

Prediction of grape moths dynamics using age structured models

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Abstract: Seven years of continuous monitoring of both, the flight occurrence of male adults and the following developmental stages (e.g. eggs and larvae) of two grape moth species in the Rhine and Main river region (Germany) revealed a large variance within the data. Additionally, precise associations related to the concurrently recorded weather data could not be established. With respect to the heterogeneity of the population dynamics of the grape moths through time and density, a generalised Leslie process was adopted for the quantitative and qualitative description of their developmental stages. The flexibility of the model concept was achieved by joining non-linear response functions that relate changes of developmental rates to changes in weather conditions with probability distribution functions. The required survival probabilities were estimated using results obtained from related climatic chamber experiments and from intensive monitoring in the vineyard. Further parameter values of the model equations were identified by a step-by-step procedure, which included adding model complexity in time and weather covariates and simultaneous fitting to the observations. Within the capacity of the model, it was possible to find constant transformation factors for data measured on different scales. The model represents a combination of both the understanding of biological mechanisms within a season and empirical components reconciling gaps of information. Potential and limits of the model are demonstrated in this report.

Keywords: Population dynamics, Leslie process, climatic influence, risk prognosis, *Lobesia botrana*, *Eupoecilia ambiguella*

Introduction

Seven years of continuous monitoring and forecasting of both, the flight occurrence of male adults and the following developmental stages (e.g. eggs and larvae) of two grape moth species in the Rhine region (Germany) revealed a large variance within the collected data. A statistical model using weather data is fit to describe the period of flight activity, the start and climax of the egg laying phase, and the hatch and development of larvae (Hoppmann & Holst 1992). The results of the model are supplied to vine growers by means of the so-called 'viticulture weather fax'.

The model was validated in three viticultural areas in Germany. In 80% of all cases, the calculated date for the application of pesticides coincided with the first occurrence of larvae. Ideally, the difference between calculated and observed first larvae stages should not exceed more than two days. In 20% of all cases, the statistical model failed to determine the exact date of larvae hatching. In these years, either an extreme weather course or rapid changes in the population dynamic could be observed. Other problems arise by using the results of pheromone traps, which are sometimes inadequate. With respect to the heterogeneity of the population dynamics of the grape a generalised Leslie process was adopted for the quantitative and qualitative description of the developmental stages of the grape moths (Lischke 1994). The numerical transformation should provide an analytic tool to:

- improve the understanding of the moth's biology with regard to modifications induced by climate, including developmental rate, reproduction and mortality.
- predict precisely the appearance of L1-larvae of both generations to improve the advisory system by reducing amount and frequency of spraying and optimise alternative control agents (e.g. *Bacillus thuringiensis*) and antagonistic strategies.

In principle, it is difficult to develop an appropriate strategy from observing pheromone traps exclusively. This is especially the case in years where long flight periods are prevalent. Consequently, it is necessary to give an estimated start and end of the flight period.

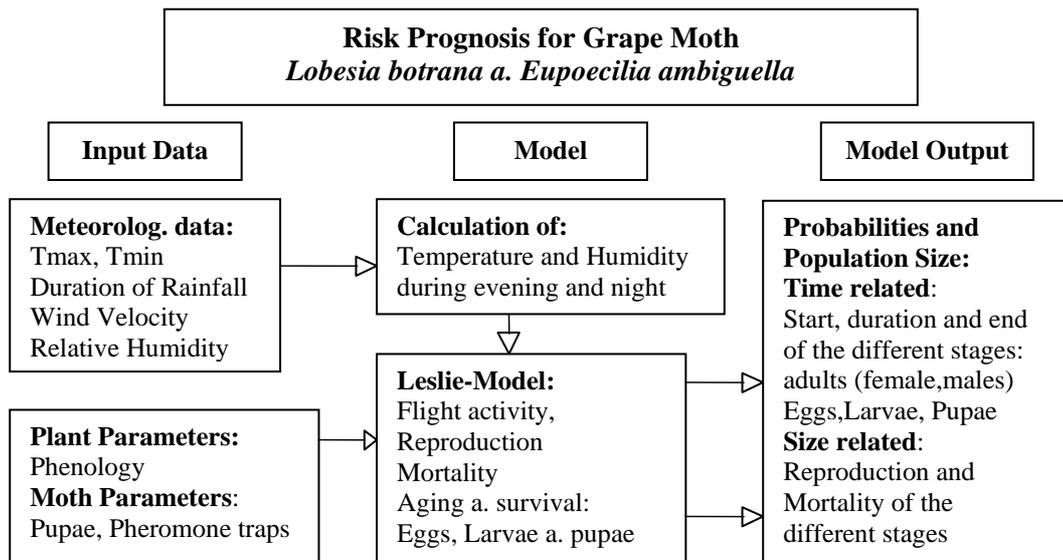


Fig. 1. Data flow risk prognosis for Grape Moth (*Lobesia botrana* and *Eupoecilia ambiguella*)

Materials and methods

The model starts off with a given number of winter pupae. In a calibration process, both flight and number of observed eggs and larvae are included. After this process, the model is validated with data obtained from other vineyards.

Figure 1 describes the data flow from the input into the model to the model results.

The input data are listed on the left-hand side of the diagram. These include: Maximum temperature (Tmax), minimum temperature (Tmin), duration of rainfall, wind velocity and relative humidity. In a later application, meteorological parameters for different topoclimatological situations could also be calculated. Additionally, phenological stages, number of winter pupae and observations from the traps are taken into account.

The model parameters are listed in the centre of the diagram. Calculations based on the Leslie process are: flight activity, egg reproduction, embryonic development, mortality, stage of larvae and pupae, all stages for two generations (normal) and for a third generation in warm seasons only.

The column at the right hand side describes the model output, which includes probabilities and population size. Start, duration and end of the different stages are time related. Quantitative results are numbers for adults (female, male), eggs, larvae and pupae, reproduction and mortality of the different stages.

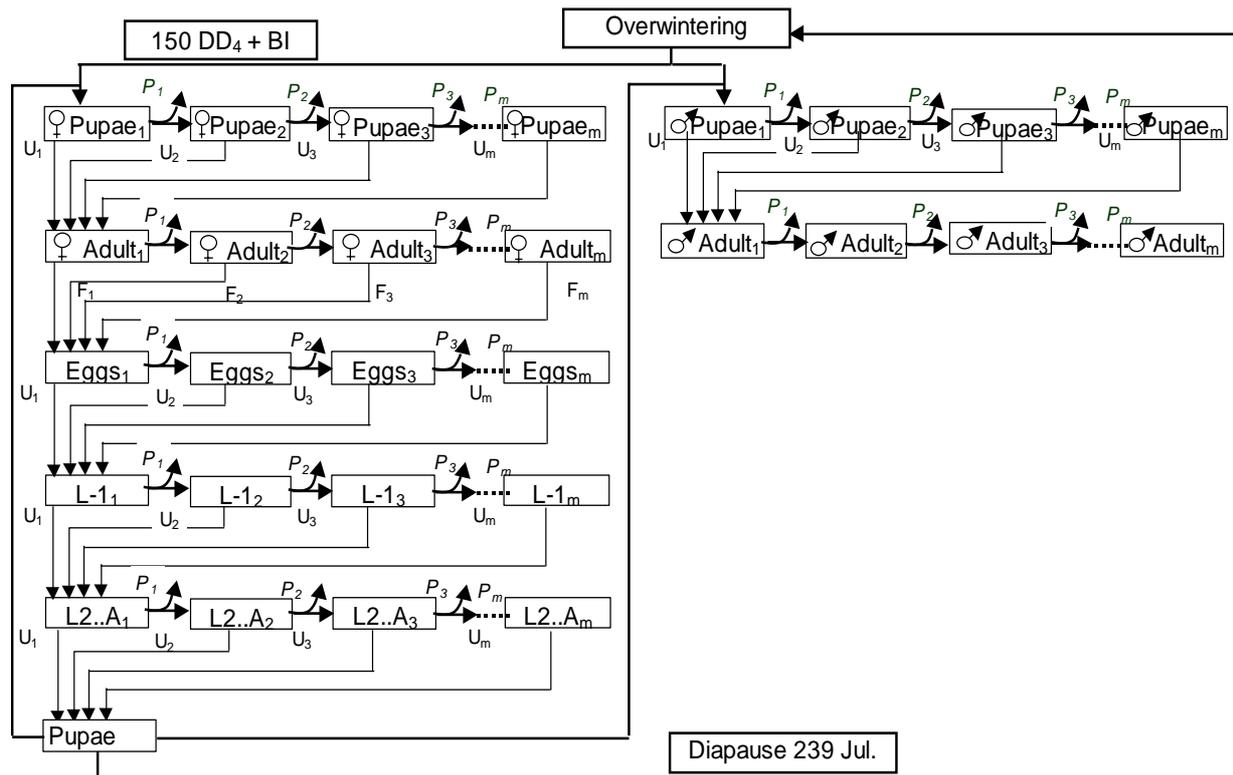


Fig. 2. Flow diagram of Leslie process describing aging and survival in different development stages

For modelling the dynamic pattern of the grape moth stages, the generalised Leslie model provides a stochastic platform, which is capable of accommodating the large variance found in the observations (Fig. 2). Current investigations regarding the biology of the grape moths help determine the developmental stages of pupae, adults, eggs and larvae. The individuals of each developmental stage of a population are distributed into age classes, emulating the varying conditions over a period of time and certain developmental probabilities are calculated. Several probabilities are computed at each time iteration:

1. The survival probability describes the move from one age class to the next (P). Contemporary the population is reduced by the fraction $(1-P)$.
2. The transition probability (U) informs about the advance from an age class of the current developmental stage to the first age class of the next stage, e.g. eggs hatch into L1-larvae.
3. The fertility rate (F) determines the size of the offspring (e.g. number of eggs), which varies with the age of adult females.

The flow diagram (Fig. 2) illustrates the above concept in detail using the following example: At the beginning of the simulation, the first age class of the first stage is loaded with the numbers of overwintering stages. These individuals survive with the given probability P in the first age class and move to the next and/or hatch, thereby advancing into the first age class of the next stage (U_1). The individuals of the specific stage together with their offspring (i.e. adult females) produce a certain amount of eggs with an age-specific rate F . Subsequently, this offspring hatches and moves into the first age class of the next stage. The process continues for each stage until the whole life cycle is completed and starts again with the given rates. The stage "adult" does not move to the next stage, but survives with a certain probability that is temperature dependent.

The flow diagram demonstrates a basic structure and is applicable to any type of organism. The model structure demands a large number of different parameters, which theoretically could be taken from related life-tables. However, such data are not commonly available. Consequently, the main challenge of modelling a specific organism, as given in this example, is the reduction of the enormous number of parameters by functional correlation of secondary orders. The development rates of insects are mainly driven by temperature. Hence, the probability U to hatch and move from one age class into the first age class of the next stage is fulfilled (or equals one), when an individual has been exposed to a certain amount of accumulated heat or temperature units in a given period of time, thereby transforming real time into "biological time". However, not all individuals of a population respond similarly to temperature. Parts of the population hatch earlier, some later. This natural variance has to be considered by suitable probability distribution functions. The same process applies to the survival of the adults. Derived from the model concept, a combination of a temperature response function in conjunction with a probability distribution function is established for each developmental stage. The mathematical functions have been explained in detail by Richter & Söndgerath (1990).

Results

Model calibration

The combination of a Weibull function as a continuous distribution function with a non-linear temperature response function has been sufficient in earlier model applications. The combined equation includes about four to five parameters, which may be derived from previously conducted experiments. For example, an experiment was carried out to assess the survival of adults under constant temperature regimes. Figure 3 illustrates this experiment, which has been performed under laboratory conditions in climate chambers for *Lobesia botrana*.

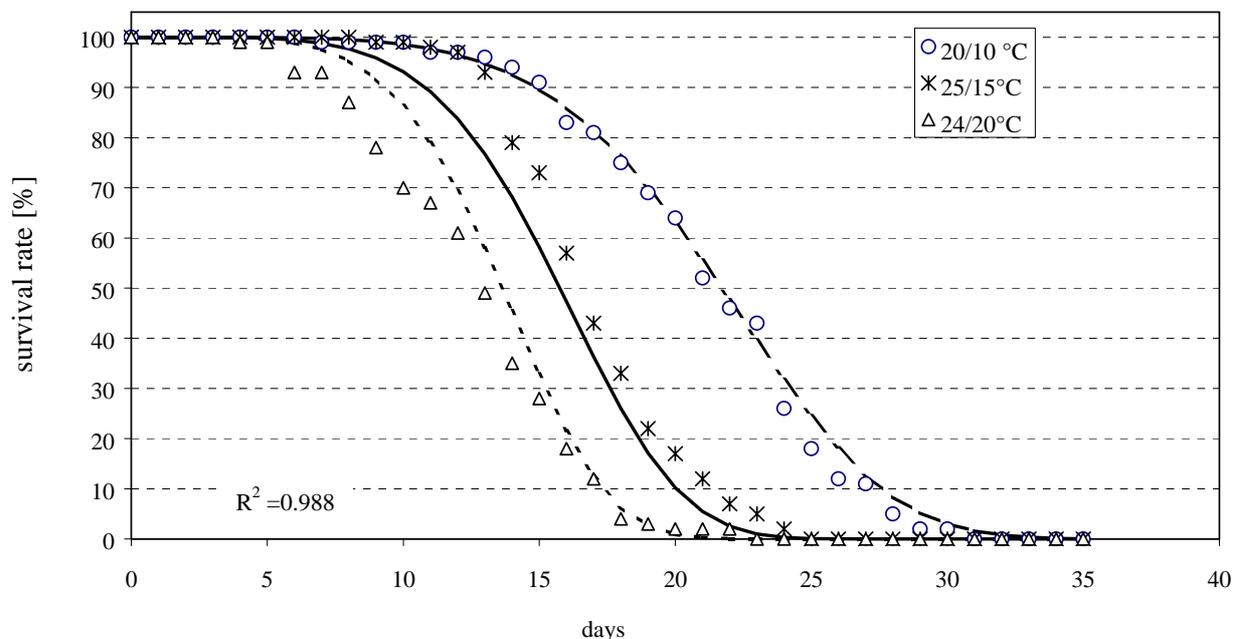


Fig. 3. Survival rate of the adult male moth (*Lobesia botrana*) under different temperature regimes

The results were fitted simultaneously to a Weibull function (the distribution function) and a quadratic temperature response function exploiting all information obtained from this and other experiments in one single step. Simultaneous fitting joins two advantages:

- the functions can be included in the model as estimated without any further transformation and
- the flight duration of both sexes under variable temperature regimes is determined.

Unfortunately, similar temperature experiments concerning the survival and development of other stages are not available. The length of egg laying periods and the amount of eggs has been investigated in climatic chamber experiments. The results were simultaneously fitted again, while a log-normal distribution was found to be the appropriate model.

Figure 4 demonstrates the curves of fertility rates of *Lobesia botrana* as a function of different constant temperatures. These experiments were conducted in climatic chambers. During a high temperature weather course, a high fertility rate over a short period of four or five days could be observed. During a cool period, the life-span of females will increase, but their fertility rate is low. During very hot periods above 30° C the fertility rate also decreases.

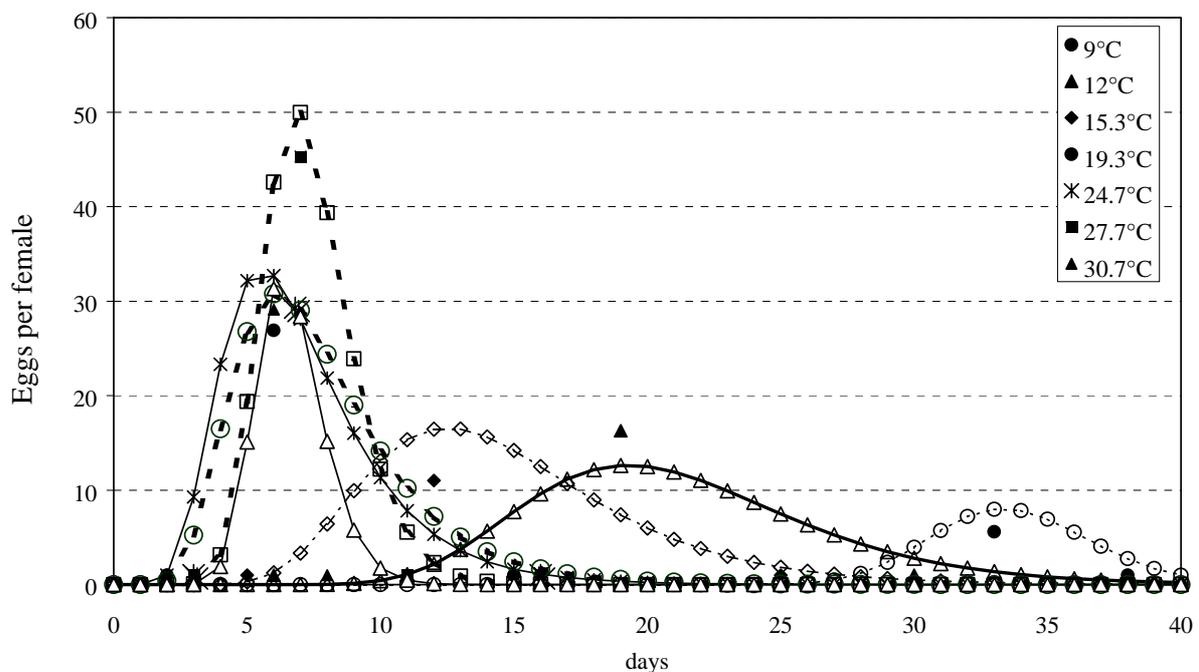


Fig. 4. Simulation of egg laying periods (*Lobesia botrana*) in dependence of different temperatures

Model validation

The model validation commences, when all model parameters are established. Figure 5 shows the first validation. The model uses only the parameter temperature and the above mentioned transformations. The compiled model, controlled by the given temperature pattern, simulated the flight duration adequately. This is true for the beginning of each developmental stage, but absolute population densities were not confirmed yet. Differences increased rapidly over a period of time.

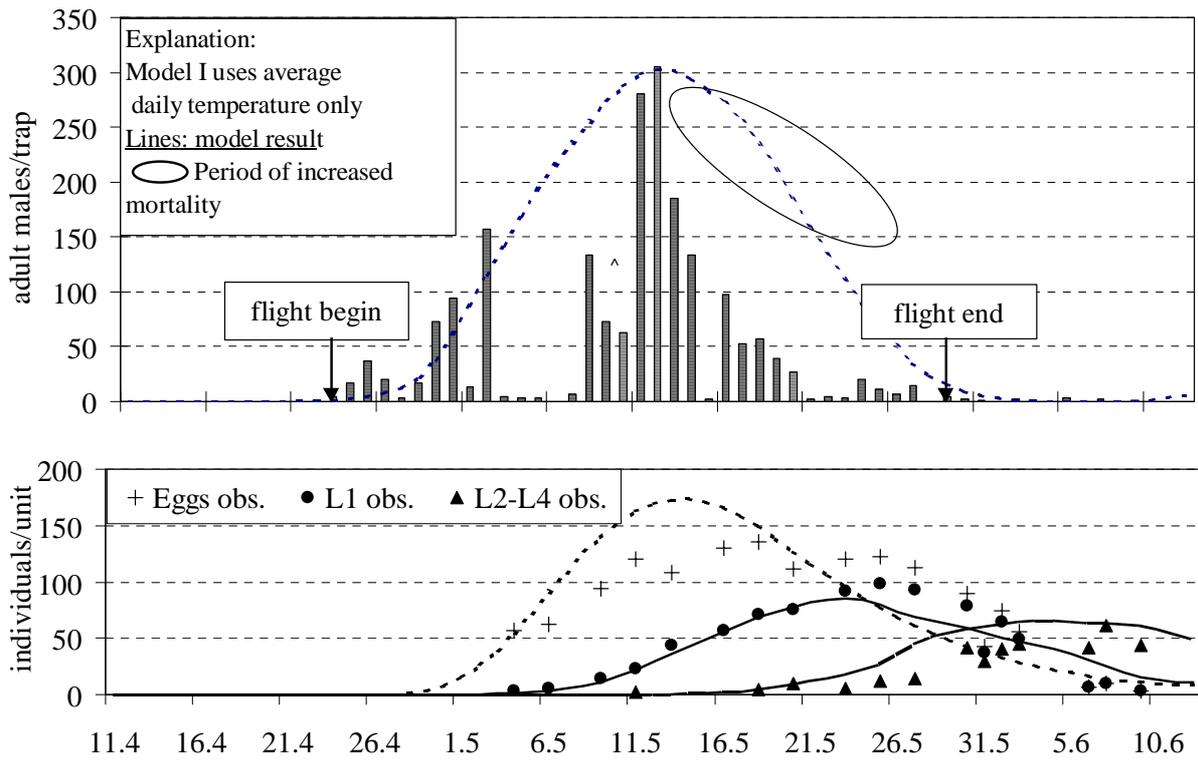


Fig. 5. Flight, egg laying and larvae period *Lobesia botrana* (Geisenheim Mäuerchen 1993)

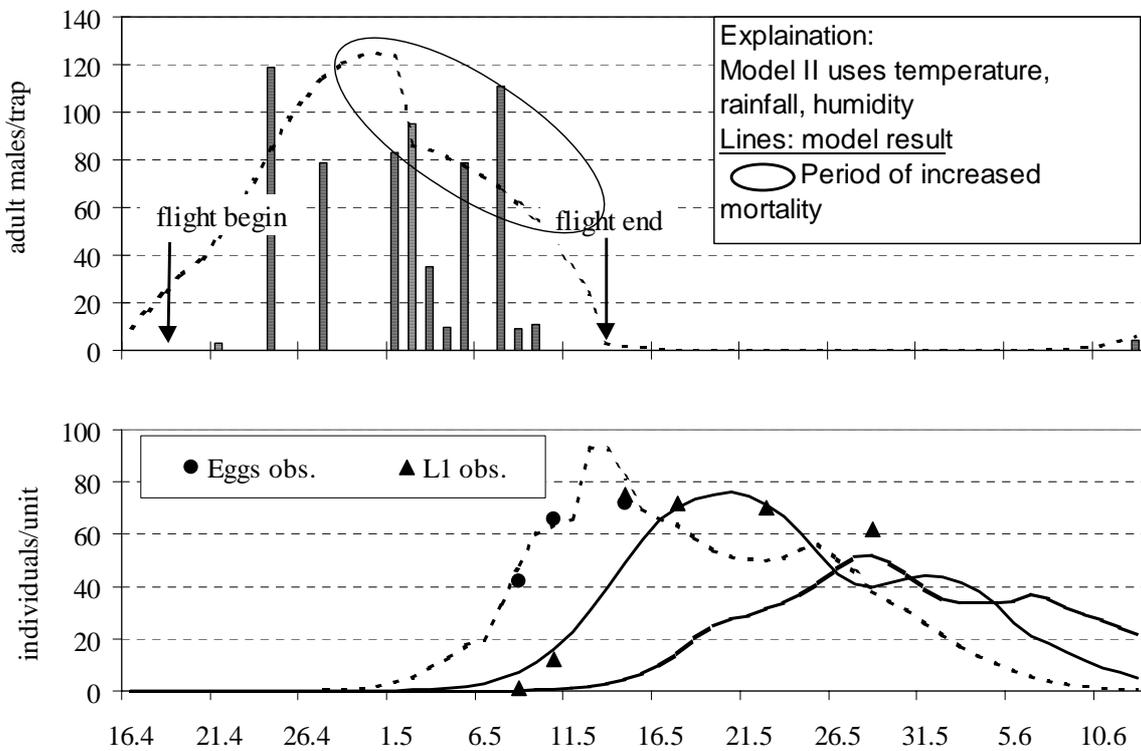


Fig. 6. Flight, egg laying and larvae period *Eupoecilia ambiguella* (Oppenheim 2000)

In the upper part of figure 5, the number of caught moths is shown together with the probability function of male moths over the whole flight period. More importantly in the lower figure, the simulated results of the egg laying phase and the larvae hatching phase are plotted. The lines represent the simulation; the discrete points are the observed numbers of eggs and larvae in field experiments. The start and duration of the stages can be simulated very confidently. Consequently, advice and recommendations for the application of biological insecticides can be competently given.

Most obviously, the simulated population declines towards the end of and was overpredicted compared to the data and the decrease had started earlier than the simulation suggested. In this consideration, the introduction of further dependencies is essential, which adjust the development or survival rate. In addition, another lethal but age independent factor should be considered. The following relations, all based on derivations of the Weibull function, have been established and were subsequently combined and tested. The factor "relative humidity" might affect the survival rates directly. Rainfall influences the mortality rates only and can be verified by the climatic files. The variable "wind" appears less influential concerning the overall outcome. This variable is primarily a delay factor for the probability of copulation and consequently the fertility rate.

Due to the high correlation of the model parameters, the entire model has to be repeatedly calibrated taking into account all important parameters at the same time. Currently, the importance of all these factors and their assumed interactions has not been thoroughly analysed and further investigations are needed. One major shortcoming is the lack of sufficient data.

The results are demonstrated for *E. ambiguella* in the year 2000 (Fig. 6). The example shows a good agreement for the first generation and the transition from the first to the second generation, both through time and population density. Furthermore, the ratio of adult males to the succeeding stages (eggs and L1-larvae) was found suitable. However, the decline of the second generation and the transition into a third generation was repeated incorrectly. Factors remain, mainly affecting the survival probabilities in this part of a season, that cannot be correlated to the weather conditions alone. Reasons for the differences have not yet been identified with the given sets of data. The model did not include any insecticide application. Consequently, a nearly explosive development of the population was observed.

Discussion

The generalised Leslie model has proven to be the correctly chosen platform for modelling the dynamics of grape moths and the results were found to be partially sound. The numerous transition and survival probabilities have been successfully transformed to weather related response functions. An overall parameter vector was identified from both, the results of experiments under controlled conditions and the empirical assumptions derived from field observations.

The appearance probability of the L1 stages is accurately predictable. A higher accuracy has been achieved for *L. botrana* due to the availability of larger data sets. a period of time continues to be a problem. The adopted Leslie process can be used for modelling the stage dynamics of both grape moths within one single generation. As shown in the presented example, the significant deviance of model and data over

The model results become more and more imprecise when initial values are less influential on the starting conditions of the model. As proven in earlier applications for other organisms, the model complexity has been easily reduced by appropriate experiments performed under constant conditions. Nevertheless, insufficient information has been

supplemented with empirical assumptions. Although these have been successfully linked to the model concept, further proof is needed. Although the model cannot be applied reliably throughout the whole season, adjustments to early stages enable an accuracy that suitably fulfils the main objective, which is the statistically derived appearance probability of the L1-stages. Thus, the model results can provide a legitimate basis for advisory systems. The clear difference between the first and the second generation within the simulation leads to the assumption of further factors involved, which may not be directly correlated to weather observations. Insecticide applications are not included in the model. Therefore, an almost explosive development of the population was observed at the change from the second to the third generation.

At this stage, the importance of all these factors and their assumed interactions has not been analysed in depth and, consequently, further investigations are necessary. The lack of sufficient data poses a major problem. For the validation process, especially with regard to the number of pupae, quantitative investigations conducted under field conditions are required. In order to solve this problem, information and data exchange with other working groups should be initiated.

Other factors still need to be identified and subsequently quantified. Further correlations or other areas of interest, for example predicting the population size in spring based on the observed dynamics of the preceding year, or determining criteria for passing into the diapause, have, as a matter of priority, not yet been addressed. With respect to both moths, a higher accuracy has been achieved for *L. botrana*, as this species has been the main subject of research within the past years and, consequently, a larger set of data is available for process identification, model fitting and calibration.

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