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Objekttyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **62 (1989)**

Heft 1-4

PDF erstellt am: **27.04.2024**

Persistenter Link: https://doi.org/10.5169/seals-402350

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MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
62, 235–245, 1989

Significance of Mortality and Temperature on the Phenology of *Orthotylus marginalis* (Heteroptera: Miridae)

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Development of the univoltine mirid, *Orthotylus marginalis* (REUTER), was simulated as a time-invariant distributed delay. Developmental time and survivorship were studied under controlled conditions, and physiological time for eggs and nymphs was defined in daydegrees above developmental thresholds. The model successfully simulated the age-distribution monitored during one year using the beating tray method. Influences of mortality and temperature are compared in the model evaluation. Phenology was only slightly affected by mortality, while the effect of microclimate was more significant and deserves more attention in future research than it has received until now.

INTRODUCTION

The predacious mirid *Orthotylus marginalis* (REUTER) is a frequent tree inhabiting insect in Swiss apple orchards (SCHAUB *et al.*, 1987). Because of its suspected economical importance it belongs to a group of insects which has been intensively studied in the analysis of the apple agroecosystem (BAUMGÄRTNER, 1985). In this work we study its phenology with particular reference to mortalities and temperature.

Phenology is the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species (LIETH, 1974). Phenology has guided agricultural activities since ancient times (WAGGONER, 1974). In agroecosystem design and management, it is a basic component in the development of models for research and implementation purposes (BAUMGÄRTNER & GUTIERREZ, 1988). For example, in supervised pest control programs knowledge of phenological events is essential to all management practices (KEMP *et al.*, 1986), including the timing of pest control operations (WELCH *et al.*, 1978). As LIETH (1974), we step beyond the prediction of the timing of key events and stress the understanding of causal relationships to construct an analytical phenology model.

To build an analytical phenology model first priority should be given to 4 basic elements: temperature, time-varying age structure, developmental variance and mortality. Because arthropods are poikilothermic organisms temperature should be considered first. This is usually accomplished by expressing time in physiological units, rather than in chronological units such as calender days (GILBERT *et al.*, 1976; STINNER *et al.*, 1974; GUTIERREZ *et al.*, 1984; CURRY & FELDMAN, 1987). However, a model representing events exclusively on a physiological time scale has serious limitations because of its restricted explicative capability (BAUMGÄRTNER & GUTIERREZ, 1988). Representation of time-var-

ying age structures is the second element in the development of an analytical phenology model. Insects pass through several life stages, and various stages may be found in the field at any point in time. Age-distribution of a field population changes with time. Proportions of each life stage may be considered as an indicator of phenology. GILBERT *et al.* (1976) explained the use of time-varying and age-specific life tables for representing such dynamic properties. In the past decade, developmental variance has become an increasingly common part of insect population models, and BELLOWS (1986) used a time distributed delay model to show how it leads to changes in population growth rates and generation time. Developmental variance is therefore considered as the third element in a phenology model for insects. One last element, mortality, is incorporated in the time distributed delay model. It has been useful to simulate insect phenology (WELCH *et al.*, 1983; CROFT & HOYT 1983) and population dynamics (GUTIERREZ *et al.*, 1984). VANSICKLE (1977) introduced attrition (i. e. proportional loss) into MANETSCH's (1976) time distributed delay model and showed, in a theoretical study, how attrition affected emergence times. Mortality is defined as the rate by which a population unit is reduced by death. We model the mortality rate as proportional to the number of individuals in a population. On the individual level this corresponds to a constant death probability of each individual. Proportional mortality takes a greater toll of individuals which require more time to pass through a life stage. As a result, the observed distribution of development times for survivors is skewed towards smaller values and observed mean and variance are reduced. From a practical standpoint proportional mortality may consequently affect phenology.

We constructed a phenology model of *O. marginalis* based on the above four elements. BAUMGÄRTNER *et al.* (1988) built a phenology model for the flight of the summerfruit tortrix, *Adoxophyes orana* (FISCHER V. ROESLERSTAMM), based on the above three elements and argued that it could be substantially improved by including mortality due to microclimatic temperature. In this case study we specifically evaluate the influence of proportional mortality and temperature as affected by microclimatic temperature on the phenology of *O. marginalis*.

The mirid, *O. marginalis,* is chosen because it is univoltine and consequently easier to study than multivoltine insects with frequent overlapping generations.

MATERIAL AND METHODS

Bionomics of O. marginalis

Like other apple tree inhabiting mirids, *O. marginalis* can be found only in apple orchards not subjected to intensive management practices (SCHAUB *et al.*, 1987). This species overwinters as eggs laid into the younger branches of apple trees. Eggs hatch in the spring, and the nymphs pass through five stages before reaching the adult life phase. All stages are predacious, feeding on a variety of insects, although aphids are assumed to be a substantial part of the diet. Feeding on apple leaves and fruit organs is observed regularly regardless of the presence of prey (unpublished data). Food quality is likely to affect mortality and fecundity of the polyphagous *O. marginalis,* but no experiments have been carried out to quantify the effect of nutrition on population development. In the field, no relationship could be established between the *O. marginalis* density and feeding punctures on young apple fruits (SCHAUB *et al.*, 1988). Consequently, this mirid

may be an innocuous or even beneficial component of the insect fauna living on apple trees. Little is known about the mirid's fecundity, but all eggs presumably diapause and hatch the following growing season (COLLYER, 1953).

Model Description

The development of *O. marginalis* life stages is considered a time-distributed process and is simulated using a distributed delay model with attrition, i. e. proportional losses occurring, during a particular life stage (VANSICKLE, 1977; GUTIERREZ *et al.*, 1984). According to this model the passage of individuals passing through the life stage, j, is represented by the set of eqn. 1

$$\begin{aligned}
\frac{dQ_{1,j}(t)}{dt} &= x_j(t) - r_{1,j}(t) - \alpha_j(t) \bullet Q_{1,j}(t) \\
\frac{dQ_{2,j}(t)}{dt} &= r_{1,j}(t) - r_{2,j}(t) - \alpha_j(t) \bullet Q_{2,j}(t) \qquad 1) \\
&\vdots \\
\frac{dQ_{k_j,j}(t)}{dt} &= r_{k_j-1,j}(t) - y_j(t) - \alpha_j(t) \bullet Q_{k_j,j}(t)
\end{aligned}$$

while t : time in daydegrees

i : index denoting the i^{th} out of k_j substages ($i=1,2,\ldots,k_j$)

j : index denoting the life stage (egg, 5 nymphal stages, adults: j=1,2,...,7)

$Q_{i,j}$: number of individuals in substage i of life stage j. The dynamics of the delay model are specified by the flow rates

α_j : instantaneous attrition rate representing mortality (see eqn. 3)

k_j : number of substages (i.e. order of the delay) for each life stage j

$$k_j = \frac{D_j^2}{s_j^2}$$

while D_j : transit time (duration or developmental time of life stage j)

s_j^2 : variance in transit time of life stage j

$r_{i,j}$: flow rate out of substage i of life stage j

$$r_{i,j} = \frac{k_j}{D_j} \bullet Q_{i;j}$$

x_j : input into first substage of life stage j (initial input into the egg stage, output of previous stages for all subsequent life stages)

y_j : output from last substage of life stage j

Developmental rates in the temperature range usually experienced by *O. marginalis* in Swiss orchards are linear (see below). Thus transit time D_j becomes the thermal constant of the life stage expressed in units of daydegrees (GILBERT *et al.*, 1976). When D_j is constant a time invariant distributed delay formulated on a physiological time horizon is an appropriate model.

The number of daydegrees accumulated during a given day is calculated from the daily maximum and minimum temperatures recorded by a meteorological station in the same region. A sine curve is forced through these temperature extremes and integrated above the developmental thresholds to update physiological time under field conditions (GILBERT *et al.*, 1976; FRAZER & GILBERT, 1976). For simulation purposes it is convenient to write eqn. 1 solely in terms of flow rates represented in eqn. 2 (VANSICKLE, 1977). Thus, eqn. 2 forms the base for simulating the passage of individual insects through the i^{th} substage in life stage j

$$\frac{dr_{i,j}(t)}{dt} = \frac{k_j}{D_j} \bullet \left(r_{i-1,j}(t) - \left(1 + \alpha_j(t)\frac{D_j}{k_j}\right) \bullet r_{i,j}(t) \right) \qquad 2)$$

with $r_{0,j}(t) = x_j(t)$ and $r_{k_j,j}(t) = y_j(t)$

The constant transit time, D_j, and the number of substages k_j can be estimated from the mean developmental time and its variance obtained in experiments carried out under controlled conditions (WELCH *et al.*, 1978). Such experiments, however, yield only developmental time (transit time) and variance for surviving individuals (m_j and s_j^2), but stage specific survivorship (ε_j) needs to be taken into account for calculating the correct values of D_j and α_j (VANSICKLE, 1977).

$$k_j = \frac{m_j^2}{s_j^2} \qquad 3a)$$

$$D_j = m_j \bullet \varepsilon_j^{-1/k_j} \qquad 3b)$$

$$\alpha_j = k_j \bullet \left(\frac{1}{m_j} - \frac{1}{D_j}\right) \qquad 3c)$$

Parameter Estimation

The equations 2 and 3 are parameterized with information summarized in Tab. 1. At a time when the eggs had presumably passed through diapause but weather conditions didn't allow further development, twigs with eggs were collected in an orchard in northeastern Switzerland and exposed in environmental chambers to temperatures of 15 °C, 20 °C and 25 °C. When eggs in the field had

hatched, first instar nymphs were collected in the same orchard and reared under the same conditions with a surplus of *Aphis pomi* (DE GEER) offered on a fresh apple leaf. The number of individuals of each instar observed is given Tab. 1. Hatching of eggs and molting of nymphs were recorded twice a day (25 °C), once a day (20 °C), or every 1.5 days (15 °C). Developmental rates as the inverse of the duration in days were calculated. The variance in developmental rates was generally higher with temperature, hence the data were weighted by the inverse of the variance. The developmental rates of all life stages except the third nymphal stage are linearly related to temperatures in the temperature range of 15 °C to 25 °C (Tab. 1). By choice, the linear model was used to describe the developmental rates of each life stage, including the third. The thermal constant (i. e. the transit time D_j) of each life stage is the inverse of the developmental rate and is expressed in daydegrees above a threshold of 9.2 °C for eggs and 10.7 °C for all nymphal stages and adults respectively (Tab. 1). A more general model representing a nonlinear relationship between developmental rates and temperatures for a wider temperature range would require the use of proportional development as appropriate time units (CURRY & FELDMAN, 1987; BAUMGÄRTNER & GUTIERREZ, 1988). In this case a time-varying instead of a time-invariant delay is applicable (MANETSCH, 1976; VANSICKLE, 1977; BAUMGÄRTNER *et al.*, 1988).

The stage specific survivorship was taken into account, and developmental time as well as a mortality rates per daydegree were calculated after eqn. 3. Thereby, for simplifying the model, each immature life stage was assumed to have the same survival rate (Tab. 1). Nevertheless, the procedure takes into account only the mortality observed in experiments under controlled conditions and neglects any additional mortality expected to reduce mirid numbers under field conditions.

Simulation Studies

Three model versions, denoted with letters A to C, were built on the above information and run simultaneously with a simulation model of Golden Delicious apple tree growth and development designed by BAUMGÄRTNER *et al.* (1986). The latter model version simulates the different phenological stages of fruit development such as bud break (a), full bloom (b), the beginning of stem hollow formation (c), and the date of harvest. Model version A is based on eqn. 2 but does not include mortality. Model version B is equal to model version A but includes mortality as observed under controlled conditions (Tab. 1). To evaluate the effect of an unknown field mortality on the phenology, a sensitivity analysis with model version A is carried out, modifying the proportional mortality by 10%. Model version C is similar to model version B but includes microclimatic conditions in the following way. While in model versions A and B ambient air temperature is used, in model version C ambient air temperature is replaced with bud temperature (LANDSBERG *et al.*, 1973). Bud temperature is assumed to represent the temperatures of the insect body. LANDSBERG *et al.* (1973) calculated bud temperature maxima (T_{mx}) from ambient temperature maxima (T_{max}), the net radiation maxima (RN), and the average windspeed (z) for two growing periods according to eqns. 4a, 4b. Before full bloom (timing of bloom simulated with the tree model):

$$T_{mx} = T_{max} + z^{-0.5} (0.0099 \bullet RN + 0.77) \qquad 4a)$$

After full bloom:

$$T_{mx} = T_{max} + z^{-0.5} (0.0113 \bullet RN - 12.2) \qquad 4b)$$

The units are as follows T: [°C], z: [m/sec] and RN: [watt/m^2]. The net radiation (RN) is approximated by the global radiation (GR) in [watt/m^2] at midday with eqn. 5 also proposed by LANDSBERG *et al.* (1973):

$$RN = 0.667 \bullet GR - 14.7 \qquad 5)$$

Model Initialization

At the beginning of the year the model is initialized with all individuals in the first substage of the egg life stage. The proportion of this initial input in the different life stages is then followed through the growing season.

Model Validation and Evaluation

In 1981 a standardized beating tray (OILB/SROP 1975) was used to record weekly *O. marginalis* densities in an orchard located in northeastern Switzerland (SCHAUB *et al.*, 1988). The ratio of nymphs to the sum of all postembryonic life stages is depicted in Fig. 1 and used for visual model validation. To evaluate influences of proportional mortality and microclimate, the curves for cumulative egg hatching and nymphal molting to the adult stage are presented in Fig. 2.

RESULTS AND DISCUSSION

The validation base is restricted to one year. Therefore, the validation base is of little value for testing the predictive capabilities of the model. Although this was not the main objective of the study, the model's versions are very useful for exploring relative influences of relevant ecological factors. Better insight of ecological processes which determine phenology may help to build models for predicting occurrence of economically important organisms with a more complicated field ecology than *O. marginalis*. Furthermore, the model can be used as a building block for a population model (BAUMGÄRTNER & GUTIERREZ, 1988) which will help to replace the empirical predation function in the apple aphid model by GRAF *et al.* (1985).

If population development is conceived as a time distributed delay, the real transit time is longer than the one observed on surviving organisms reared under controlled conditions (eqn. 3). Thus, mortality factors lead to an underestimation of developmental times, expressed in both physiological or chronological time. For *O. marginalis* the difference was small (Tab. 1), but workers are advised to be careful when estimating and specifying developmental times from life table studies, particularly if they have high variance and comprise high mortality.

Both field data and model versions show abrupt changes in the age structure (Figs. 1, 2). For example, egg hatching and adult molting, occur over a relatively short period of time (Fig. 1). Low variability in developmental time observed under controlled conditions (Tab. 1) appears thus confirmed by field studies. In addition, field data indicate that *O. marginalis* eggs terminate the suspected diapause simultaneously, thus justifying our approach to initialize the model. Egg

Tab. 1. The estimation of model parameters from standard statistics on poikilothermic development of *Orthotylus marginalis* life stages (eggs, and L1, L2, L3, L4, L5: nymphal stages, Ad: adults, N: number of replicates, THR_a: threshold with standard error SE after CAMPBELL *et al.* [1974], P: significance level for the test of linearity, m_a: observed mean [[c]: median] of developmental time in day degrees above the stage specific threshold THR_b, m_b: observed mean developmental time above a common threshold of 10.7 °C, s^2: observed variance of developmental time [[d]: calculated after SHAFFER (1983)], μ: observed mortality per stage and ε: estimated average survival per stage, k: order of the delay, D: stage-specific transit time in daydegrees, α: proportional attrition rate [[e]: estimate]).

Parameter	Life Stages						
	Egg	L1	L2	L3	L4	L5	Ad
N	71	-	12	18	34	36	24
THR_a	9.2	-	11.0	10.7	10.8	10.7	-
SE	0.13	-	0.66	0.17	0.20	0.17	-
P	0.16	-	0.08	0.01	0.47	0.52	-
m_a	171.0	-	42.3	43.0	46.8	69.6	193.0[c]
THR_b	9.2	-	10.7	10.7	10.7	10.7	10.7
m_b	-	-	44.3	43.0	47.4	69.6	193.0[c]
s^2	182.2	-	70.1	60.4	32.7	32.1	387.0[d]
μ	-	-	0.33	0.33	0.18	0.24	-
ε	0.72	0.72	0.72	0.72	0.72	0.72	0.72
k	161	28[e]	28	31	69	151	96
D	171.8	44.8[e]	44.8	43.5	47.6	69.8	193.7
α	.0044	.0071[e]	.0071	.0083	.0061	.0062	.1008

hatching occurs after bud break but before full bloom of the Golden Delicious cultivar. This suggests that postembryonic development coincides with tree growth, and that abundant plant food should be available at the time *O. marginalis* is found in Swiss apple orchards.

A comparison of the model versions A and B in Figs. 1, 2 shows that phenology varies very little. Eqn. 3b indicates that the combined effect of two factors may be responsible for this result. First, the proportional mortality (28% for each instar) may not have been high enough to affect the observed developmental time. However, the sensitivity analysis clearly shows that differences in phenology also remain small if the survivorships are modified according to Tab. 2, there is little change in the calendar day on which 50% of the population has reached the adult stage. Second, the little variation of phenology may be due to an exceptionally low variability found for the development of *O. marginalis* life stages. Variability in some life stages is so low that one can consider a model without incorporating variability. Literature referring to heterogeneity in developmental time suggests higher variability in developmental time and consequently lower k's for arthropods in general (SHAFFER, 1983). However, if we use a smaller (and

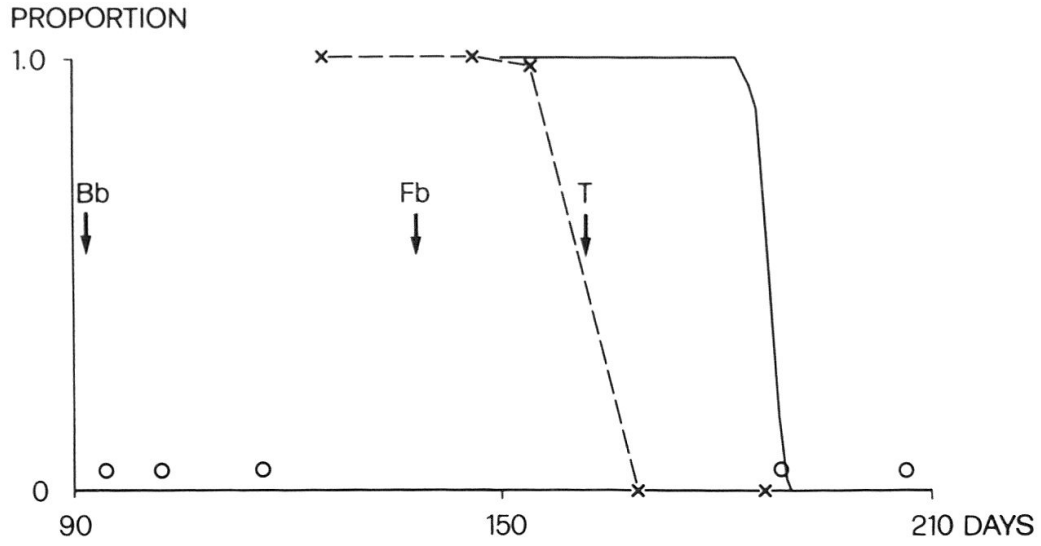

Fig. 1. Visual validation of the *Orthotylus marginalis* phenology model without considering the proportional mortality and the microclimatic influences (x: observed, — : calculated proportion (PROPORTION) of the number of nymphs divided by the total number of postembryonic life stages, and o: samples without *O. marginalis;* DAYS: number days from January first 1982; Bb: calculated bud break, Fb: full bloom and T: stem hollow formation for the Golden Delicious apple cultivar).

more generally applicable) variability derived from SHAFFER (1983) and subsequently carry out a similar sensitivity analysis as above the differences in phenology remain approximately the same. Thus, the incorporation of proportional mortality as the fourth element in an analytical phenology model improves only slightly the predictive capability of the model. Consequently, if one attempts to simulate the phenology but not the densities of *O. marginalis* or of another species with similar life tables attributes, there is no need to consider proportional time constant mortality. However, this conclusion is valid exclusively for a particular mortality type. For example, our work does not permit the discussion of stage-specific and time-varying mortality nor of mortality factors operating independently from the physiological time horizon. At temperatures below the developmental threshold, the model assumes that no mortality occurs. However, a severe frost may kill a substantial part of a sensitive substage or even a complete life stage. Both types of mortality are likely to change profoundly the phenology and should be considered in future research work. If the phenology model is used as a building block for a realistic population model (BAUMGÄRTNER & GUTIERREZ, 1988), a better incorporation of mortality is likewise necessary.

Tab. 2. The influence of a proportional life stage specific mortality on the 50% cumulative appearance day of adult *Orthotylus marginalis*.

	Mortality							
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7
Day	188	188	188	188	187	187	187	187

The temperature experienced by tree crown-inhabiting *O. marginalis* is different from the air temperature, and egg hatching as well as adult appearance occurs earlier than predicted by model version A (Fig. 2). A closer agreement between observed and predicted values is achieved with model version C (Fig. 1, 2).

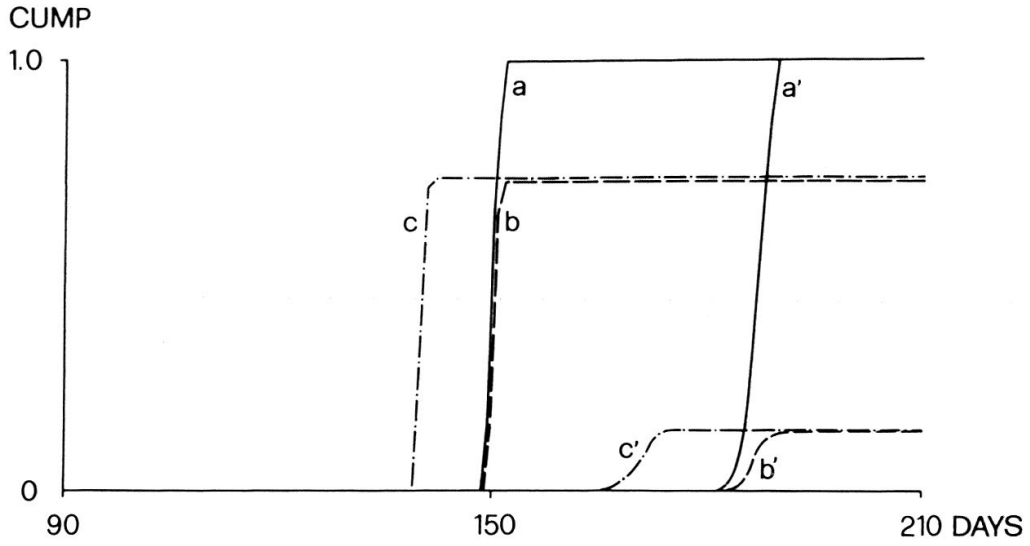

Fig. 2. The influence of proportional time constant mortality and of the microclimate on the cumulative proportion (CUMP) of hatching eggs and emerging adults predicted by different model versions detailed in the text (DAYS = number of days from January first 1982; a, a' = eggs and adults predicted by model version A; b, b' = eggs and adults predicted by model version B; c, c' = eggs and adults predicted by model version C).

Nevertheless, a comparison of the predicted patterns in Fig. 2 with the observed values in Fig. 1 shows that the predicted appearance of nymphs and adults is still later than observed in the field. This is not unexpected, since climatic conditions in Swiss apple orchard may be quite different from the climate in British orchards on which the eqns. 4, 5 are based. For example, in Switzerland snow cover during winter is more frequent. Hence high temperature differences between air temperature and wooden frame of an apple tree are observed when high radiation coincides with a snow covered orchard floor. Nevertheless, it is premature to conclude that eqns. 4, 5 underestimate microclimatic influences in Swiss apple orchards. The suspected diapause is not considered directly in the model and the model does not consider within-plant movements of mirids. The microclimate simulator of LANDSBERG *et al.* (1973) is built on a spatially and temporally restricted data set. We recognize the improvements obtained when considering microclimatic conditions, but refrain from further adjusting the model in order to get a closer agreement between observed and calculated values. Instead, we recommend making direct microclimatic measurements for evaluating their influence on mirid phenology.

ACKNOWLEDGEMENTS

We would like to thank Prof. V. DELUCCHI for his advice and encouragement. We are indebted to Prof. A. GUTIERREZ, Dr. N. STONE and Dr. J. JACKMAN for their reviewing the manuscript.

ZUSAMMENFASSUNG

Die Entwicklung der univoltinen Miride *Orthotylus marginalis* (REUTER) wurde als zeitverteilter Alterungsprozess simuliert. Die Entwicklungszeit und das Überleben wurden unter kontrollierten Bedingungen beobachtet. Die physiologische Zeit der Eier und Nymphen wurde in Gradtagen über ihren Entwicklungs-Nullpunkten definiert. Das Modell simulierte die Altersverteilung erfolgreich, die während eines Jahres mit der Klopfmethode im Feld verfolgt wurde. In der Evaluation des Modelles wurde der Einfluss von Mortalität und Temperatur verglichen. Die Phänologie wurde durch die Mortalität wenig beeinflusst. Das Mikroklima hingegen war wichtiger und verdient in zukünftigen Untersuchungen mehr Beachtung als bisher.

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(received July 12, 1989)