



Identifying weather related covariates controlling the grape moths dynamics

K. Schmidt¹, D. Hoppmann², H. Holst³, B. Berkelmann-Löhnertz³

¹ Nemaplot, Bergstr. 103, D-53129 Bonn, Germany, Kai.Schmidt@uni-bonn.de

² German Weather Service, Agro-Meteorological Research Station Geisenheim, Kreuzweg 25, D-65366 Geisenheim;

³ State Research Station Geisenheim, Department of Phytomedicine, Von-Lade-Str.1, D-65366 Geisenheim;

Keywords: Population dynamics, Leslie process, survival function, climatic influence, *Lobesia botrana*, *Eupoecilia ambiguella*, grape moth;

Published 2003 OEPP/EPPO Bulletin 33, 517-524

Summary

The use of control agents demands the precise prediction of the susceptible larvae stages of the grape moths *Lobesia botrana* and *Eupoecilia ambiguella* as these dynamics are varying with the weather pattern of a particular year. Hence the objective has been to partition the relative influence of a specific climatic factor on the insect dynamics. Data taken from 7 years of continuous monitoring of both the flight occurrence of male adults and the following development stages (i.e. eggs and larvae) were analysed by a generalised Leslie process. The model type reduces the population to three probabilities: development, survival and fertility. Each probability can be modelled as a function of the associated weather factors, while a) the functional relationships and b) the model parameters has to be established. The analysis started with the most simple approach, and in a step by step procedure model complexity was added until a sufficient fit to the overall data set was achieved. Within the magnitude of the model, the development rates were controlled solely by temperature, but the duration of single stages (i.e. survival) was found to be a combination of temperature and relative humidity. The model represents a combination of both the understanding of the mechanisms within a season and empirical components reconciling gaps of information.

Introduction

Both grape moths *Lobesia botrana* and *Eupoecilia ambiguella* cause severe problems in the Northern European wine production areas. The prediction in time and density of the L1-larvae of the two moth species are the main concerns of an advisory system as a) only these development stages are susceptible to control agents and b) facilitate the optimisation in terms of spraying amount and frequency reduction. The population dynamics of the moths vary with the particular weather situation within a season. Two generation are completed under normal conditions, while occasionally a third generation is observed. Hence the objectives are the development of a suitable framework to identify the relative impact of a single climatic factors (i.e. temperature, relative humidity and others) and to transform these climatic factors into appropriate response functions. The functional relationships must fulfil the conditions for all the first and the second generation and the dynamics of a whole season.

Material and methods

Several vineyards under field conditions in the Rhine and Main river region (Germany) have been continuously monitored for a decade using pheromone traps. The method determine the flight periods of both moths and the total numbers of flying males, but do not provide any

information about the egg producing females (Hoppmann & Holst, 1993). To improve the understanding of the population dynamics, the seasonal time courses of eggs and larvae stages of *Lobesia botrana* were additionally studied in one location from 1992 to 1998. Further information were provided from climate chambers experiments under a range of constant temperature conditions (Holst, unpub. data, Scholten-Thoma, 1995). Concurrent to the biological history the weather conditions were recorded. Figure 1a demonstrates a typical example of the observations. The time courses show clearly an overlapping of different development stages. A suitable analysis tool for the observed data structure is the generalised Leslie process published by Richter & Söndgerath (1990). Figure 1b shows an arbitrary example of three, overlapping stages. Within this model type the individuals of each developmental stage of a population are distributed into age classes, emulating the varying conditions over a period of time. The partition into age classes reduces the population dynamics to three probabilities: fertility, development and survival. The last two probabilities can be modelled in terms of the biological time. To achieve the objective the pattern of the model has to be synchronised with the observations. Hence related response functions of an associated weather factor has to be established for each development stage, while a) the functional relationship and b) the model parameters are essential. The underlying hypothesis supposed that the “best” model would fit all data of 1992 to 1998 simultaneously with one constant parameter vector.

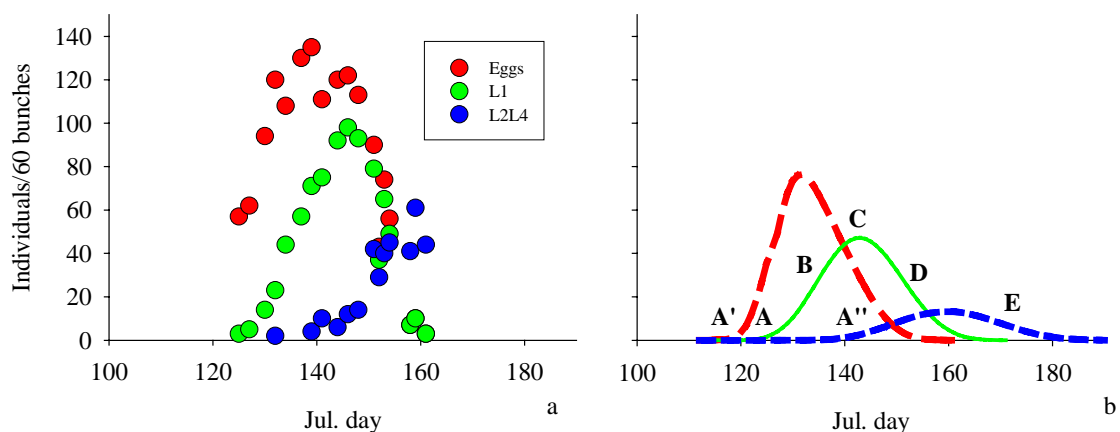


Fig. 1: a) observed sequence of development stages of *Lobesia botrana* in 1993; b) time course of a three-stage Leslie model; (Letters denote cardinal points)

Modelling principles

The flow diagram (Fig. 2) demonstrate the model structure with respect to the specific biology of the moths. 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 into the first age class of the next stage (U_1). The adult females produce a certain amount of eggs with an age-specific rate F . This offspring hatches and moves into the first age class of the stage L1. The following larvae stages were summarised to the stage L2L4. The process starts again with completion of the whole life cycle. For the mathematical details how to calculate the transition probabilities of a generalised Leslie model we refer to Richter et al. (1990). The survival rates of the adults and the age-specific fertility rate were estimated from the mentioned climate chambers

experiments. The development rates were determined by the transformation of the real time to the biological time. The related temperature response function were calibrated to the appearance rate of each stage (points A', A, A'' in fig. 1b), leaving the survival probability of the stages eggs, L1 and L2L4 as the unknown elements of the model. The related response functions have to be identified from the time courses of the 1992-1998 data. It has to be in mind that the procedure has to be repeated for each development stage. Avoiding to much complexity the matter will be limited to the L1-stage.

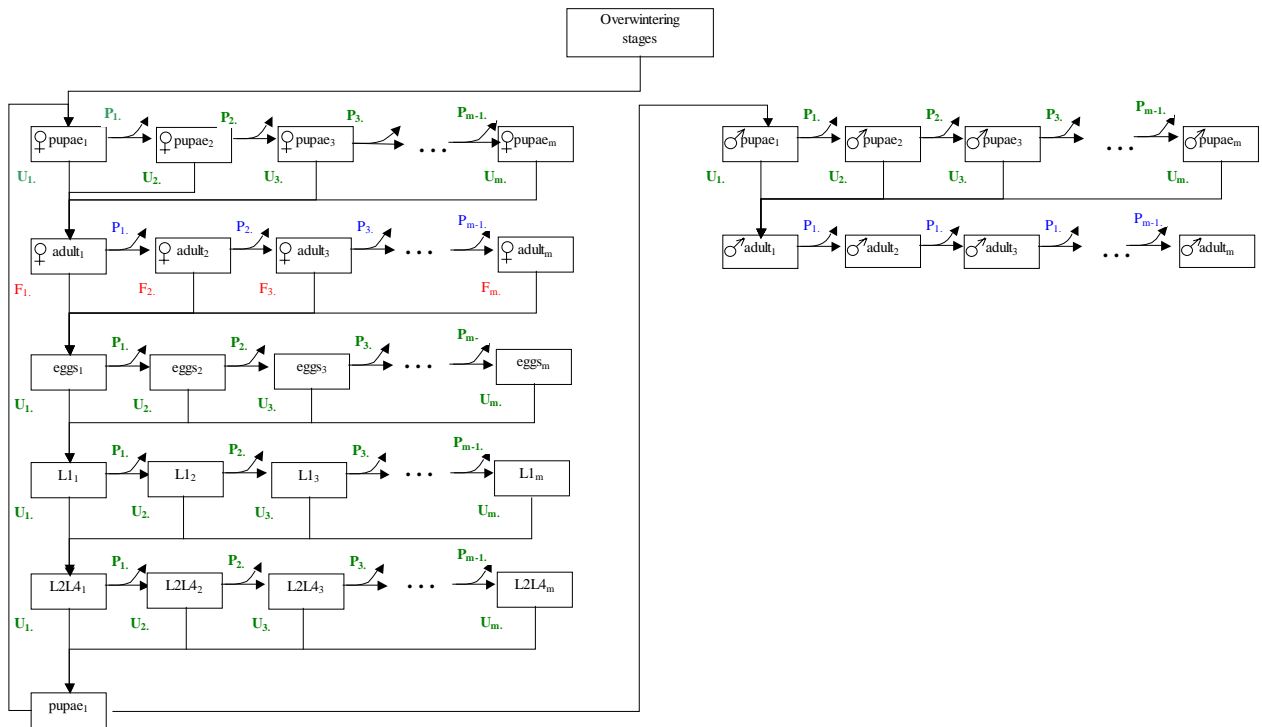
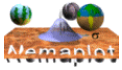


Fig. 2: The age structured compartment model

The observed pattern in time and density (fig 1a) represents the outcome of unknown and assumed processes and their interactions. It is assumed beforehand that the climatic conditions are the major factors controlling the biology. Adopting the Leslie model allows the discrimination of a single climatic factors based on the model behaviour. But similar to the observations, the model trajectory for one stage is the output of different processes, which are simultaneous calculated. Fig. 1b demonstrates the relevant periods. As already mentioned, the begin of stage L1 varies with the development rate of the previous stage eggs. The shape of slope B (fig. 1b), the maximum C, the decreasing slope D and the end E are controlled by the influx of individuals of the previous stage and the outflow of individuals due to hatch into the next stage and due to death. The maximum C also varies with the density of the previous stage. The relative influence of these processes on the shape of the model trajectory changes over time. Exactly this change over time provides the potential to discriminate the process of concern, when the masking effects of one process over the others are small.

The survival models

The probability to survive from one age class i to the age class $i+1$ at time t for any development stage s can be modelled by the choice of a distribution function G , reducing the survival probabilities $P_1 \dots P_m$ to a few secondary functional parameters (Richter et al., 1990).



For any stage s in the age class i at time t it holds the general form

$$P_{s,i,t} = \frac{G_s(i+1)}{G_s(i)} \quad (\text{eq. 1})$$

Model 1

The most simple form would be the choice of an exponential distribution function with one parameter λ . The model represents a constant mortality rate throughout the lifespan of the stage:

$$G(P)_{s,i,t} = e^{-\lambda} \quad (\text{eq. 2})$$

The m primary parameter for each age class are reduced to one secondary parameter λ for each development stage.

The second choice is a Weibull distribution, in which groups of individuals die concurrent at the end of the lifespan.

$$G(P)_{s,i,t} = \exp \left(- \left(\sum_{j=1}^i \frac{1}{\delta \cdot \theta_t \cdot (T_t - T_{crit})^2} \right)^{\beta_P} \right) \quad \text{for } T_t < T_{crit} \quad (\text{eq. 3})$$

with the special case $\theta_t = 1$

The end of the lifespan is attained when a certain amount of heat units is fulfilled. The rate is described by a quadratic response function, considering the temperature T at time t . The survival probability is 1 in the beginning, but get significantly smaller, when the denominator becomes larger. Obviously the rate is small with cooler temperatures and large in warm situations. The effect is a variation in the longevity of a stage with respect to temperature. The model requires 3 parameters.

The third model tested, again based on the Weibull distribution, is an extension of equation 3 while the actual rate is both a function of temperature and relative humidity (H_t) at time t .

$$\theta_t = \gamma + (1 - \gamma) \cdot \left(1 - \exp \left(- \left(\frac{H_t}{H_{Low}} \right)^{\alpha_H} \right) \right) \cdot \exp \left(- \left(\frac{H_t}{H_{High}} \right)^{\beta_H} \right) \quad (\text{eq. 4})$$

Equation 4 generates a plateau with $\theta = 1$ using a certain ratio of the parameter α_H to β_H . This plateau represents the range of the relative humidity not affecting the rate. The parameter H_{Low} and H_{High} describe approximately an upper and lower boundary. A physiologically plausible range is about 50 to 80 % rH (Savescu et al., 1969; Savescu & Rafaila, 1978). Beyond these boundaries the rate increases and consequently shorten the longevity. For clarity, the parameter H_{Low} and H_{High} are in fact the points of inflection of equation 4, therefore a suitable parameter value for H_{Low} is in the range of about 40% and 90-100% for H_{High} . The further parameter γ varies between 0 and 1 and limits the effect of unfavourable humidity conditions, as even very dry or wet conditions might not be directly lethal or, taken from the biology, the larvae within the canopy/bunches are less affected by extreme weather situations. Suitable values for γ are in the range of 0.6. The extended model requires several

more parameters compared to the second model. But equation 4 should hold a specific curvature, therefore most of the parameters are predetermined.

Fitting criteria and parameter identification:

a) Numerics

To solve the parameter estimation problem the Levenberg-Marquardt-algorithm was programmed and adopted to the current non-linear regression (Press et al., 1992), while the iterative fitting procedure was undertaken using an initial value approach. The algorithm had to minimise the residual sum of squares (RSS) for each stage, while the minimising criteria were weighted by the logarithm:

$$RSS_{L1} = \sum_{i=1}^n (\ln(1 + y_i) - \ln(1 + D(t_i, \Theta)))^2 = \min \quad (\text{eq. 5})$$

with

n sample size

y_i denotes the measurement at time t_i

D Result of Model D at time t_i with parameter vector Θ

b) Biology

The discrete model structure is too complex and the cascade of dependencies from stage to stage yield in such high correlation that no finite solution is possible. Despite the potential to reduce the numbers of parameter to secondary functional parameters and initial values were derived from climate chambers experiment, the remaining parameters suggest the existence of numerous parameter vectors producing the same or similar model trajectories. Therefore the parameter estimation problem is not straight forward. Restricting the choices of solutions the analysis of the dynamics were partitioned into three phases:

- 1st generation, related to an average daily temperature of 14 °C
- 2nd generation, related to an average daily temperature of 18.5 °C
- complete season with the emphasis on the transition from 1st to 2nd generation

A successful approach (i.e. a specific parameter vector for all components) must not only repeat the population dynamics of the generations through time, but also through density.

c) specific fitting methods

To verify the suitability of the three survival models, each model is fitted to the data of each year, stressing the first generation first. Secondly the procedure is repeated for the second generation, but concurrent the parameter range must be plausible to the results of the first step. Thirdly the procedure is done again for the whole season, again maintaining the results of step one and two. Each fit produces one parameter vector. Averaging the parameter vectors over the years, generates a model applicable for all years.

Results

Table 1 compares the RSS of each survival model, applied to the 1st, 2nd generation and the complete season for the first larvae stage. Despite the difference in complexity from model I to model II, there seems to be no progress in quality in terms of a statistical comparison. The average residuals for model II indicate even a weaker performance than model I. In most of the cases the smallest RSS are achieved by the most complex model III.

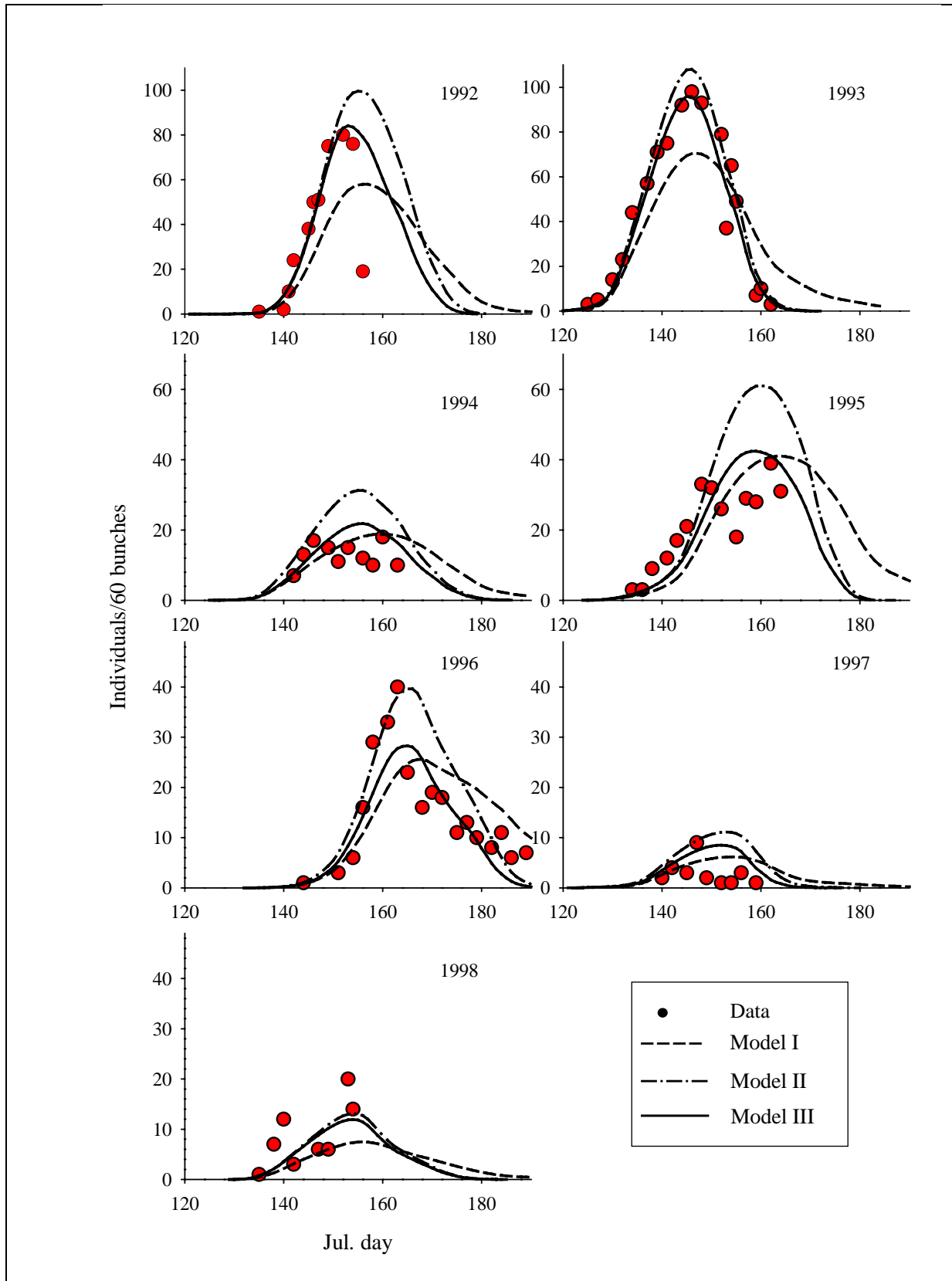


Fig. 3: Comparison of three survival models to L1-observations from 1992 to 1998



Tab. 1: RSS¹ comparison of survival models and data (Ex. L1)

	I ²			II			III		
	1 ³	2	3	1	2	3	1	2	3
1992	4.1	0.6	13.8	4.2	0.2	17.3	3.5	0.2	7.9
1993	8.5	3.4	33.3	1.9	1.8	6.1	1.4	2.3	3.0
1994	1.1	2.2	18.3	4.5	1.5	7.4	1.4	1.5	5.6
1995	3.5	3.5	13.1	3.9	6.8	6.2	1.9	10.4	4.5
1996	3.9	8.6	27.8	5.5	20.4	26.4	7.0	21.4	22.7
1997	5.9	1.6	7.8	12.4	2.0	37.6	7.6	1.8	9.5
1998	4.9	2.9	6.9	2.8	4.7	21.4	2.8	3.9	17.4
∅	4.6	3.3	17.3	5.0	5.3	17.5	3.7	5.9	10.1

¹ Logarithm of residual sum of squares

² Model type

³ Generation (1,2, 3 = whole season)

A visual comparison of data and model results for the first generation highlights significant differences. In Fig. 3 the three survival models are shown for each year as they behave with the estimated parameter vector and are controlled by the underlying weather files. Comparing the exponential distribution (model I) to the whole data set revealed a plausible solution for single years, but the time courses are insufficiently repeated. Due to the constant mortality rate the increase of the population and the maximum is underestimated. Contemporarily the decreasing period is overestimated and the end of the stage is delayed. The structural output of model I is inappropriate and must be rejected. The Weibull distribution, established with a temperature response function (model II), repeats well the beginning and increasing slope, indicating that the entire dynamics at this time are controlled by the influx of the previous stage and nearly all individuals survive. In all years the maximum is overestimated due to a delayed onset of the mortality processes. The continuous overestimating indicates that the temperature driven rates might be too small. But smaller rates would not have fit the data of the second generation. Despite model II performs better than model I and than indicated by the RSS, it also demonstrates structural weakness. Model III, driven by the seasonal temperature and relative humidity pattern, performs best. Most of all the trajectories repeats well all phases of the observations and does not show a structural deviance. Solely in 1996 maximum and longevity are underestimated. The results supports not only the hypothesis that longevity of the larvae stage is controlled both by temperature and relative humidity, but also provide reasonable parameter range for the factor humidity. Fig. 4 visualise the Weibull distribution under constant temperature and constant humidity conditions after 20 days and shows the proportional survival .

Tab. 2: Estimated parameters for the survival functions

stage	δ	T_{crit}	β	H_{Low}	H_{High}
eggs	0.0154	56.0	5	43	100
L1	0.0115	56.0	19	41	100
L2L4	0.0165	55.9	8	41	110
pupae	0.0177	64.0	8	30	110

fixed parameters: $\alpha_H = 15$; $\beta_H = 41$; $\gamma = 0.6$ (eq. 4)

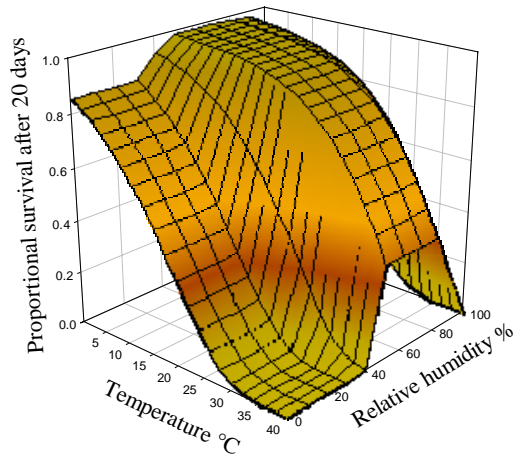


Fig. 4: Varying survival proportions under constant temperature and relative humidity after 20 days (stage L1)

The fitting techniques are also applicable for the stages eggs, L2L4 and pupae. The latter ones are fitted to the observations of the second generations due to lack of appropriate data. Tab. 2 shows the estimated parameters. The parameter T_{crit} are consistent over all egg and larvae stages. Only the rate parameter δ varies. The second parameter β of the Weibull distribution describes the sharpness of transition for the survival function. A large β demonstrates a sudden death of all individuals when they have been exposed to a certain amount of heat and humidity units or the biological time is over 1 (fig. 4). A small β describes a smooth transition. Drought periods shorten the lifespan of eggs and larvae stages, while the rates start to accelerate below 50% rH. Eggs and L1 seem to be influenced by very humid conditions as well, which is not noticed for the following larvae stages. The stage pupae seems to be less affected by changes in rH as the parameters suggest.

Figure 5 shows an example of the synthesised model, combining parameters estimated from climate chambers experiments and the techniques introduced here. The model repeats well the dynamics of all development stages for one generation, but calculating the dynamics of the second generations from the dynamics of the first generation overpredicts the density of some stages later in the season.

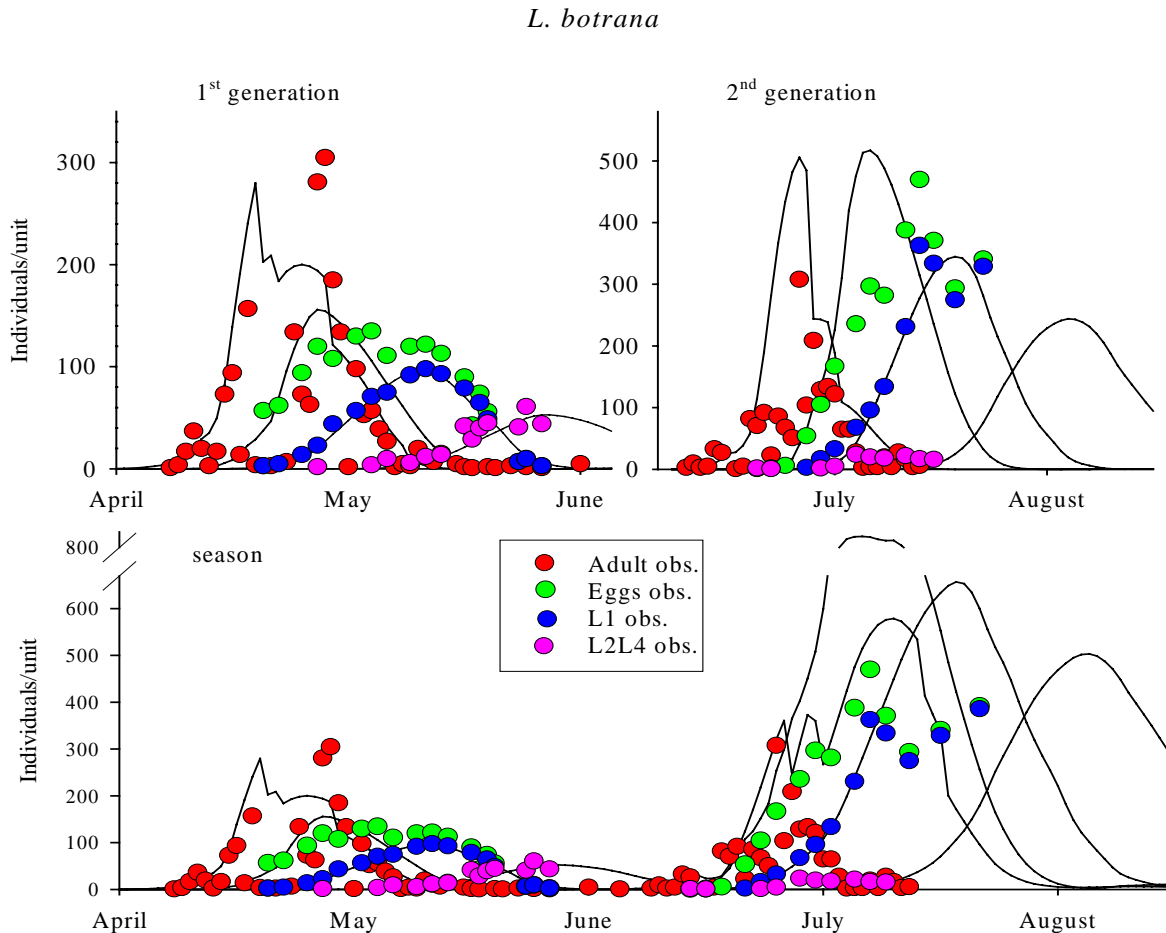


Fig. 5: Comparison of the parameterised Leslie model and observations, separated in first, second and both generations (site Mäuerchen, 1993)

Conclusion

The open structure of the Leslie model provides a suitable frame to test different dependencies as the population dynamics of the grape moths are controlled by the underlying weather pattern. Within the range of this model longevity and therefore population density of the larvae stages are controlled by both temperature and relative humidity. The chosen combination of response functions (Model III) is an example how to consider both factors simultaneously. Other climatic factors, for example rainfall or wind speed, have been tested but are found of no importance on the longevity of the larvae stages. The introduced techniques allow to discriminate between several physiological processes, which occur concurrent within a season. Intensive experiments under constant temperature and constant humidity conditions would be the alternative. In most cases these experiments are not available or not even possible. It is assumed that the method is applicable for other species with similar data sources. The analysis emphasised *Lobesia botrana* due to a sufficient data source. Similar relations might be valid for *Eupoecilia ambiguella*, but with a different



parameter vector. As related data are not available a similar analysis for this moth was not possible. The synthesised model explained a large proportion of the variation found in the field data and represents the successful synchronisation of model and data. Despite fitting to data, it also implies many assumptions, reconciles gaps of information and might not be a direct prove for reality. It should be kept in mind, that the complex of survival is reduced to some basic processes, but many more factors are likely as seen in the simulation of a whole season. The model results agree well with the data sets for one generation, but simulating a complete season shows inconsistency later in time. Apparently more factors than considered here and probably are not related to weather conditions, might control the dynamics later in the season.

Acknowledgement

The project is funded by the Hofgeisbergstiftung, Rüdesheim, Germany

5. References

- Hoppmann, D. & Holst, H. (1993): Forecasting of the cycles in the developmental cycles of the grape moths (*Eupoecilia ambiguella* and *Lobesia botrana*) and their relationships on weather conditions. *Vitic. Enol. Sci.* 48, 172-175
- Lischke, H. (1991): Ein Modell zur Simulation der Populationsdynamik des Apfelwicklers (*Cydia pomonella* L. (Lepidoptera, Tortricidae)), PhD-Thesis, Heidelberg, 139 pp.
- Press, W.H., Teukolsky, S.A., Vetterling, W.T. & Flannery, B.P. (1992) Numerical recipes in Fortran, The Art of Scientific Computing, 2nd Ed., Cambridge University Press, 963 pp.
- Richter, O & Söndgerath D. (1990), Parameter Estimation in Ecology, the link between data and models, VCH Weinheim, 218 pp.
- Savescu, A., Iacob, N., Cristea, N., Lefter, G., Vionica, I. (1969), Prognoza si avertizarea in protectia plantelor “, Edit. Agro-Silvica, Bucuresti, 199-207;
- Savescu, A., Rafaila, C. (1978), Prognoza in protectia plantelor “, Edit. CERES, Bucuresti, 302-305;
- Scholten-Thoma, F. (1995) Optimierung eines Prognosemodells für Traubenwickler, Spezielle Untersuchung zur Flugaktivität und Eiablage bei *Lobesia botrana* (Schiff.) und *Eupoecila ambiguella* (Hübner.), PhD-Thesis, Mainz, 121 pp.