (April 18 in 1979, May first in 1980) the leaf area was measured with a leaf surface integrator. The earthworm density was not estimated. For our purpose an exponential model appeared to be a reasonable approximation for describing the proportional losses with respect to the initial leaf surface ($\Omega = 1.0$):

$$L(\tau) = \Omega \cdot e^{-u \cdot \tau v} \quad [11]$$

Via least square techniques $u = 0.1411 \cdot 10^{-5}$ and $v = 2.299$ were obtained. For an initial leaf mass $\Omega < > 1$, i.e. a defined initial mine density, Ω had to be changed accordingly. τ is the time for earthworm activity, expressed in units of daydegrees above the 2°C threshold (RAW, 1962). It is calculated by forcing a sine wave through the temperature extremes in the herbal layer and integrating it above the threshold (GILBERT *et al.*, 1976). After differentiating eqn. [11] with respect to τ we obtain $B_2(\tau)$ which we can subsequently transform into the daily loss $B_2[T_j]$

$$B_2[T_j] \Leftarrow B_2(\tau) \quad [12]$$

because the number of day-degrees for a particular day can be calculated. In the simulation model it is convenient to calculate them via the rate summation method (eqn. 7) for 16 simulation time increments per day. As opposed to the first loss term $B_1[T_j]$ in eqn. [10], $B_2[T_j]$ does not operate as a constant proportion through the developmental time of pupae. It acts instead on a time horizon which reflects the earthworm activity.

The combined losses per day, i.e., the overall mortality in the simulation model [1], were calculated as follows

$$B[T_j] = B_1[T_j] + B_2[T_j] / \left(\sum_{h=1}^H r_h[T_j] \cdot DEL[T_{j-1}] / H \right) - B_1[T_j] \cdot B_2[T_j] / \left(\sum_{h=1}^H r_h[T_j] \cdot DEL[T_{j-1}] / H \right) \quad [13]$$

Presumably, earthworms do not distinguish between leaves inhabited by living or dead pupae. Hence, $B_2[T_j]$ would also include population losses which have already been eliminated via $B_1[T_j]$. This is important if parasitoid survival is to be taken into account (JOHNSON *et al.*, 1979).

Model validation and evaluation

The flight of the overwintering males was recorded over 4 years with 2 pheromone traps, which were put into the neglected orchard in Chur and checked weekly. In all except the first year (1978/79) the genitalia of all the males caught were prepared, the *P. blancardella* males were identified and counted. In 1978/79 all males found in the pheromone traps were assumed to belong to the species *P. blancardella*. The cumulative flight of *P. blancardella* males was compared with the predictions of the model, computed with an initial mine number $\Omega = 100.0$.

Some observations made by JOHNSON *et al.* (1976) in Canada were also used for validation purposes.

RESULTS AND DISCUSSION

SEVERINI *et al.* (1990b) have identified the cohort as the basic unit for studies on population development. If the cohort members are poikilothermic organisms, any function which relates the developmental rate to the temperature can be used to calculate the time-varying transit time for eqn. [1]. In this case a modified function proposed by LOGAN *et al.* (1976) was already parametrized for non-diapausing conditions and could be used directly for this work (BAUMGÄRTNER *et al.*, 1981b).

Fig. 1 shows that an Erlang function of the order $H=54$ satisfactorily describes the observed data as represented in histograms. Thus, the method proposed by SEVERINI *et al.* (1990a, 1990b) for apricot flowering phases can be successfully applied to arthropods. However, as pointed out by SEVERINI *et al.* (1990b), the parameter estimation procedure relies on experiments in which no losses were observed. This deficiency was overcome in this work by using the data obtained at the temperatures of 15, 20 and 25°C under which negligible mortality was observed (BAUMGÄRTNER *et al.*, 1981b).

During the overwintering phase pupal development is prolonged due to exposure to short-day conditions (BAUMGÄRTNER *et al.*, 1981b) and mortality occurs. Thus the model requires the estimation of parameters for developmental time under diapausing conditions as well as mortality functions. Clearly, the observed transit time and survival are related and, a priori, cannot be treated separately in parameter estimation procedures (MANLY, 1989b; SCHAUB & BAUMGÄRT-

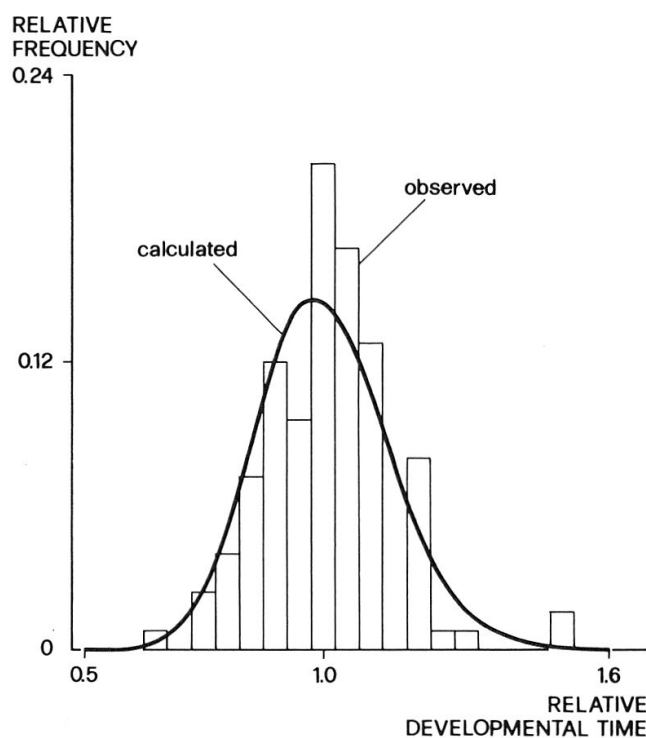


Fig. 1: The relative frequency of emerging adults during an 0.05 wide interval of the relative developmental time. An Erlang function of order $H = 54$ is fitted to the data in the histogram.

NER, 1989). This is illustrated in Fig. 2 in which the median development for surviving pupae is less than the theoretical median in the absence of mortality. Our approach differs from many proposed in the ecological literature in that it is built entirely on the theory of the delay model. We assume that the time distributed delay model is a mechanistic representation of cohort development (SEVERINI *et al.*, 1990b), consequently we can use its principles to design parameter estimation procedures. For example, the theoretical developmental time can be calculated from observations of survivors provided there is a proportional mortality acting on a cohort with variability in developmental time.

Fig. 2 shows that the model predicts a higher variability in emergence patterns than observed in the shelter. This difference is difficult to explain and may be due to an overly simplistic treatment of the diapause process which includes the losses. We had expected that the model would more likely underestimate the variability in emergence patterns, because it considers the development of one cohort only, while the shelter group presumably consisted of several cohorts each having its own emergence pattern. The value of the correction factor $\Psi = 3.76$ cannot be compared to the factor $f_{P,T}$ which represents the relative lengthening of pupal development to account for a short day effect (BAUMGÄRTNER *et al.*, 1981b). First, $f_{P,T}$ appears to be temperature-dependent and not constant as assumed here. Second, the age and the age structure of the shelter group, possibly also comprising of larvae, which entered the observation phase on December 1st was unknown, while the beginning of the individual development was known in the experiments of BAUMGÄRTNER *et al.* (1981b). Third, as opposed to the controlled conditions under which $f_{P,T}$ was obtained, the group in the shelter was ex-

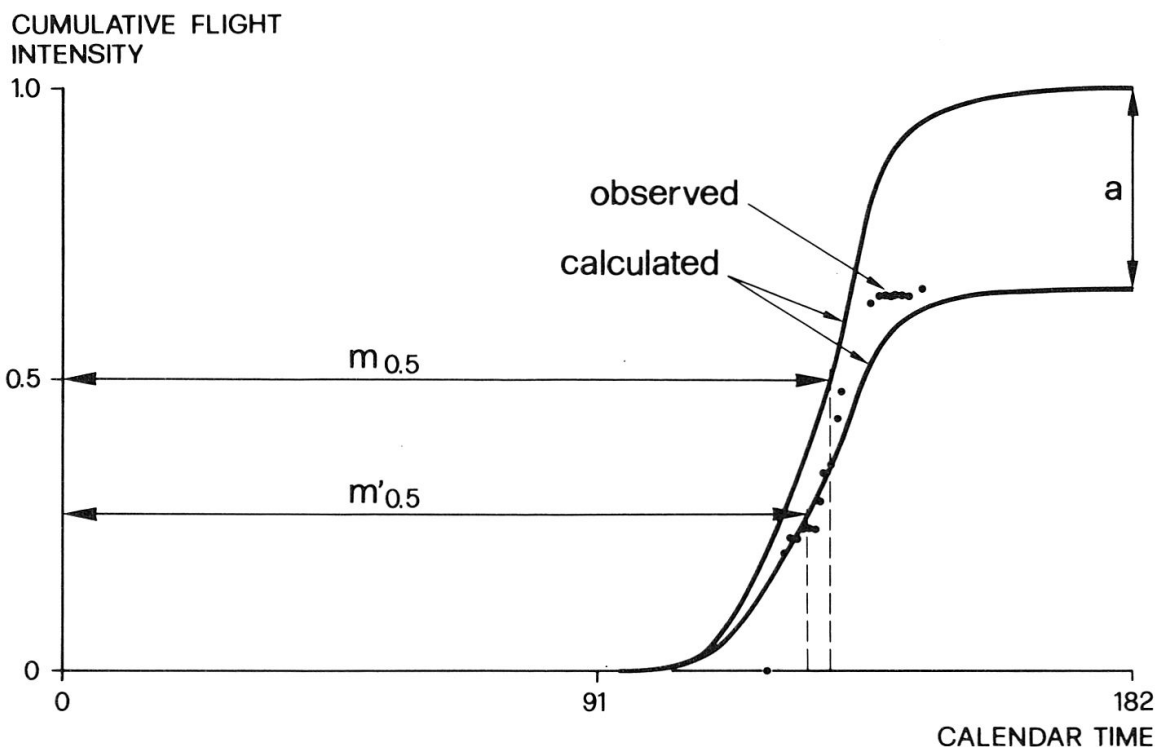


Fig. 2: The relative flight intensity, expressed as the cumulative proportion of emerging moths, in the shelter. The intensity is calculated with and without attrition (a), i.e. a time constant proportional mortality, and compared to the observed intensity ($m_{0.5}$ and $m'_{0.5}$ are the developmental time in days for 50% of the cohort without and with losses, respectively).

posed to continually changing daylengths, the effects of which on population development have not been investigated.

As stressed above no attempt was made to predict the population development at a given location, and a high degree of uncertainty in parameter estimation procedures and model prediction was accepted. Nevertheless, some tentative remarks can be made with respect to the model's ability to reproduce pheromone catches. For Chur, the model predicts a very low survivorship, less than 0.02%, and stresses the importance of earthworm activities for the overwintering *P. blancardella* pupae. By the same token, however, the parasitoids which emerge later may be even more affected, so that no final assessment of leaf burial in the *P. blancardella* life system can be made. The simulated emergence of adults occurs systematically earlier than observed, despite the calibration work. This is not unexpected, however, because the model assumes that the fallen leaves pass the winter on the orchard floor underneath the trees while the wind may have transported them to locations with different conditions for survival (POTTINGER & LE ROUX, 1971). In the Chur orchard, for example, leaves are often blown to a wall on the south side of the orchard where they accumulate in higher densities than those used in the experiments on leaf burial (eqn. 11). Furthermore, the soil near this wall is frozen longer, or covered by snow, than the remaining orchard, hence a substantial proportion of the overwintering pupae and in particular the soil inhabiting earthworms, may experience temperatures different from the ones in the remaining orchard. Another reason for the discrepancy between the predicted and the observed emergence patterns may be the inadequacy of pheromone traps to serve as a validation base: first, they attract only males which emerge earlier than females (JOHNSON *et al.*, 1976), second, the response to the trap depends on physiological and behavioral aspects which have only partially been included in the model.

The predictions of the model indicate furthermore that, at least for the two years under study, the predicted survivorship was more variable at Meaford, Canada than in the Swiss orchard: in Chur the values were remarkably stable between 0.01% and 0.02%, while at Meaford the corresponding values differed between 0.05% (1973/74) and 0.006% (1974/75). 1973/74 was a warmer overwintering period than 1974/75: the number of day-degrees above 2°C, accumulated until May 15, was 273.9 in the former and 199.9 in the latter year. Thus, the model appears to confirm the observation of LAING *et al.* (1986) who found that the population suffers from heavier losses in a cold overwintering period. If a model with more reliable predictive capabilities confirmed these observations it would be interesting to discuss the differences with respect to the area of origin/area of distribution (*P. blancardella* was accidentally introduced from Europe to North America, MAIER, 1983), and with respect to management considerations.

From a practical stand-point this work shows how a diapause effect and a calibration factor can be added to the temperature effect on cohort development, and how VANSICKLE's (1977) attrition, i.e. a constant proportional loss, can efficiently be built into the model to account for mortality. Moreover, the work demonstrates how easily a second mortality term, not directly related to the developmental process under consideration, can be incorporated into the model. This is more difficult to accomplish when the time invariant delay is used: attrition factors operating on the physiological time horizon were treated separately from the factors operating with respect to calendar time (ZAHNER & BAUMGÄRTNER, 1988). Thus, the basic equation [1] for the time-varying version has been

proven flexible enough that diapause effects can be incorporated directly into the transit time, while different mortalities can easily be combined into the attrition term. From a theoretical stand-point a simple model on the development of a single cohort has enabled us to demonstrate how the area of applicability of the time-varying distributed delay model can be extended to deal with phenomena of great importance in arthropod and plant population ecology.

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ZUSAMMENFASSUNG

Ein zeitabhängiges Delay-Modell mit Verlusten ist für die Simulation der Entwicklung von *Phyllonorycter blancardella* (Fabr.)-Puppen in Obstanlagen verwendet worden. Die Temperatur in der Krautschicht ist die einzige Steuervariable. Die folgenden Elemente sind im Modell berücksichtigt worden: die temperaturabhängige Entwicklung und ihre Streuung, der Einfluss der Diapause auf die Populationsentwicklung und die Mortalität, welche entweder den Parasitoiden und andern unbekannteren Faktoren zugeschrieben werden oder für die Regenwürmer verantwortlich sind, welche die Blätter mit den Puppen in den Boden einarbeiten. Das Modell ist hauptsächlich entwickelt worden, um zu zeigen, wie diese Effekte direkt in die Grundgleichung eingebaut werden können. Dennoch können einige Schlussfolgerungen bezüglich der Populationsentwicklung im Winter gezogen werden: Die Verluste infolge der Regenwurm-Aktivitäten sind hoch, aber relativ konstant während 4 Beobachtungsjahren in einer schweizerischen Obstanlage, während grosse Unterschiede zwischen zwei Jahren unter kanadischen Bedingungen vorausgesagt werden.

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