Modelling the population dynamics of the grape moths *L. botrana* and *E. ambiguella* stages using age-structured models - the analysis of climate chamber experiments
Part 1: from adult survival to first larvae hatch

K. Schmidt [1], D. Hoppmann, H. Holst [3], B. Berkelmann-Löhnertz [3]

[1] Nemaplot, Bergstr. 103, D-53129 Bonn, Germany, Kai.Schmidt@nemaplot.de
[2] German Weather Service, Agro-Meterological 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 model, survival function, development, biological time, *Lobesia botrana, Eupoecilia ambiguella*, grape berry moth, climate chamber;

Abstract

Two grape berry moths, *Lobesia botrana* and *Eupoecilia ambiguella*, were kept under controlled conditions in climate chambers at different constant temperature levels. In total, three independent experiments were conducted within the last years. The data provide information about the longevity of adult males and females, egg production and the population dynamics of the developmental stage eggs, as these vary with different temperatures. The obtained data were used to estimate the parameters of environmental response functions, which determine the different probabilities of an age-structured Leslie model. These probabilities are described by sub-models of different complexity. In addition, the Leslie model was used to analyse parts of the experiments concerning the population dynamics of the observed development stages of both moths. In a first step, the relevant parameters were estimated on a real time scale separately for each temperature level. In a second step, these estimates were calibrated to an appropriate response function. Thirdly, the model was used to determine the influence of the factor relative humidity on the population dynamics by the analysis of related trials. The experiments together with the way of analysis may be regarded as a first step towards the development of a model, which predicts the population dynamics of both moths under field conditions.

1. Introduction

The population dynamics of most insects, including the two grape berry moths *Lobesia botrana* and *Eupoecilia ambiguella*, are directly controlled by the specific climatic conditions of a location and year. However, due to several interactions it is much more uncertain, how a small change in one of the controlling climatic factors, such as temperature or relative humidity, relates to a relative impact on the mass changes of the population through time and magnitude. Taking into account several climatic factors simultaneously we can hardly distinguish between one or the other factor.
In this study, our initial hypothesis is that temperature has the highest impact on the population dynamics, while other factors, such as relative humidity, take a secondary effect and vary the influence of the main factor. Our aim was first to identify the relative influence of temperature and then second to distinguish between temperature and the additional factor “relative humidity”. Related climate chambers experiments were chosen and newly initiated. Obtained data are then

analysed with an age-structured Leslie model (Richter & Söndgerath, 1990). Such models reduce the population dynamics to three probabilities: a developmental rate, a survival rate and a fertility rate. The first probability is applicable to all development stages, which hatch into another stage. The second is applicable to all stages, while the last one is restricted to adult females only. These probabilities vary with the underlying climatic conditions. Hence, it is essential a) to define the related response functions, which provide the link from climatic conditions to biological responses and b) to estimate the parameters of those functions with data taken from climate chamber experiments.

2. Materials and Methods

2.1. Climate chamber experiments

The results of three types of climate chamber experiments are available for the identification of the functional relationships and parameter estimations:

a) Survival times of the adults

The longevity of adult males and females have been observed under three levels of controlled temperature regimes ranging in average from 15 °C to 21 °C for *L. botrana*. *E. ambiguella* was tested at 21°C only. The progress of an initial population of 100 adults was monitored twice a week. The experiments were concluded once all insects had died at each temperature level.

b) Extended experiments

As the previous experiments have been insufficient with regard to *E. ambiguella*, similarly designed experiments have been repeated for both moths. Freshly hatched adults were collected and transferred to growth cylinders. Each cylinder contained 5 pairs of adults of both sexes. The cylinders were kept in climatic chambers at different temperatures (table 1). Each experiment was repeated four times. The insects were fed on a specific diet. It was presumed that a relative humidity (rH) of 80% would have no limiting effect on the population dynamics. Consequently, most parts of the trials were run within this rH-range. At daily or twice weekly intervals, the development of the population was observed until all adults had died. Additionally, the period of egg laying, the number of eggs per cylinder and their time courses were recorded at each temperature level. Finally, the empty eggshells were removed from the growth cylinders and counted at each sampling date.

Table 1: Layout for population dynamics experiments with constant temperatures,
5 pairs of moths, n=4;

L. botrana			***E. ambiguella***		
trial name	temperature °C	relative humidity	trial name	temperature °C	relative humidity
LB A	16/18-22/24	set 70-80%	EA A	16/18-22/24	set 70-80%
LB B	18/20-24/26	set 70-80%	EA B	12/14-18/20 (16.9)	set 80% (64%)
LB E	16/18-22/24	var. at night	EA C	16/18-22/24 (18.1)	set 80% (77%)
LB F	12/14-18/20	set 70-80%	EA D	16/18-22/24 (19.3)	var. day/night (57%)
LB G	16/18-22/24	var. day/night	EA K	23/24-27/28 (26.0)	set 80% (65%)
LB K	23/24-27/28	set 80% (65%)			

(Numbers in brackets denote averaged values per day if available)

c) Fertility and egg laying

Previous data were available from Scholten-Thoma (1995). The experiments were conducted with an average temperature range of 9°C to approximately 31°C. For details of night/day temperatures refer to figure 4. Egg laying was monitored at 1 to 3 day intervals, whereby the maximum and total number of eggs/female, the period of pre-oviposition and the duration of egg laying was determined.

2.2. Mathematical components

2.2.1. The Leslie process

The generalized Leslie model (Richter et al., 1990) provides the mathematical model that takes environmental co-variates into account in form of related response functions. The principles applied are straightforward: With respect to the biology, an insect population is divided into their specific developmental stages and the individuals of each development stage are subdivided into age-classes, considering varying conditions with increasing age or time. Such models are multidimensional difference equations. At each iteration over a discrete time step t, the following probabilities are calculated for each development stage:

1. The survival probability ($P_{s,i}$) describes the proportion of individuals of one development stage, which moves from one age class i to the next age class i+1 of the same stage s. Concurrent the individuals are reduced by the fraction 1-P;
2. The transition probability $U_{s,i}(t)$ to move from age class i of stage s into the first age class of stage s+1 at time t; e.g. eggs hatch into L1-larvae.
3. The fertility rate F_i denotes the number of eggs per female in age class i;

The probabilities are multiplied with the number of individuals X in age class i and stage s at time t, in short $X_{s,i}(t)$. The individuals in age class i + 1 at time t + 1 are then calculated by:

$$x_{s,i+1}(t+1) = (1 - U_{s,i}(t)) \cdot P_{s,i} \cdot x_{s,i}(t) \qquad \text{(eq. 1)}$$

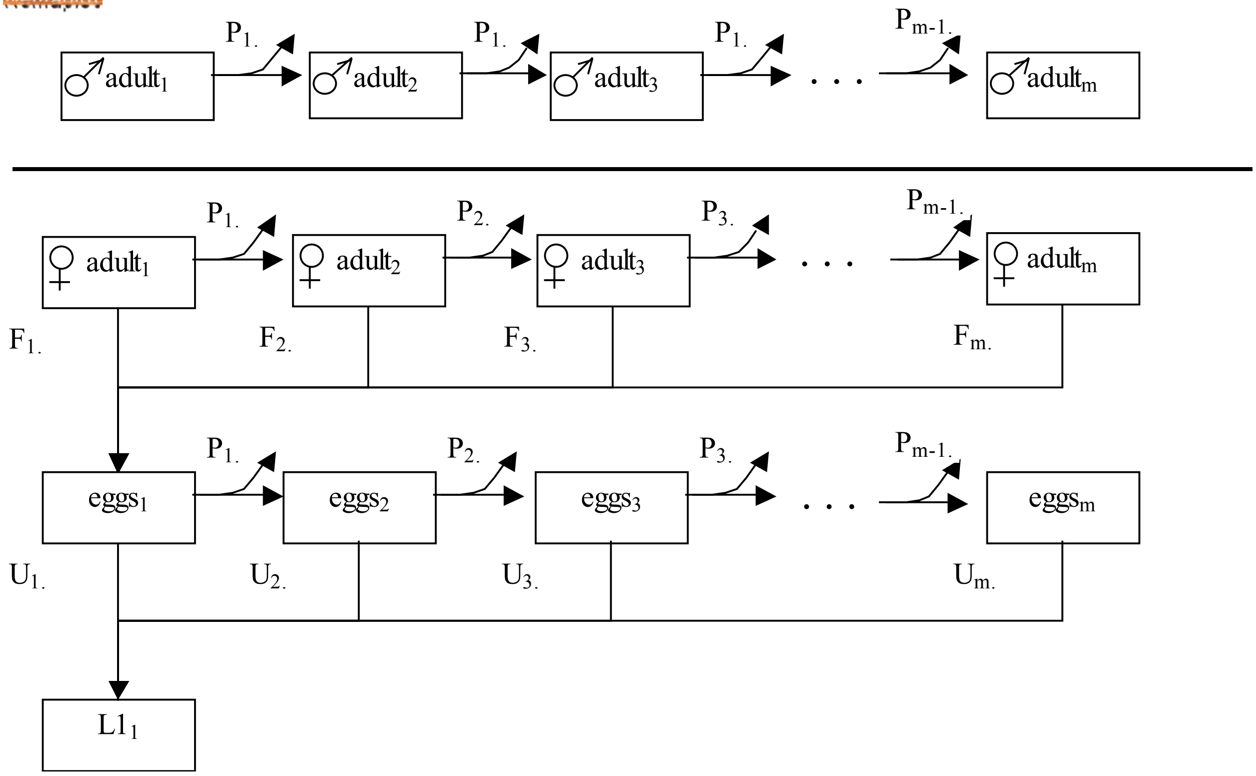


Figure 1: Compartments of the Leslie model for the given experimental design and moths; L1 represents the collection of empty egg shells in age class 1

The flow diagram (fig. 1) illustrates the above concept, while the model size was restricted to the design of the initiated climate chamber experiments. The freshly hatched adults are put in age class 1. These individuals survive with the given probability P_1 and advance to the next age class 2. From age class 2, the individuals survive with the probability P_2 and advance to the next age class and so on. Based on biological principles, adults cannot hatch into another stage, but the adult females produce a certain amount of eggs at age class i (F_i), which varies with increasing age. Newly produced eggs get into age class 1 of the egg stage and the survival process is calculated as before. When the development of the eggs is completed, the individuals hatch into the first age class of the first larvae stage L1. In theory, these processes are repeated for all successive stages of the moths. With respect to the experiments, the sampled empty eggshells represent the first age class of the stage L1 and are collected there.

2.2.2. Introduction of environmental response functions

The model structure demands a large number of different parameters. As the introduced probabilities vary considerably with varying environmental conditions, the main challenge is the reduction of the number of parameters to functional correlations of secondary orders. For many species, the time required to complete a developmental stage and to hatch into the next stage varies with temperature. The duration of a stage is shorter at higher temperatures until a certain temperature level is exceeded. Beyond an optimal temperature, biological processes retard again. The functional response is therefore non-linear. Additionally, not all individuals of one stage respond equally to temperature. A natural variation has to be considered, as some individuals hatch earlier, some later. Therefore, the response functions are embedded in a suitable probability distribution function. These response and distribution functions have been developed earlier

(O'Neill et al., 1972; Richter et al., 1990; Selhorst, 1995) and are briefly introduced in the following. A suitable temperature response function valid for a wide range of temperatures is the O'Neill function (O'Neill et al., 1972) for any development stage s:

$$d_s(T) = k_{\max} \cdot \left(\frac{T_{\max} - T}{T_{\max} - T_{opt}} \right)^x \cdot e^{\frac{x \cdot \left(T - T_{opt}\right)}{\left(T_{\max} - T_{opt}\right)}}$$

with (eq. 2)

$$x = \frac{w^2 \cdot \left(1 + \sqrt{1 + \frac{40}{w}} \right)^2}{400}$$

and

$$w = (Q10 - 1) \cdot \left(T_{\max} - T_{opt}\right)$$

for temperature T in °C and $T < T_{\max}$. The parameters $k_{\max}$, $T_{\max}$, T_{opt} and Q_{10} have to be estimated for each stage. A trajectory of the function is shown in figure 3 or figure 7. Integrating over the temperature response function allows the calculation of the biological time of stage s, as the progress rate of the individuals of stage s changes with temperature. Using a Weibull distribution as the normalized distribution function, we obtain at time t the following relationships (Richter et al., 1990):

$$G_s(t) = 1 - \exp^{-\left(\int_{t_{s,0}}^{t} d_s(T(\tau)) d\tau \right)^{\beta_{s,U}}} \qquad \text{(eq. 3)}$$

The transition probability to advance from age class i of stage s to the first age class of stage s+1 is calculated by

$$U_{s,i}(t) = \frac{G_s(t) - G_s(t-1)}{1 - G_s(t)} \quad \text{for } 1 - G_s(t) > 0 \qquad \text{(eq. 4)}$$

Similar relations apply to the determination of the survival probabilities. For any stage s in the age class i at the time t, it holds the general form

$$P_{s,i,t} = \frac{G(P)_s(i+1)}{G(P)_s(i)} \qquad \text{(eq. 5)}$$

while G of the stage s represents a Weibull distribution again, in which groups of individuals die concurrently at the end of their lifespan.

$$G(P)_{s,i,t} = \exp^{-\left(\sum_{j=1}^{i} \frac{1}{\lambda_s \cdot \left(T_j - T_{crit}\right)^2}\right)^{\beta_{s,P}}} \quad \text{for } T_j < T_{crit} \qquad \text{(eq. 6)}$$

The end of the lifespan is reached when a certain amount of heat units have been fulfilled. The rate is described by a quadratic response function (Selhorst, 1995), considering the accumulated temperature T from age class 1 to age class i. The integral was simplified to a sum, as time t and age class i were chosen on the same scale. The survival probability is 1 in the beginning, but gets significantly smaller, when the denominator becomes larger. Obviously, the rate is small with cooler temperatures and high in warm situations, and accordingly, longevity is either prolonged or shortened. The effect is a variation in the longevity of a stage with respect to temperature. The accumulated heat sum is again embedded in a Weibull distribution function G_s. This procedure reduces the number of parameters to two for the quadratic temperature response function plus one for the Weibull exponent for each stage. For a detailed mathematical background, we refer to Richter et al. (1990).

3. Results

3.1. Estimating the parameters of the survival functions.

The Weibull distribution with the embedded quadratic temperature response function (eq. 6) was simultaneously fitted to all data for both males and females. A high proportion of variance found in the data is explained by the model as shown by the coefficient of determination ($R^2 = 0.97$-0.98). Exploiting all information in one step holds the advantage that the functions can be included in the model as estimated without further transformation. Fig. 2 shows the results for the females only, yielding the following parameters for the quadratic temperature response function and the distribution function of eq. 6:

Table 2: Parameter estimates of the survival probabilities for both moths

	L. botrana		***E. ambiguella***	
Parameter (eq. 6)	adult ♂	adult ♀	adult ♂	adult ♀
$\lambda_{s,P}$	0.0124	0.0154	0.0456	0.0326
$Tcrit_s$	57.17	48.05	41.66	43.26
$\beta_{s,P}$	5	5	5	5

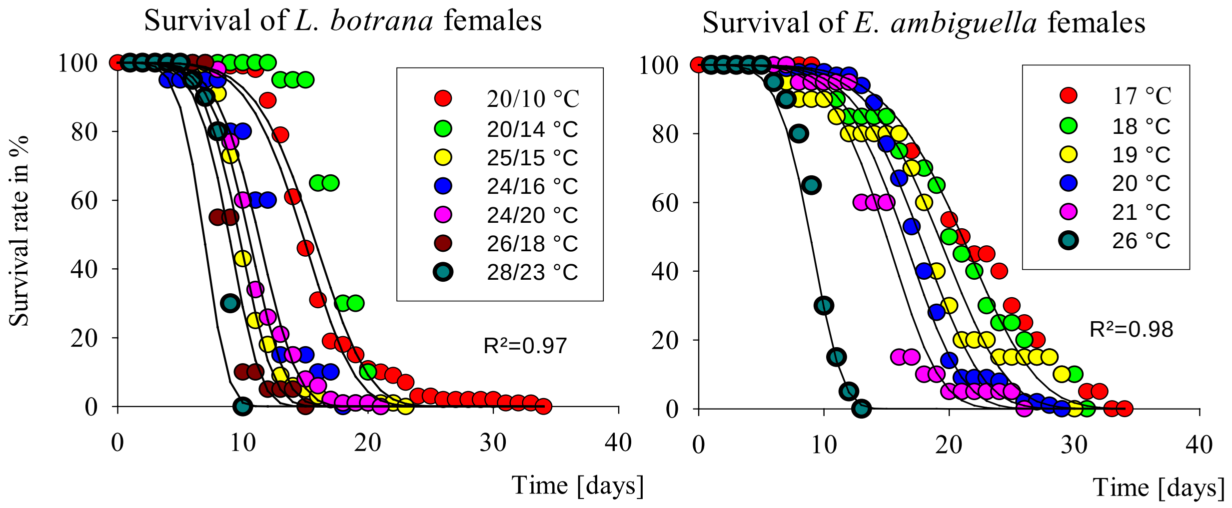


Fig. 2: Simultaneous estimated survival rates of *L. botrana* and *E. ambiguella* at different constant temperature levels.

3.2 Estimating the fertility rates F_i of age class i at time t

Data taken from Scholten-Thoma (1995) have clearly shown the temperature dependency of the egg laying duration and quantities. For the analysis the complete data set was divided into three biological plausible components:

1. Adult female longevity;
2. Maximum egg laying varied with temperature;
3. Pre-oviposition period;

While the component "longevity" has been estimated before, the two additional components can be identified by the determination of the developmental rate for the pre-oviposition time and the maximum amount of laid eggs at different temperatures. The O'Neill function (eq. 2) was fitted to the maximum egg data (fig. 3 c). Egg laying starts after the adult females have been exposed to a certain amount of heat units. The egg laying period starts after 2 days at optimal temperature conditions and is delayed in either cooler or warmer conditions. K_{max} of a temperature response function is therefore at a value of approximately 0.5 (= 1/time). Again, fitting a O'Neill function to the data (fig. 3 b), integrating over the estimated function and embedding the integral into a Weibull function, as previously executed (eq. 3), determines the start of the egg laying period. The product of the three components computes the fertility rate in each age class at a given time and temperature:

$$F_i(t) = P_i * d(T) * S_i \qquad \text{(eq. 8)}$$

with
$F_i(t)$ = Number of eggs/female in age class i at time t
P_i = fraction of adults with the condition of age class i (range 0 to 1)

d(T) = max. number of eggs at temperature T (°C)
S_i = Switch to determine end of the pre-oviposition period at age class i (range 0 to 1)

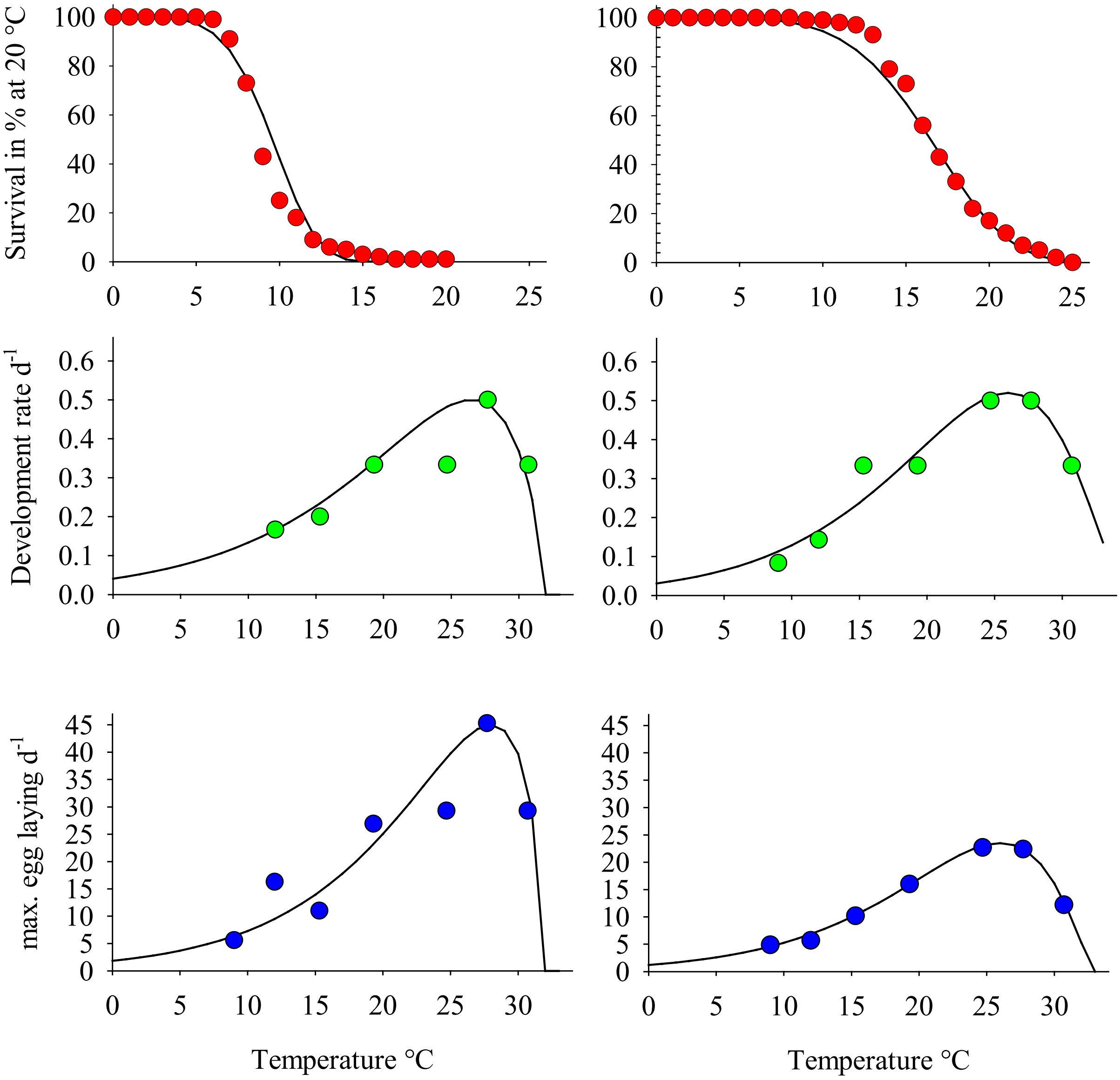


Figure 3 a,b,c: Estimated response functions describing the fertility rate; left column: *L. botrana*; right column: *E. ambiguella*

To explain the mechanism in detail: young females have the potential of a full offspring rate (P_i=1), but if the developmental time of the pre-oviposition period is not yet fulfilled (S_i=0), the egg laying rate is zero. When the pre-oviposition time has passed, the adults switch to fertile conditions (S_i = 1). The final number of eggs produced is a function of d(T) at given temperature T. The amount of laid eggs decreases with the females' ageing (P_i < 1). The given example at 20°C (fig. 4 a) shows the decrease starting after 8 days and egg laying stops approximately after 14 days for *L. botrana*. For *E. ambiguella*, the decrease starts after 14 days and stops eventually after 24 days at the given temperature level.

Table 3: Parameter estimates of the fertility probabilities for both moths

Para-meter	*L. botrana*	*E. ambiguella*	description
	adult survival (fig. 3a)		
P_i	as table 2		Adult female survival
	pre-oviposition time (fig. 3b)		
k_{max}	0.42	0.52	max. development rate
Q_{10}	1.792	1.87	rate change with temperature change by 10 °C
T_{opt}*	24.5	26	optimum temperature
T_{max}*	33	35	max. temperature
β_F	6	6	2nd Weibull parameter
	max. egg laying (fig. 3c)		
F_{max}	45	23	max. egg laying rate/female/day
Q_{10}	1.9	1.87	rate change with temperature change by 10 °C
T_{opt}	28	26	optimum temperature
T_{max}	32	33	max. temperature

* parameter calibrated, fixed

The sub- model is applicable to all temperature ranges (fig. 4) of the underlying experiment without varying a parameter. The fertility rate of both moths is described by an individual parameter vector. Although the results of different climate chamber experiments have been combined for model development, the synthesized model agrees well with the observations made for most of the temperature levels. Only the trial under very hot conditions (31 °C) was not repeatable. Compared to the longevity of *L. botrana*, the adults of *E. ambiguella* stayed alive longer, but concurrent the actual maximum egg laying rate is smaller. The pre-oviposition period of both appeared to be similar.

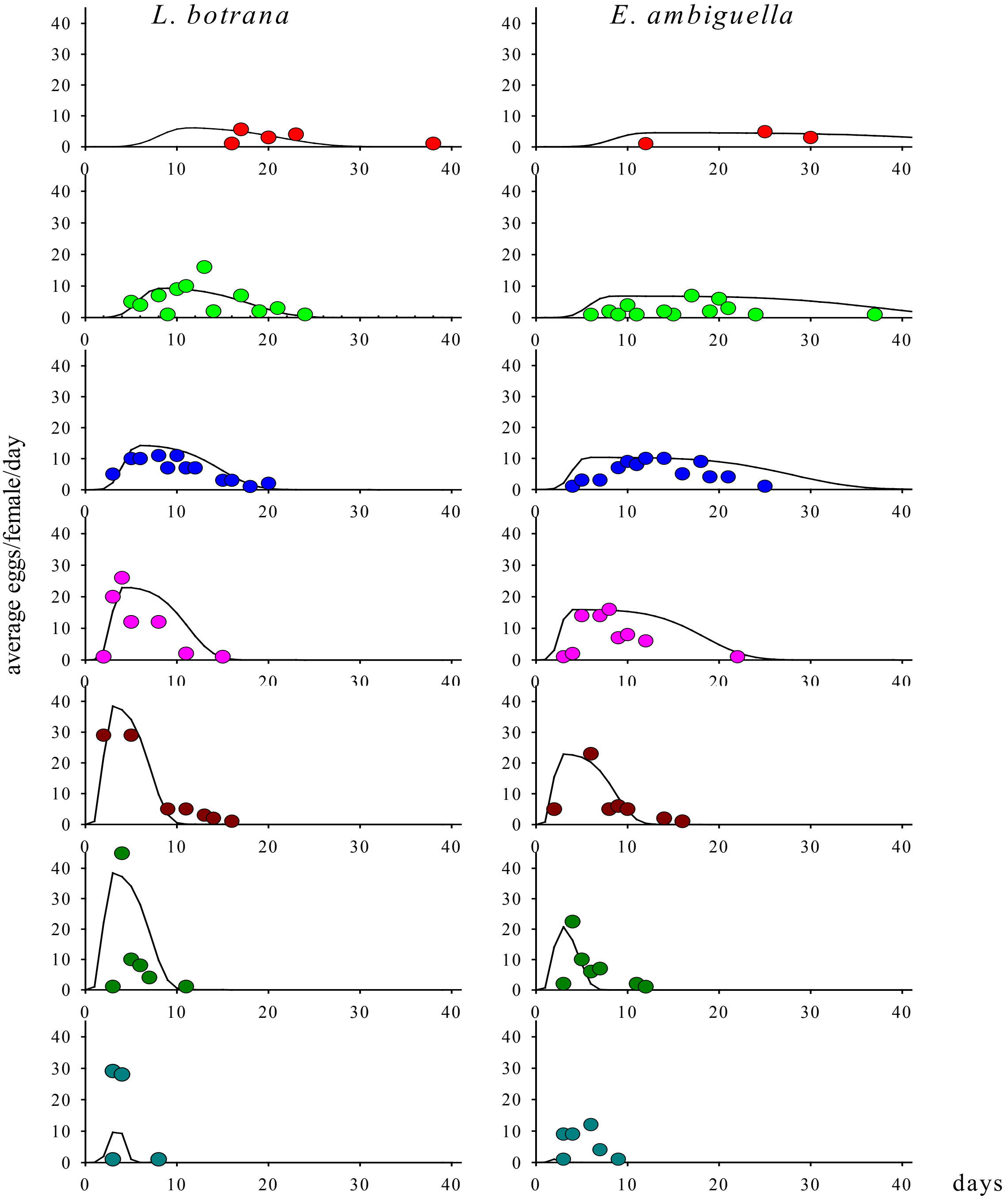


Figure 4: Comparison of the fertility sub-model with observations at different temperature levels (night/day temperatures) for both moths.

3.3. Estimating the development and survival rates of the stage eggs

So far, the first compartments (adult longevity and fertility) of the Leslie model shown in figure 1 have been identified and parameterized for both moths. These results in conjunction with the Leslie model were used to analyse the third complex of climate chamber experiments. The progress of the egg population was monitored over time. For this stage, we require the appropriate transition and survival probabilities as introduced before. Parameter estimation can be performed in two ways: a) all data are used for all parameters simultaneously or b) separate estimates are obtained for each temperature level. In a subsequent step, the estimates are fitted or calibrated to the introduced response functions. The first method is not applicable to the task ahead, as the data have no clear distinction between transition and survival probabilities. Hence, the probability distribution functions for the transition probabilities and the survival probabilities of the stages s (here s = eggs) were estimated on the real time scale instead of the biological time by using the Leslie model. The survival probability becomes then

$$P_s(t) \quad = \quad \exp^{-\left(\frac{t}{tc_s}\right)^{\beta_{sP}}} \qquad \text{(eq. 9)}$$

and the normalized distribution function to estimate the transition probability becomes

$$G_s(t) \quad = \quad 1 - \exp^{-\left(\frac{t}{td_s}\right)^{\beta_{sU}}} \qquad \text{(eq. 10)}$$

while tc_s and td_s denote the points of inflection in days. The parameters β_{sU} and td_s of the distribution function can be estimated according to the shape and maximum of the trajectory of the accumulated egg shells. It represents the appearance rate of the stage L1. The parameter tc_s is estimated to the observed magnitude of the eggs. To solve the fitting problem, the Leslie model was linked to a least square fitting procedure estimating the parameters iteratively (Press et al., 1992).

Figure 5 summarize the results of the complete Leslie model fitted to the data of both moths at different constant temperature levels. The survival pattern of the adults is the result of the simultaneous fittings. The error bars denote the 95% confidence intervals (n=4). All figures of one temperature experiment should be regarded as one regression unit.

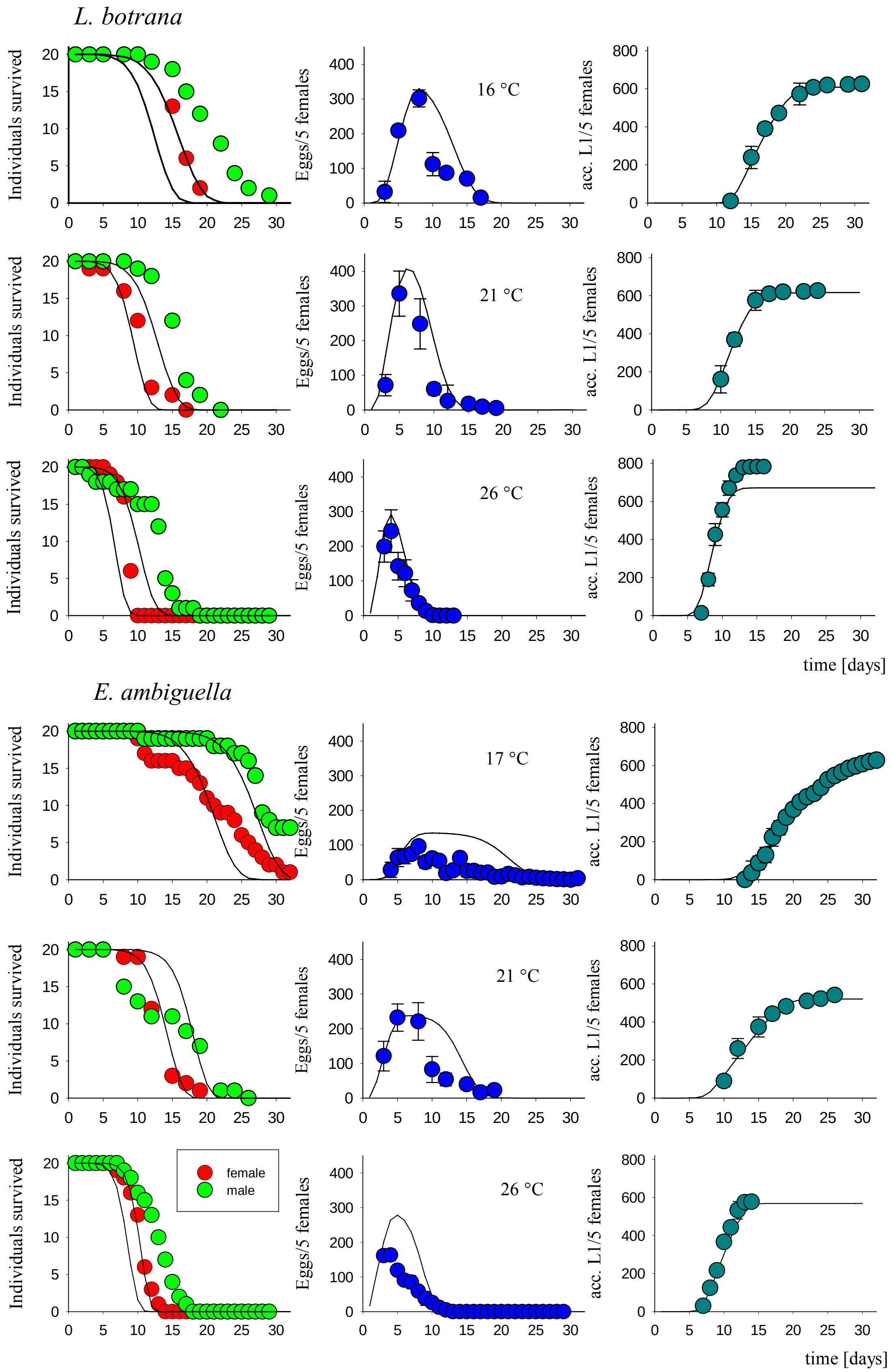


Figure 5: Fitted Leslie model for the stage dynamics at different temperature levels for both moths; error bars denote the 95% CI, n=4; (read graphs from left to right as one regression unit)

The estimated parameters (unit = days) are shown in the following tables 4:

Table 4: Fitted parameters (in days) for the stage eggs

	L. botrana			*E. ambiguella*	
	development	survival		development	survival
Temperature trial	Td_{egg}	Tc_{egg}	Temperature trial	Td_{egg}	Tc_{egg}
LB F ø 16 °C	22.1	9.3	EA B ø 17 °C	23.5	4.7
LB A ø 20 °C	10.1	3.9	EA C ø 18 °C	13.4	2.7
LB B ø 23 °C	7.6	3.5	EA D ø 19 °C	10.5	2.8
LB K ø 26 °C	6.1	3.1	EA A ø 21	6.5	2.0
			EA K ø 26	7.5	1.4

By determining the normalized developmental and survival times (i.e. 1/tc or 1/td), the following response functions were obtained (eq. 2 in figure 6 and eq. 6 in 7), yielding the following list of parameters (table 5):

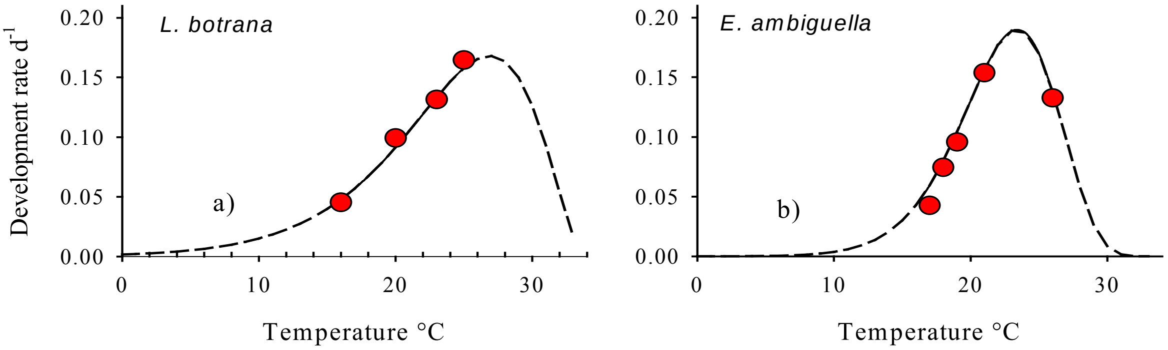


Figure 6: Calibrated response functions (eq. 2) for the determination of the development time;

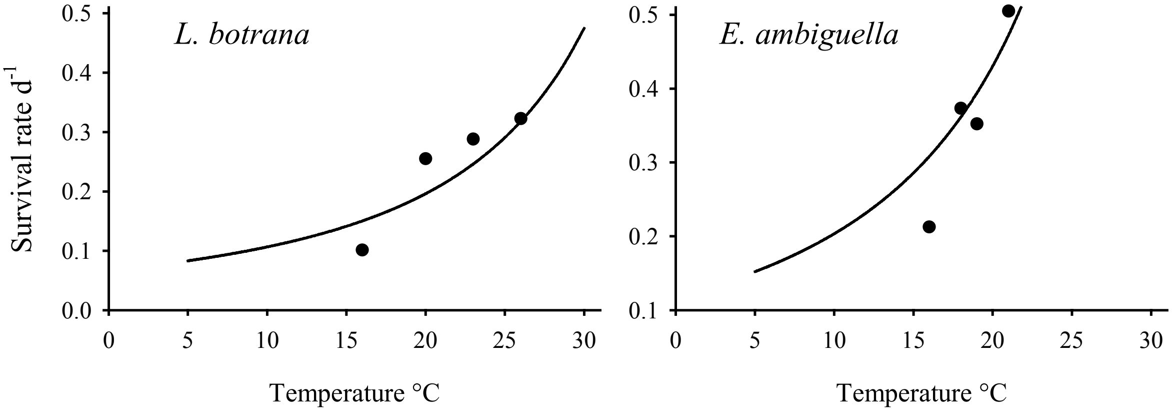


Figure 7: Calibrated response functions (eq. 6) for the determination of the survival time;

Table 5: Calibrated temperature response functions

Parameter	*L. botrana*	*E. ambiguella*	Parameter	*L. botrana*	*E. ambiguella*
	Egg development			Egg survival	
k_{max}	0.17	0.19	λ	0.0065	0.0048
Q_{10}	2.2	3.1	T_{crit}	48	42
T_{opt}	26.5*	23.4			
T_{max}	34*	34*			
$\beta_{s,U}$	1.65	13.69	$\beta_{s,P}$	5	5

* parameter fixed

The O'Neill function (eq. 2) and the quadratic response function (eq. 6) were calibrated to the observations. Four or five temperature levels alone are not sufficient for a valid estimation, since these represent just a small range of potential temperatures. Therefore, the extrapolation into ranges beyond the observed ones appears rather empirical. However, we have to accept this weakness for the time being until more data become available.

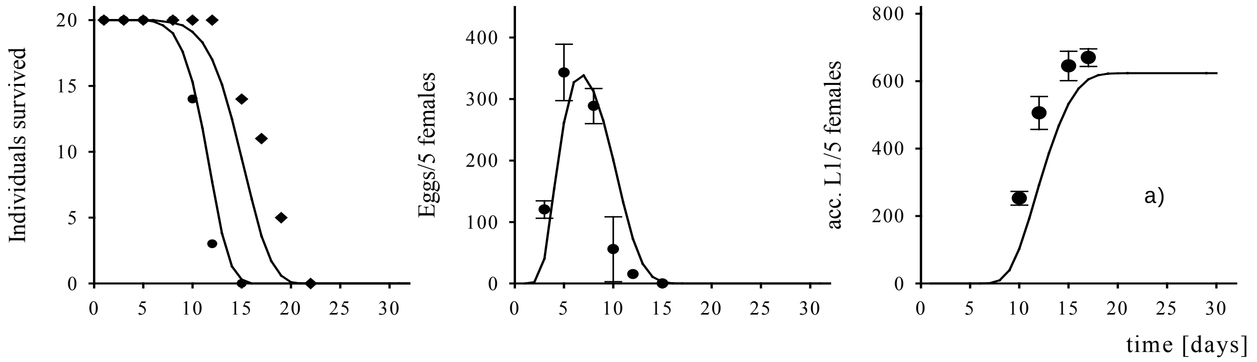
3.4. The influence of the factor relative humidity (rH)

Most of the third group experiments were run with an adjusted rH of approximately 80%, presuming a response plateau, which does not disturb the developmental rates, neither the survival nor the fertility rates. Beside one experiment for *E. ambiguella*, two experiments were conducted for *L. botrana* without controlled rH at the temperature level of 18/24°C. In one experiment, the rH concentrations were allowed to vary naturally during night time only, while in the second one, rH varied day and night (LB G and EA D). Especially during the latter experiments, the individuals were exposed to certain periods during the day when rH fell below the range of 45% to 50%. If the factor rH had no influence on the population dynamics of *L. botrana*, the experiments should be repeated by the model without parameter change as the trial conducted with controlled rH conditions at the same temperature level. While the variation of rH during the night did not demonstrate a significant deviance (fig. 8 a), the situation changed in the second experiment. Figure 8 b shows an over-prediction concerning the population densities of eggs. The appearance rates in time agreed well with the observations. Apparently, the factor rH affects the population density, but not the development rates. Two hypotheses were assumed: The factor rH controls the fertility rate or the life span of eggs. Both hypotheses were tested within the given model approach. Reducing the longevity of eggs did not improve the divergence between data and model. Reducing the parameter F_{max} (eq. 2) resulted in a satisfying agreement for eggs, but the quantity of empty egg shells remained too low (fig. 8 c). Nevertheless, the underlying egg laying response function was be extended by an additional response function of the factor rH. A double Weibull function is suitable to vary F_{max} by a factor θ_t (eq. 11) .

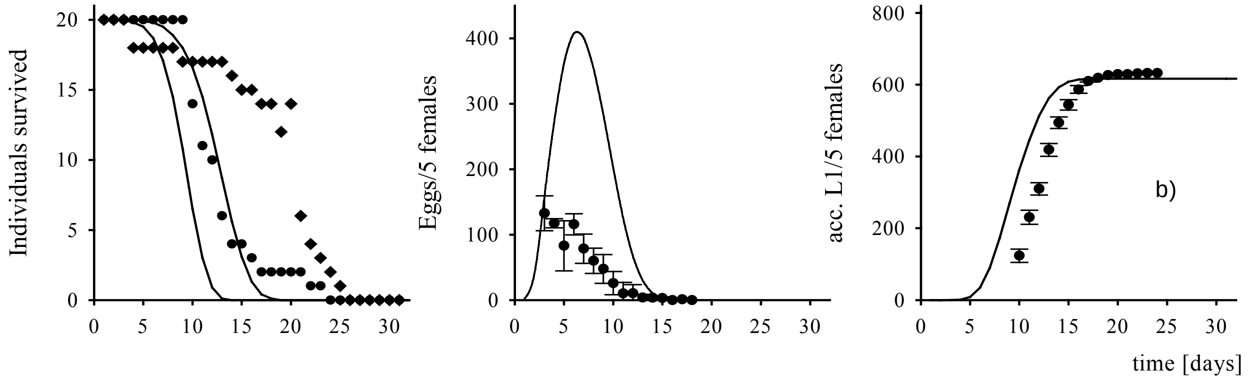
$$\theta_t = \left(1 - \exp^{-\left(\frac{H_t}{H_{Low}}\right)^{\alpha_H}} \right) \cdot \exp^{-\left(\frac{H_t}{H_{High}}\right)^{\beta_H}} \qquad \text{(eq. 11)}$$

H_t is the relative humidity in % at time t and H_{low} and H_{high} represent the points of inflection. Equation 11 generates a plateau with $\theta = 1$ using a certain ratio of the parameters α_H to β_H. As already mentioned above, Figure 9 shows a potential outcome of the product of both response functions. It is obvious, that we cannot extrapolate to the whole mesh of combined response functions with just few measurements. The lack of information is completed with empirical assumptions.

L. botrana, 21°C, variablel rH% at night



L. botrana, 21°C, variablel rH%



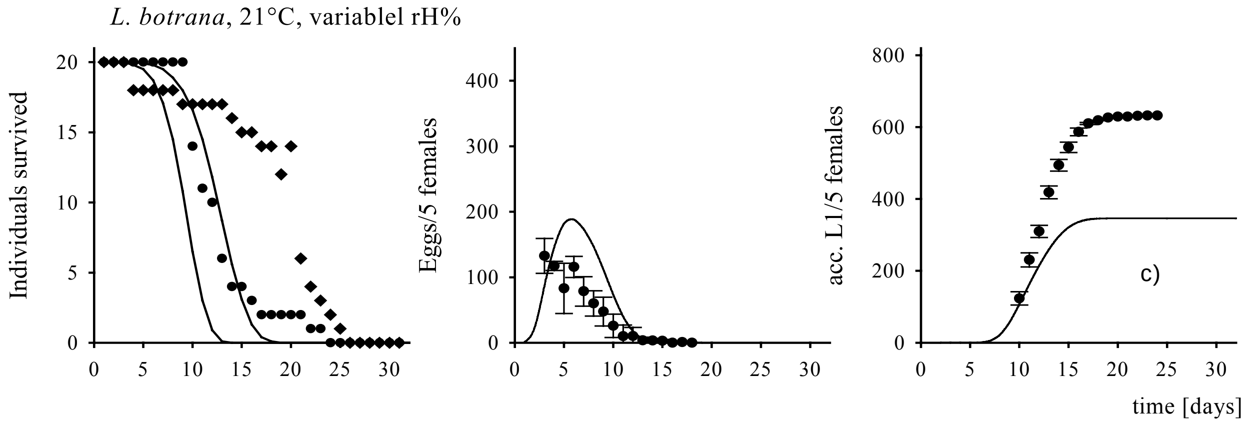


Figure 8 a, b, c: Testing the influence of the factor relative humidity and model output; a) rH variable during night time only; b) rH variable all the time; c) newly calibrated with changed fertility rates for *L. botrana;* for legend see figure 5

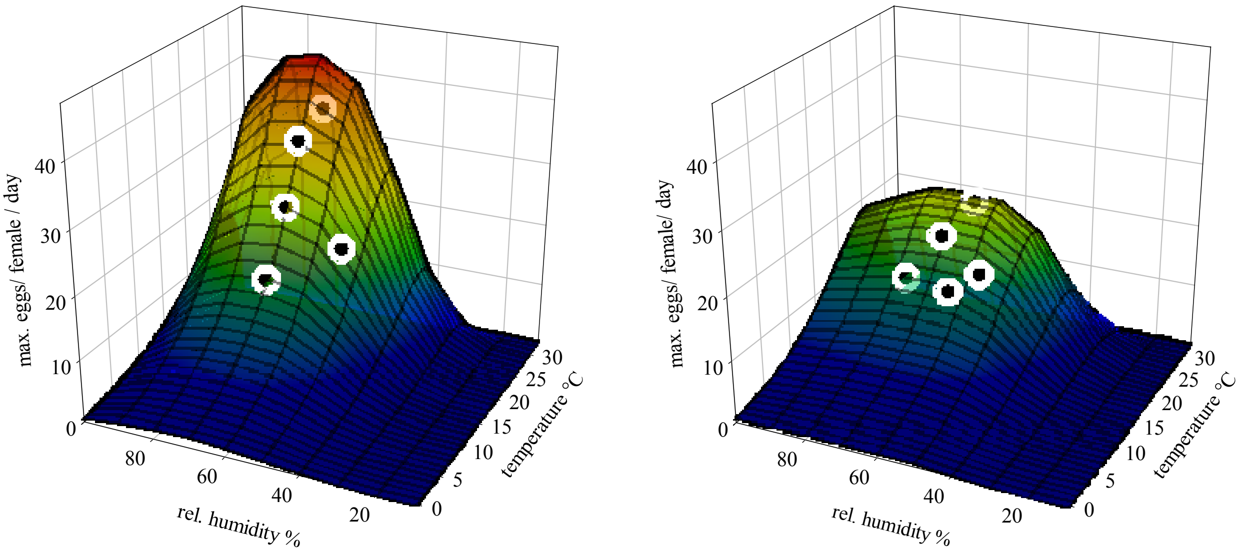


Figure 9 a, b: Changed fertility rates as a combined function of temperature and relative humidity; a) *L. botrana*; b) *E. ambiguella*

4. Discussion

Despite conditions of the experiments were kept as constant as possible, the observed variability in the data confirmed the complexity of the climate driven population dynamics of the two moths. The pattern observed in neither of the experiments revealed a straightforward image of the underlying mechanism. The analysis presented here demonstrates a way as to how to reduce information of parallel processes to parameters of environmental response functions. For the analysis of the adult's longevity data, known techniques have been adopted (Richter et al, 1990; Selhorst, 1995). Simultaneous fitting exploits all information completely, but deviance between single sets of data and model occur.

The analysis of the fertility trials required an allocation to three biological based components. Each of the three components were fitted to a sufficient amount of data over a wide temperature interval, thereby providing estimates of the related response functions. It was possible to transfer the results of the longevity analysis to identify the egg laying duration. This does not substantiate the correctness of the underlying assumptions, but was well-suited to solve the problem. It must be mentioned that other and probably simpler dependencies than those introduced here may be valid also. Hoppmann & Holst (1993) suggested that the number of eggs is predetermined by temperature. Once the respective amount of eggs is achieved, the adults die. Reducing the moths to some few key parameters, it is obvious that both moths occupy the same habitat but exploit the same climate with different efficiency. *E. ambiguella* has a preference for cooler temperatures, which is expressed by longer life spans of the adults. However, the maximum number of eggs per female at optimum temperatures is reduced. *L. botrana* seems to be better adapted to higher temperatures. Despite the longevity being shorter at a given temperature, the maximum fertility rate F_{max} is higher at higher temperatures. The otherwise contrary behaviour was approximately balanced in the 14/22 °C trial (fig. 4). The compiled fertility sub-model did not show major deviance compared to the observations, but the model trajectories pass the data to the outer boundary. Nevertheless, some deviation occurred as the model represents idealized conditions, which were probably not maintained in the experiments. Only at very high temperatures, (25/33 °C), the model failed to repeat the observed numbers of eggs. The underlying temperature response function shortens the adult longevity in such a way that no eggs are produced.

Both preliminary analysis steps have been essential to understand the temporal pattern of the following stage eggs. The data represent the two parallel processes, which are defined by the Leslie model: development and survival. The Leslie model has been the tool to distinguish between both, while the introduced model structure has been used as a regression approach. Fitting the relevant parameters on a real time scale provided the source for estimating the response functions for both development and survival. The temporal pattern of eggs and the appearance rate of larvae were repeated well, even though the trajectories sometimes missed the confidence intervals. It must be mentioned that temperature is the only driving variable in the model during the iterative fitting, and therefore represents strongly idealized trajectories. Within the climate chambers, the environmental conditions have been variable, although constant conditions were targeted. The unexpected death of one out of five females should have a significantly changed the total amount of eggs produced.

The fitted model provided an appropriate tool to analyze the experiments, which were conducted at the same temperature level but with different relative humidity levels. With one trial only for each moth, conclusions are difficult to generalize. Within the spectrum of data and model, there is evidence that the maximum fertility rate is controlled by the combination of the two factors under investigation, and fertility decreases with increasing dry conditions. The critical values of the double Weibull function used to describe the effect of rH correspond with observations made by Savescu et al., (1969) and Savescu & Rafaila (1978). Figure 9 demonstrates a potential outcome of the combined response functions, but also highlights the immense lack of proper information. No evidence was found for a shortened life span of the further developmental stages with reduced rH levels. This does not mean that these stages remain unaffected by rH. The rH could have stayed above the biological critical level that no changes in behaviour occurred. In fact, a similar analysis of field data related to climate records revealed an impact of rH on the survival probabilities of the stages eggs and L1 (Schmidt et al., 2002). Ranking the impact of climatic factors, it seems to be realistic that temperature is the main factor, while the factor relative humidity varies the temperature effects.

The model and analysis approach introduced here merges three independent experiments. The data were used to identify components of a theoretical model, and in return, the model was applied to reveal processes, which are normally hidden in the variance of data. A comparison of the estimated model with field data is premature, as further factors should be considered and the complete life cycle of the moths must be established first. Nevertheless, the experiments and the analysis conducted so far improve the required knowledge for the assessment of relative changes of one climatic factor in relation to the biological response. An initial contribution was made towards the final objective of the project, namely the prediction of the population dynamics of both moths under field conditions.

Acknowledgements

We like to thank Miriam Hauck and Silvia Pieper for their patience to keep the trials running smoothly and for their efforts of data collection. The project was funded by the “Stiftung Hofgeisberg”, 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

O'Neill, R.V., Oldstein, R.A., Shugart, H.H. & J.B. Makin (1972): Terrestrial ecosystem energy model. Eastern deciduous forest biome memo report, No. 72-19: 38 pp.

Press, W.H., Teukolsky, S.A., Vetterling, W.T. & Flannery, B.P. (1992) Numerical recipies 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;

Schmidt, K., Hoppmann, D.,Holst, H. & B. Berkelmann-Löhnertz (2002), Identifying weather related covariates controlling the grape moths dynamics, EPPO Bulletin 33, 517-524;

Scholten-Thoma, F, (1995) Optimierung eines Prognosemodells für Traubenwickler, Spezielle Untersuchung zur Flugaktivität und Eiablage bei *Lobesia botrana (Schiff.)* und *Eupoecila ambiguella (Hübn.)*, PhD-Thesis, Mainz, 121 pp.

Selhorst, T. 1995. Modelling the temperature effect on bimodally distributed life times. Ecological Modelling, 27-34