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Computer Modeling of Insect Growth and its Application to Forensic Entomology

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Introduction

It is obvious that temperature is of critical importance to insect development, and much research has been devoted to this area. Developmental theories, mathematical equations, and even computer simulations of insect growth have all been created and published within the relevant literature. However, the use and application of computer modeling in forensic entomology is largely unexplored. The reason for this is that many widely used entomological computer models do not provide acceptable results for predicting development times of insect field populations under variable temperature (Stinner et al. 1974), and this is a critical drawback for forensic applications. The only published accounts of established statistical protocol or computer simulation of the arthropod fauna inhabiting carrion is by Schoenly (1992), and Schoenly et al. (1992). Schoenly et al. (1992) developed a computer algorithm in the BASIC language to calculate the postmortem interval from arthropod succession data. The required input for this program is the identity of arthropod taxa recovered from the death scene, data on carrion-associated arthropod taxa, known succession patterns, and data on developmental duration of the immature stages.

Schoenly (1992) also developed a set of statistical protocols proposed for analyzing carrion-arthropod succession in forensic entomological investigations. This protocol analyzed data in three ways: 1) Patterns of arthropod visitation (arthropods divided into reoccurring or non-reoccurring taxa); 2) Temporal changes in taxonomic

composition of the carrion-arthropod community; and 3) Applying sampled random tests (Monte Carlo simulation) to community wide arthropod visitation times.

Most published computer assisted entomological techniques use succession (= species replacement) timetables of certain taxa to estimate the upper and lower limits of the postmortem interval in days. Williams (1984) published a model for aging fly larvae in which a method is described for determining the time of egg hatch based on larval weight, with respect to temperature. Two programs were developed, one computes the parameters for logistic equations, and the other estimates the time elapsed from when a sample is removed from a body to the estimated egg hatch time. However, in this model temperature and the insect species serve as independent variables while the growth rate and parameters of a logistic growth curve are the dependent variables.

In order to advance the applicability of computer simulations to forensic entomology, the baseline understanding of adult behavior and its effect on oviposition patterns needs to be expanded and adult emergence patterns need to be charted. Our objectives were to determine the mean and standard deviation of the development of immature life stages, compare the development of immature insects under constant and cyclic temperature regimes, and compare the various development model theories with the baseline data to determine the optimum model format. In addition to these goals, we also feel that advanced computer models should be developed which compensate for adult activity periods; ambient temperature fluctuations, inter-species competition, and the excess metabolic heat generated by actively feeding second and third instar larvae. With such technology it is hoped that increased accuracy and understanding of the use of entomological evidence in crime scene investigation will be developed.

Computer Modeling Theory

The need to predict insect development time has led to many mathematical models that describe the effects of temperature on insect development. Of these mathematical models, two general types are relevant to this work. These are the degree-day summation method, first introduced by Candolle (1855), used in a non-linear model by Sharpe & DeMichele (1977), and the non-linear temperature inhibition model (Johnson and Lewin 1946).

Linear Development Rate Models

The most common development rate model, often called degree-day summation, assumes a linear relationship between development rate and temperature between thresholds (Allen 1976). This method works well for intermediate temperatures, but because of nonlinear effects at high and low temperatures it does produce some errors at temperature extremes (Stinner et al. 1974). The linear model assumes that rates are proportional to temperature, and since amounts are integrals of rates, the amount of development is the integral of temperature (or a linear function of it) along a time axis and has units of temperature-time (e.g., degree-days). Temperature-dependent development in poikilothermic insects can be approached using either time or rate of development. Rate of development is traditionally utilized because rate models were created from biochemical and biophysical properties (Sharpe and DeMichele 1977, and Wagner et al. 1984). Kramer et al. (1991) addresses several of the complications that arise when using rate instead of time. However, Allen (1976) presented a method for calculating degree-days and allowing for an upper and lower threshold.

Non-linear Development Rate Models

Since some temperatures are lethal to organisms, it is obvious that development must be a nonlinear temperature function at the temperature extremes. Non-linear development rate functions based on enzyme kinetics were developed to describe high temperature inhibition by Johnson and Lewin (1946) and low temperature inhibition Hultin (1955). Sharpe and DeMichele (1977) described a general model incorporating both high and low temperature inhibitions based on control enzyme inactivation. Another nonlinear model of temperature-dependent development, (Stinner et al. 1974) utilized a function that is a simple sigmoid curve with an inverted relationship when the temperature is above the optimum. This model, as originally given, assumed symmetry about the optimum temperature, but can be easily modified for asymmetry. A nonlinear model by Logan et al. (1976) uses an equation that is asymmetric about the optimum, but becomes negative for very high temperatures.

Of the Sharpe and DeMichele model, Wagner et al. (1984) states that there is no other poikilotherm development rate model with greater flexibility, goodness of fit capability, or stronger theoretical foundation. However, this model is a bit complicated. It possesses six constants that must be determined by nonlinear least squares and, in some situations, it may be 'overkill' (particularly in cases which temperature extremes are not often encountered). Recently, Schoolfield et al. (1981) modified the Sharpe and DeMichele model to enhance its overall utility and simplify parameter estimation. As pointed out by Worner (1992), the interaction of cyclic temperatures with nonlinear development can introduce significant deviations from the linear development rate

model, especially in the low and high temperature regions of the development rate function.

To accomplish our objectives of enhancing postmortem interval estimation techniques, an insect phenology model with particular reference to the unique problems of forensic entomology has been developed using Simulink flow diagram software for IBM compatible PC-type desktop computers. The development of this model employed a linear chain of differential equations to represent each of the insect life stages. This technique, called a distributed delay, is broadly used in engineering to model delay processes (Manetsch 1976, Vansickle 1977) and has been used by others to model insect developmental delays (Gutierrez et al. 1975, Gutierrez et al. 1984a, b). Distributed delays as models of biological time lags are also described in Cushing (1977) and MacDonald (1978) who referred to it as the 'linear chain trick'. A distributed delay is simply a linear chain of rate (i.e., differential) equations representing flow through a system of 'boxes', each having the same flow rate (a) in equation 1.

Equation 1:

$$\begin{aligned}\frac{dx_1}{dt} &= f(t) - ax_1 - \mu x_1 \\ \frac{dx_2}{dt} &= ax_1 - ax_2 - \mu x_2 \\ &\vdots \\ \frac{dx_n}{dt} &= ax_{n-1} - ax_n - \mu x_n\end{aligned}$$

This chain of equations represents an entire life stage (e.g. the egg stage) in which the x_i 's are the number of eggs in each substage, and the flow rate, a , is the same for all substages, giving the name *distributed* delay. Some mortality is indicated from each substage at rate " $-\mu x_i$ ". The 'input' is represented as $f(t)$, i.e., some general function of

time. In forensic cases involving entomological evidence, $f(t)$ would be oviposition by adult flies. This method has two major advantages: (1) It is easy to model such systems with simulation software (e.g., MATLAB/Simulink (The MathWorks Inc.) which is a ‘boxes-and-arrows’ modeling environment, and (2) everything in the model can be obtained from the mean time in a life stage and the variance of the time. These things are usually reported with the relevant developmental literature since they are easily measured empirically. Thus, by simply measuring the mean and standard deviation of the time to complete a stage, one can obtain the data needed to construct a stage model using a distributed delay. The number of stages required, n , is given by $n = \tau^2/s^2$ (rounded to the nearest whole number) where τ and s are the mean and standard deviation of the time required to complete a life stage (e.g., the egg stage). The flow rate a in the distributed delay equation (1) is equal to n/τ . A single differential equation flow diagram from Simulink is shown in Figure 9, while a cascade of these diagrams is shown in Figure 10 representing the equations in (1) above. The useful “single substage” formula is shown below in equation 2 where we have included mortality with the per capita rate “ μ ”.

Equation 2:

$$\frac{dx_i}{dt} = ax_{i-1} - ax_i - \mu x_i$$

Development rate functions were obtained at different temperatures under controlled conditions and through comparison with larval development under field conditions. Field comparison was based insect collections made from two *Sus scrofa* (L.) (domestic pig) carcasses, less than 24 hours postmortem, obtained as mortality from local hog producers. These carcasses were placed outdoors simultaneously under identical

conditions with one left exposed to the insects throughout decomposition, while the other was covered with a screen cage to exclude further insect colonization after 3.5 days exposure. Insect samples were collected daily from the center of the maggot mass (or masses) to duplicate the entomological sampling techniques utilized by crime scene technicians and other death investigators. The samples were identified to species and sorted according to developmental stage. The observed sample data time series was then compared to the computer model output.

Creation of a Computer Model

For the carcass exposure study, results were interpreted only for insects in the family Calliphoridae (Diptera), and from this family only two species colonized the remains; *Cochliomyia macellaria* (Fabricius), and *Chrysomya rufifacies* (Macquart). With the covered carcass, all ovipositions ceased once the screen and frame structure was in place proving that the enclosure was an effective barrier to colonization. After the initial oviposition input of 3.5 days, development proceeded normally and all life stages are shown in Figure 1A, and 1B. The first instar was recovered on days 3-9 for both species, the second instar of *C. rufifacies* was found on days 4-10, while the second instar of *C. macellaria* was present in samples until day 14. The third instar of *C. rufifacies* was recovered during the morning hours of experimental day 5, and this stage displayed a duration 24 hours longer than that of the *C. macellaria* third instar. Similarly, the pupal stage of *C. rufifacies* also formed 24 hours later than the pupae of *C. macellaria*, and adult emergence of *C. rufifacies* occurred 24 hours later than for *C. macellaria* with the first adults recovered 22 and 23 days (respectfully) after exposure.

Larval development on the carcass that remained exposed to continual insect colonization was not as easily interpreted as that of the covered carcass. Generally, the residence time of an instar on the carcass was longer, presumably due to longer exposure to oviposition input. With *C. macellaria*, the time in which the first instar was recovered increased by seven days, and the duration of the second instar was lengthened by four days (Figure 1B and Figure 2B). Onset of the third instar was also lengthened by four days, with the start of the pupal stage having an almost equal delay of 3.8 days for both species. This same delay period also held true for the onset of adult emergence for both species.

On the exposed carcass, *C. rufifacies* was able to develop for a period of four days before the carcass population was decimated by *Solenopsis invicta* Buren (red imported fire ant). The ants effectively removed all of the eggs and first instar larvae of *C. rufifacies* during the late morning to mid afternoon hours of day four, and the adults of this species did not re-colonize the corpse until the late morning hours of day six (Figure 2A). After re-colonization of the carcass (the 2nd oviposition peak in Figure 2A), development proceeded much the same as occurred on the covered carcass (Figure 1A). However, the ants did not significantly reduce the enormous numbers *C. macellaria* eggs and first instar larvae that were laid on other areas of the carcass. Therefore oviposition and initial colonization of *C. macellaria* continued over an extended period of time as eggs were recovered throughout the first five days of exposure, and the first instar larvae were found for a total duration of 16 days. Ovipositions, although reduced in number, probably continued on the exposed carcass for a period longer than was actually reported.

However, the large number of *C. macellaria* maggots made recovery of the relatively few eggs an unlikely event.

The complete maggot model is shown as a Simulink flow diagram (Figure 3) where each life stage (egg, first instar, second instar, third instar, pupa, and the adult) consists of a chain of equations like the distributed delay, equation (1). Each of these life stages has an input for the development rate function for that particular stage, an input from the previous life stage, plus an input for the mortality rate. The output (emergence) of each stage is passed to the next, and it is also sent to a multiplexer so that output can be graphed. Two types of graphs are available: one that plots the proportion of the population against time, and the other that plots relative abundance against time. The proportion in each stage is particularly useful for crime scene comparison since it is independent of absolute abundance. The graphical output can then be used for postmortem interval estimation based on entomological evidence through direct inspection.

One of the main complications with which a forensic entomologist must contend when utilizing a computer model for postmortem interval estimation is the effect of temperature on development and hence the rate of flow through the substages. However, this can be accounted for by making either the development rate, or the time to complete a stage, a function of temperature.

The model is driven by input from both the temperature submodel (Figure 10.4) and the oviposition submodel (Figure 5). The temperature submodel accounts for ambient temperature, and it can be adjusted to fit constant or cyclic conditions. This is accomplished by the use of a constant value that represents the average temperature, and

a wave function that cycles around the average temperature specified by the user. If the user has empirical temperature observations, either daily or hourly, they can be entered as data in an ASCII text spreadsheet and imported directly into the model in place of the temperature submodel. The oviposition submodel accounts for the behavior and diurnal activity of adult flies, as well as the added effect of cadaver age and its attractiveness to various fly species. Additionally, the threshold activity temperature can be specified with this submodel so the rate of oviposition can be more accurately predicted. Through the use of a "constant box", a clock function, and a "relational operator", the time at which oviposition would cease (either through normal adult oviposition behavior or by exclusion such as concealment with a structure or container) can be specified if it is known (Figure 5).

Figure 6 demonstrates the cadaver attractiveness function as a curve with a normal distribution ($\mu = 24\text{hr}$, $\sigma = 20\text{hr}$) plotted against time. The model output shown in Figure 7 illustrates the flight behavior of flies that exhibit a diurnal periodicity, which must be accounted for as flies are not active at night. Thus no oviposition should occur during these hours and the time of cadaver deposition, which is also the starting time for the model, is an important variable.

Figure 8 shows the combined effect of cadaver age, ambient temperature, and flight activity on oviposition. The black line represents the cadaver age effect, the dotted line represents the expected oviposition rate at optimum developmental temperatures, and the gray line represents actual ovipositions with a diurnal periodicity. The substage model, or the single development substage (Figure 9), is the core of the model as it combines the development rate input, data flow from previous stages, the mortality rate,

and passes the combined output to the next substage. This substage model represents equation (2) in the linear cascade process. The output of the oviposition submodel flows through the life stages of egg, larval instar 1, 2, 3, pupa, and adult. Each of these life stages is configured as a series of single developmental sub-stages linked together forming a “distributed delay” as shown in Figure 10. The shape of the simulated developmental curve for each of the insect life stages can be controlled by increasing or decreasing the number of these substages within a particular life stage. The relation between mean (τ) and variance (σ^2) of the emergence curve and n (the number of stages) is represented by equation 3 so n can be easily calculated from the mean and variance of the data.

Equation 3:

$$n = \frac{\tau^2}{\sigma^2}$$

This mimics the effect of temperature on an insect by regulating the time required to complete a stage, as altering the number of substages thereby changes the mean and SD of the growth curve. For simulation purposes the number of substages were varied for each life stage to match the mean and SD of growth curves obtained through laboratory rearing. This was accomplished through equation 4.

Equation 4:

$$\tau = a + \frac{b}{T - c}$$

The development rate input for each life stage is controlled through the development rate submodel (Figure 11). This submodel is based on actual developmental

data obtained under laboratory conditions and must be specified for various species under differing conditions. The settings that must be specified by the user are the minimum developmental time (a), the accumulated degree hours required for development at that temperature (b), and the minimum threshold developmental temperature (c).

Simulation output is illustrated in Figures 12-16. The output from the overall model is represented in Figure 12 showing the relative abundance of each life stage on a time axis. Figure 12 also shows the simulation output for a body deposited at dawn, with average ambient temperatures of 25°C for the developmental period. However, the change of body deposition time can be easily accomplished by a time shift of ± 12 h, as in Figure 13, where simulation input (the oviposition submodel) was phase-shifted by 12 h to reflect deposition of a body at dusk as opposed to a dawn deposition, with an average ambient temperature of 12°C. Not surprisingly, in simulation trials a shift in the time of first oviposition produced a corresponding shift for all subsequent life stages. Such a shift was still discernable even at the time of adult emergence.

In an actual death investigation (example case), the collected entomological evidence consisted of equal proportions of second and third instar larvae of *Chrysomya rufifacies*. Utilizing the computer model, it was possible to plot the time interval at which equal proportions of second and third instar larvae would occur. Figure 14 shows simulation output of relative stage abundance. This example illustrates the development (at 20°C) of *C. rufifacies* on a cadaver assumed to be deposited at dawn. Figure 15 demonstrates the same species and conditions, except the body is assumed to have been deposited at dusk. Obviously, a simple time shift, prolonging the estimated PMI, is the only observable difference between the two scenarios. However, if a dusk deposition is

still assumed, but the ambient temperature is increased to 30°C, then the PMI estimation based on the relative stage abundance is shortened considerably and the alteration of the PMI is easily visualized (Figure 16). One of the advantages of a computer model such as this is that many varying scenarios can be simulated in a short period of time, allowing the forensic entomologist to consider and decide on many possibilities.

Such output can allow the forensic entomologist to conduct an analysis utilizing the proportion of various life stages within a sample to estimate the postmortem interval. Such a proportional analysis was difficult to accomplish without the predictive and visualization power of computer software such as Matlab/Simulink, and the existence of a modeling program based on the actual temperature dependent development of insect species of forensic importance.

Comparisons of linearity were also conducted, and it was found that of the three species studied, development was essentially linear between 15°C and 35°C.

Development deviated from linear with the 10°C and 40°C rearings as complete development was not successful. Mean development time of each life stage for *P. regina* (Meigen), *C. macellaria*, and *C. rufifacies* was plotted and fitted to a hyperbola using TableCurve®(Jandel Scientific) in Figures 17-22.

Figures 23-26 are a comparison of laboratory data with a distributed delay model of the egg stage. Figure 23 represents the proportion of unhatched eggs remaining, and Figure 24 represents the rate of emergence at 25°C. Figures 25 and 26 are a comparison of laboratory data and model prediction of egg hatch at 30°C. Figure 27 is a comparison of model output and field data for *C. macellaria*. The model output (A) shows the relative proportion of the population with time, and (B) shows data obtained under field

conditions for *C. macellaria* developing on a *S. scrofa* carcass. Model output for *C. macellaria* compares closely to field data, with a maximum deviation of approximately 20 h, with the exception of the pupal stage. This discrepancy was due in part to being truncated by field sampling techniques for adult emergence, and by the fact that the model displays the migratory phase of the third instar as a separate output. These two factors probably account for the majority of the variance observed between model and field data for the pupal curve. However the mean times of the life stages are the same, and it is time that is the most critical value. It is important to note that Vansickle (1977) showed that, in distributed delay systems, as mortality increases the mean and variance decreased thereby reducing time estimations. With the exception of the predation on *C. rufifacies* by *S. invicta*, the field data and model output agreed well under conditions of low mortality.

This computer simulation model will help to develop increased accuracy and understanding of entomological evidence collected in human death investigations. In future applications a 'Maggot Model' such as this can be developed further so that it can be made available to qualified forensic entomologists on a CD-ROM medium. Such a version would run on IBM compatible computers and in its final form would effectively operate on common desktop computing equipment. In addition to the accuracy and precision of the actual calculations available, the graphical output of the process of insect development and model diagrams could be helpful in explaining insect development and the conclusions of a forensic entomologist to judges, juries, and attorneys.

Importance of Computer Modeling

The design and construction process of this computer model produced many interesting and unexpected results during the simulation of insect development on human cadavers. The results produced by the Matlab/Simulink program could have a pronounced effect on both the methodology and precision of future postmortem interval estimations based on entomological evidence that utilizes this technology.

The output of the computer model emphasizes the importance of knowing the flight behavior of flies when attempting to determine the time of initial oviposition. Additionally, it was discovered that the rate of oviposition was not an important factor in postmortem interval estimation. Not surprisingly a body deposited at dusk would have a much different input 'impulse' than would be expected from a colonization at dawn. If adult flies are not active and do not generally take flight during the night time hours, a dusk deposition of a body would have an initial window of no insect activity equal to the dark period. Unlike the peaks and troughs of oviposition which become smoothed out and nearly undetectable in subsequent life stages, the initial oviposition *delay* is carried through to all subsequent stages. Thus the postmortem interval estimation would be prolonged by an interval equal to the dark period unless the investigating entomologist accounted for adult flight behavior. Photoperiod-dependent oviposition is a critical factor in the computer model and of utmost consideration when constructing a PMI estimation.

Preliminary output of the computer model indicates that the peaks and troughs in oviposition rates on a body are not as critically important as once suspected. Such differences in successive ovipositions become negligible and have little significant effect on the emergence shape of subsequent life stages, in particular those of the pupa and

adult. In engineering parlance, the insect life stages constitute a "low pass" filter, i.e. a process that passes low frequency input, but not the high frequency of daily ovipositions. This knowledge is beneficial to the forensic entomologist when estimating the postmortem interval as such data are unknown in actual forensic investigations involving human death. Since such data are not collected, and impossible to obtain or estimate through larval collections made at the scene, the case of the forensic entomologist can be bolstered by the knowledge that such missing information is not a major hindrance or detrimental to his estimation.

Practical Applications of a Computer Model

In the field of forensic entomology, accurate and current developmental data for the forensically important insects are a paramount concern. It is hoped that the information contained within this work will allow for the further refinement of postmortem interval estimations based on entomological evidence. Detailed documentation of egg hatch, larval growth, and adult emergence for key blow fly species will provide forensic entomologists with current data so that they may confidently bolster their analysis. Additionally, computer models like this should provide invaluable information that can greatly aid forensic entomologists utilizing a variety of methodologies for entomological assessments in death investigations.

Further Studies in Computer Modeling

The biology of most of the forensically important insects is largely unknown. For most of those that have been researched, the data are preliminary and incomplete. Only a small portion of the insects commonly utilized in forensic entomology have their biology

adequately detailed in existing literature. For these reasons a great deal of basic biological research needs to be conducted on the more common species. Laboratory data alone are not sufficient for utilization in human death investigations. Such data need to be compared with data obtained under field conditions so that the two can be used in conjunction to obtain the most accurate postmortem interval estimation possible.

Obtaining accurate field data for forensic insects is difficult because research utilizing human cadavers is currently possible only at a very limited number of facilities. Thus, a domestic pig has been identified as a suitable surrogate and is frequently used for basic research. However, animal use restrictions involving research are increasing, and the utility of domestic pigs may be only a temporary avenue to obtain data. It is important for the continued success of forensic entomology that field research be not only sustained, but increased.

This work was the first to incorporate the use of computer modeling of insect species life cycles in the field of forensic entomology. Computer simulation is a promising new way to obtain an 'independent' analysis by which to estimate the postmortem interval. Such analyses can be compared with the standard techniques utilized by forensic entomologists so that any discrepancies are easily identified and addressed. Computer modeling introduces a new tool into crime scene investigations, which does not require modification of the forensic entomologists' standard techniques, and does not destroy evidence. This methodology deserves further exploration as a practical tool for use in death investigations.

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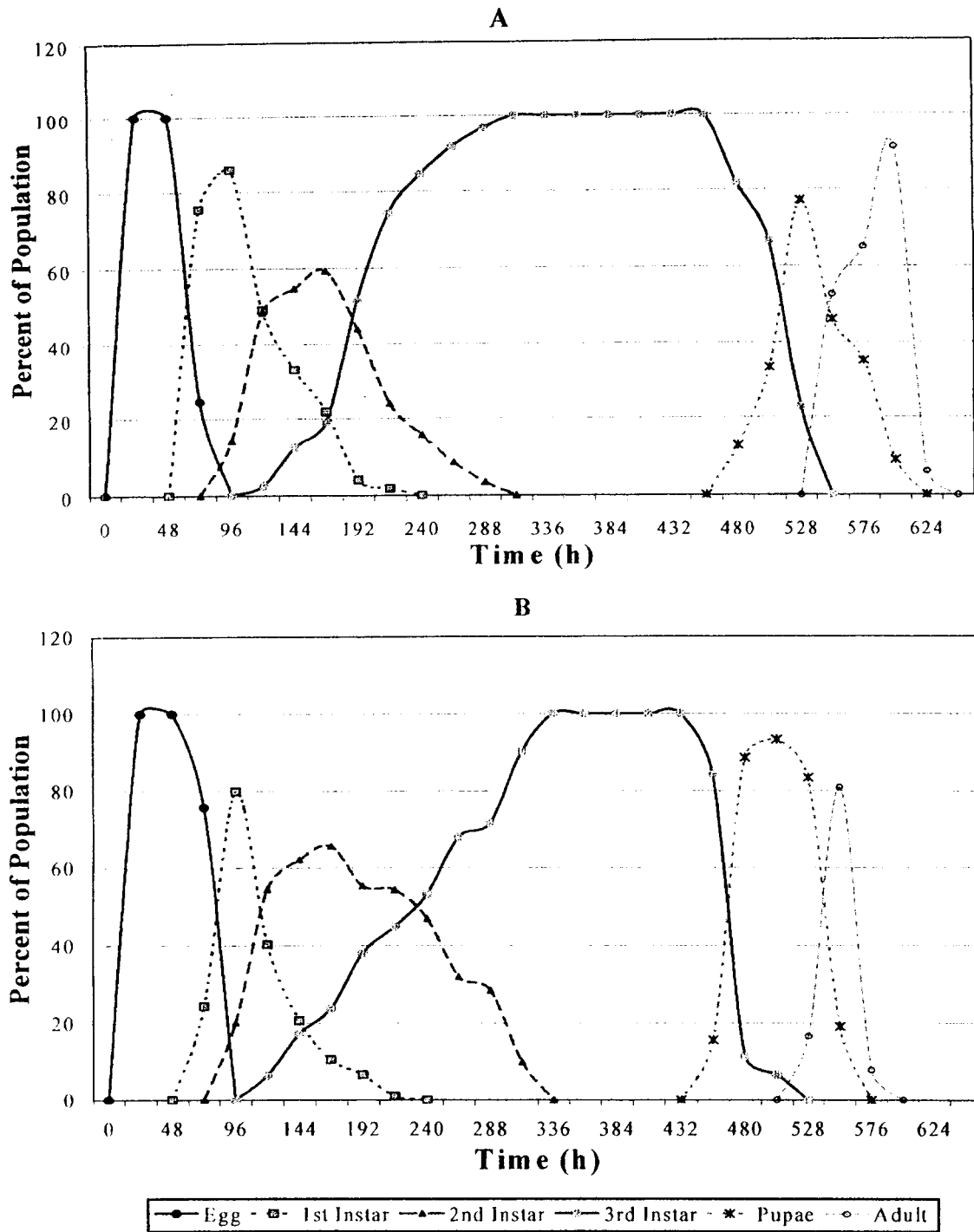


Figure 1. Development on *S. scrofa* carcass with oviposition artificially excluded after day three (Average Temperature 18°C). (A.), *C. rufifacies*; (B.), *C. macellaria*.

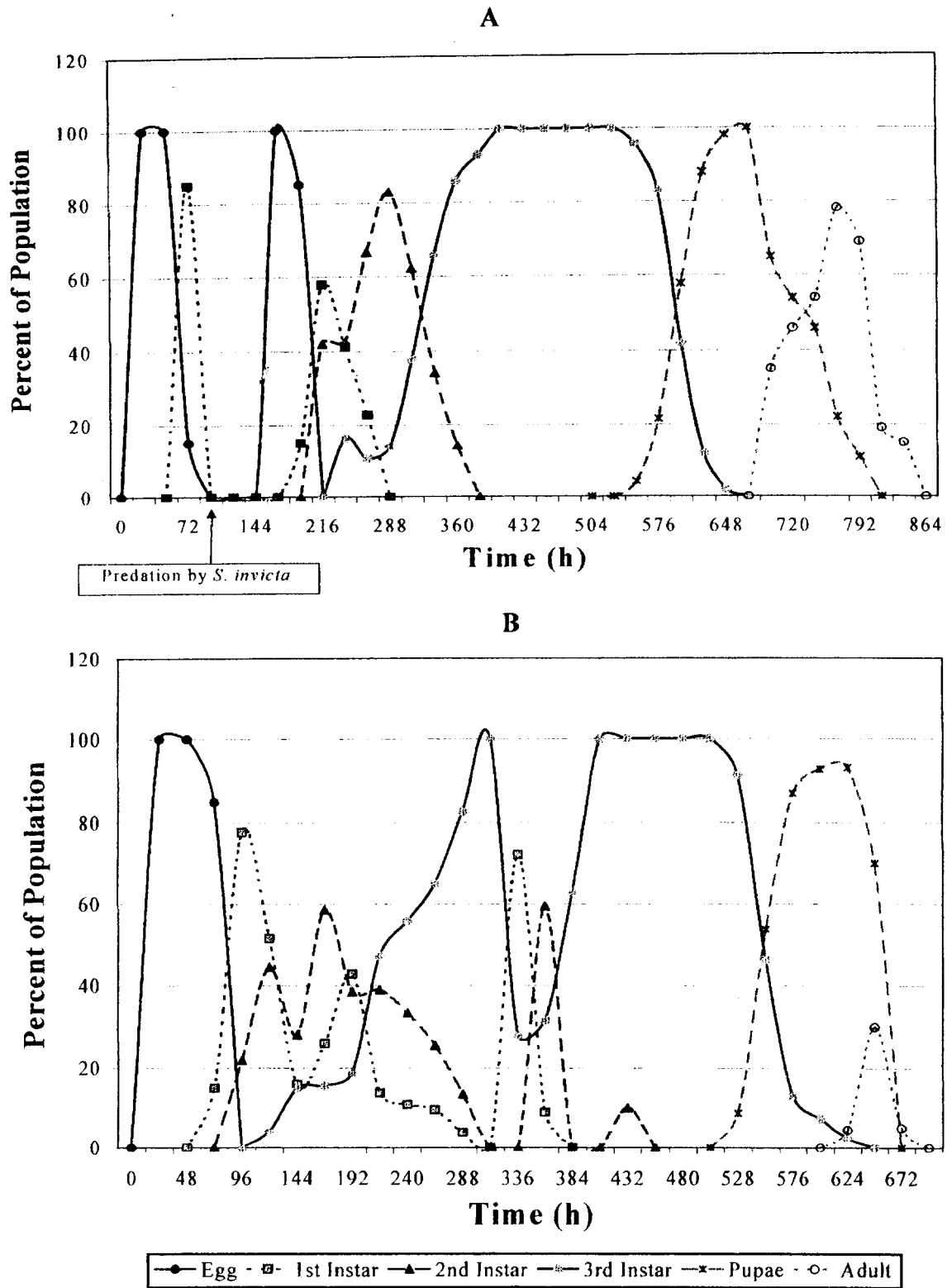


Figure 2. Development on *S. scrofa* carcass with normal oviposition (Average Temperature 18°C). (A.), *C. rufifacies*; (B.), *C. macellaria*.

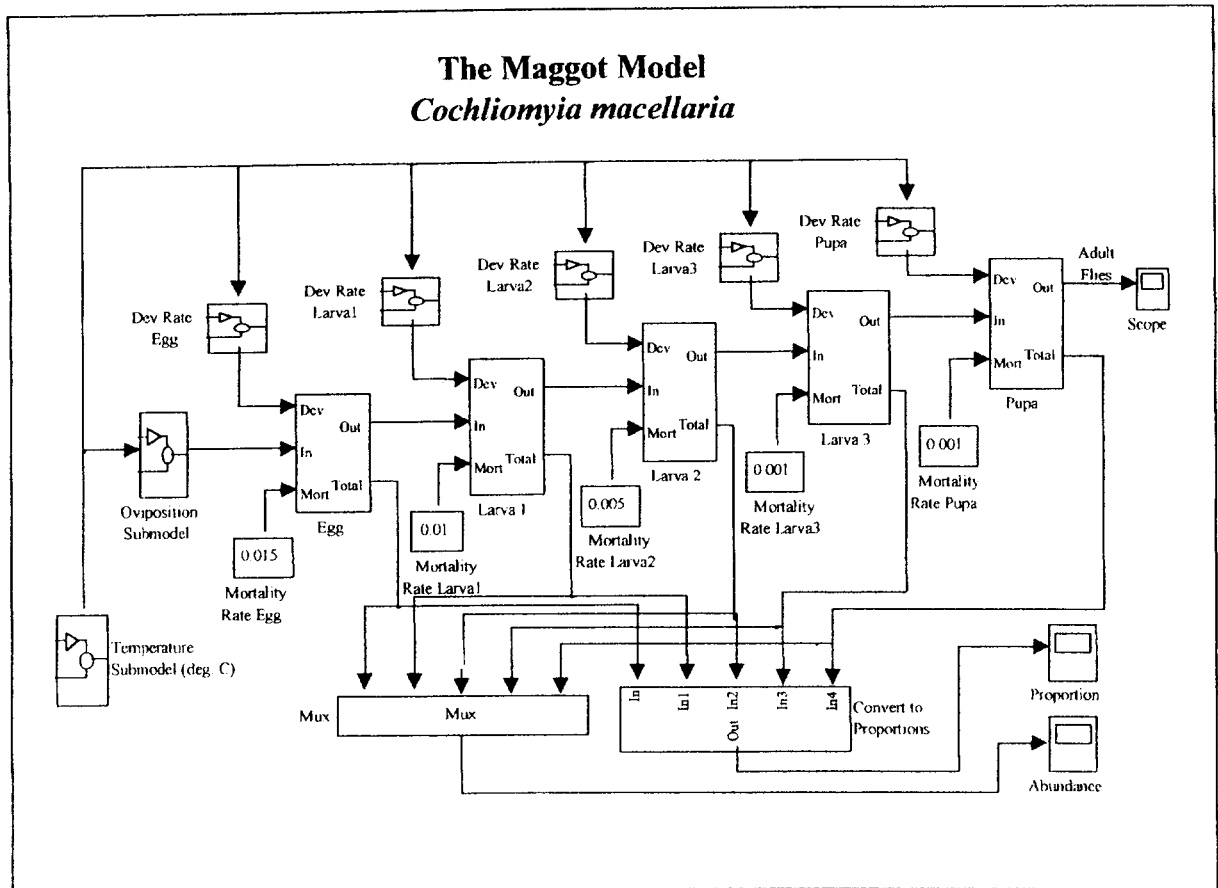


Figure 3. Insect development model as an open loop (flow through) MATLAB/Simulink diagram.

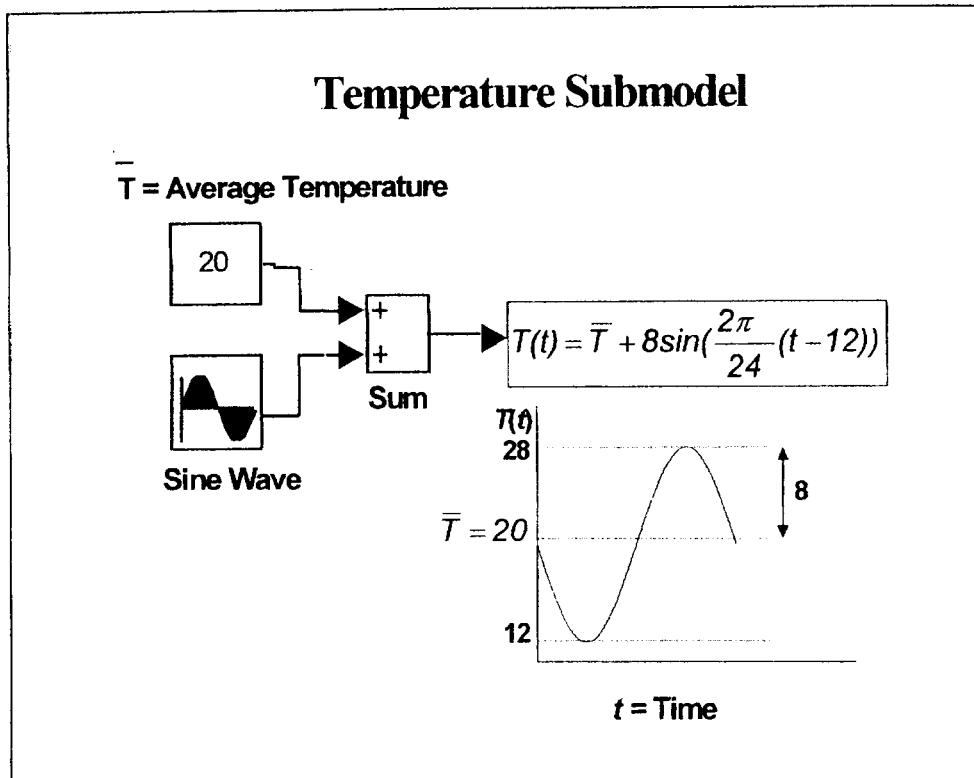


Figure 4. Temperature modeled as a sine wave, with a 8°C amplitude, around an average temperature of 20°C.

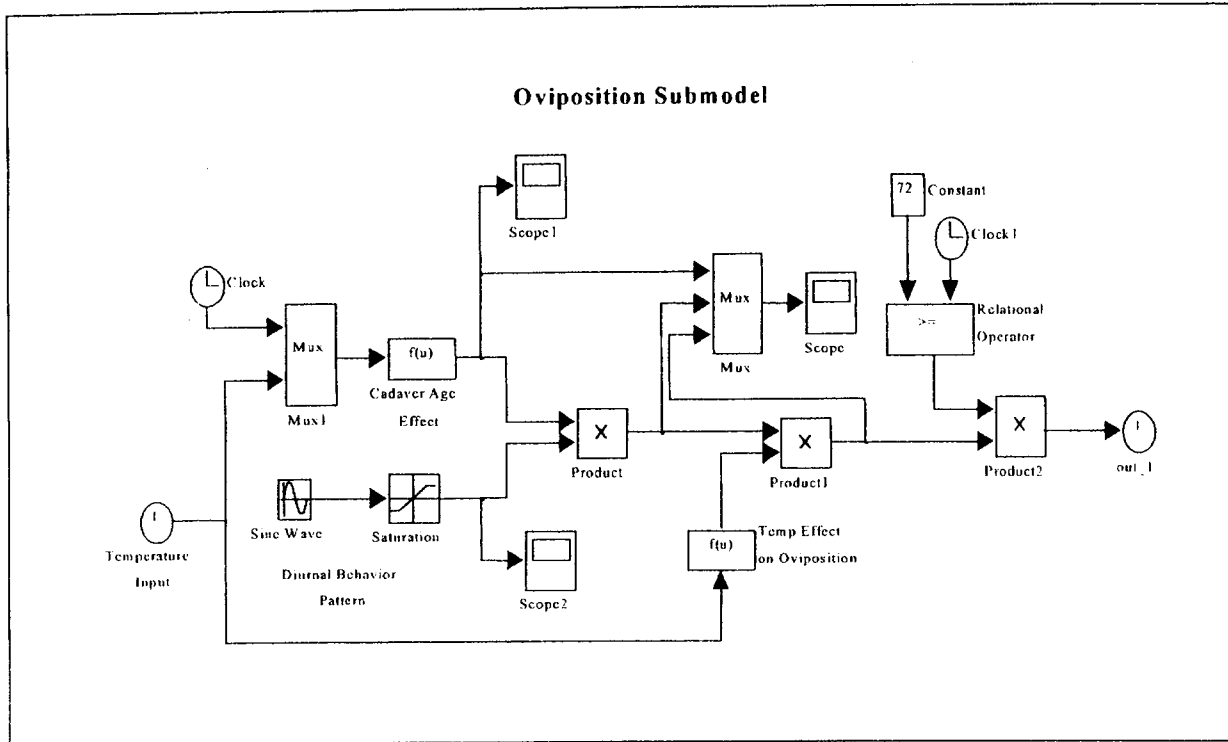


Figure 5. The oviposition submodel incorporating the diurnal activity pattern and the cadaver age effect. Note input of temperature from the temperature submodel (Figure 4).

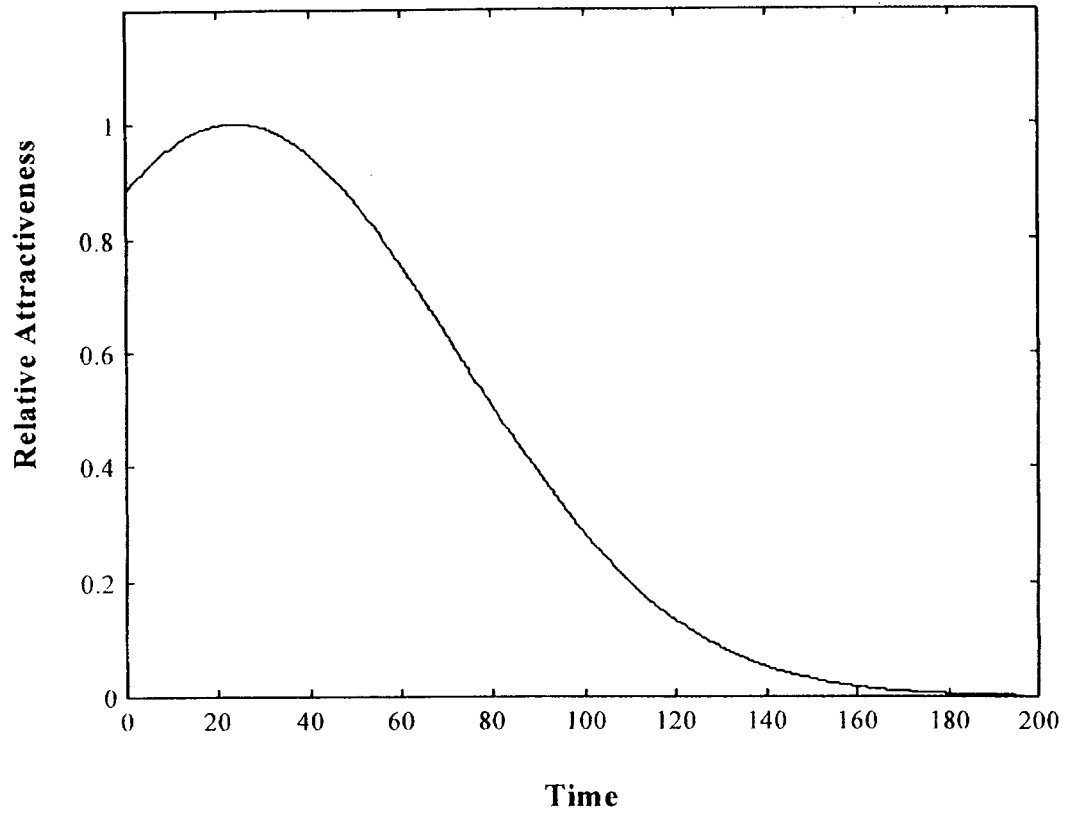


Figure 6. Example of the cadaver attractiveness function specified as a curve of normal distribution with a peak at 24 hours and a SD of 20 hours. This effect is represented as the 'cadaver age effect box' in Figure 5.

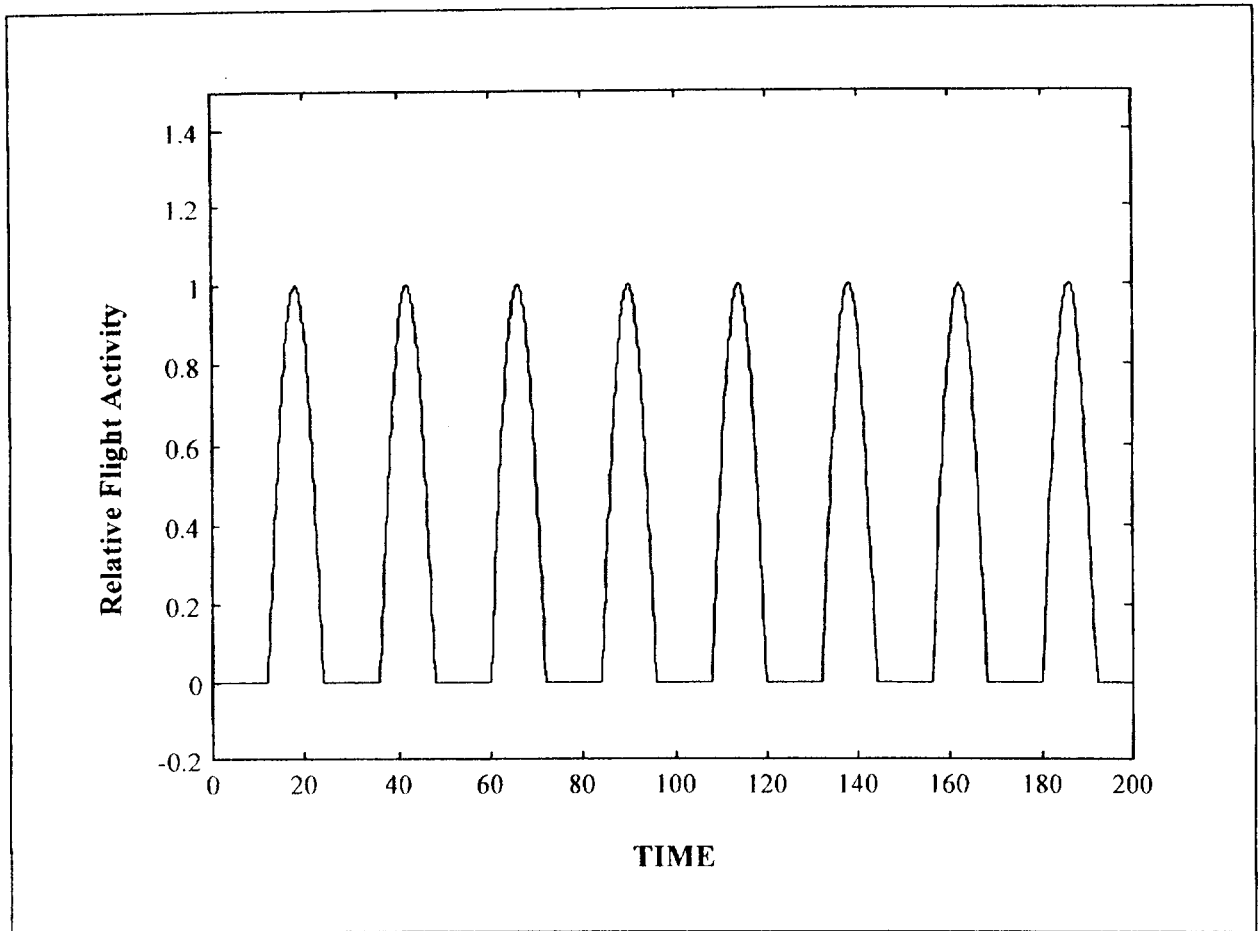


Figure 7. Example of the diurnal oviposition pattern with body deposition time at dusk. The first 12 hours of this simulation has no fly activity due to the dark period. The 'sine wave' and 'saturation' boxes in Figure 5 produce this output.

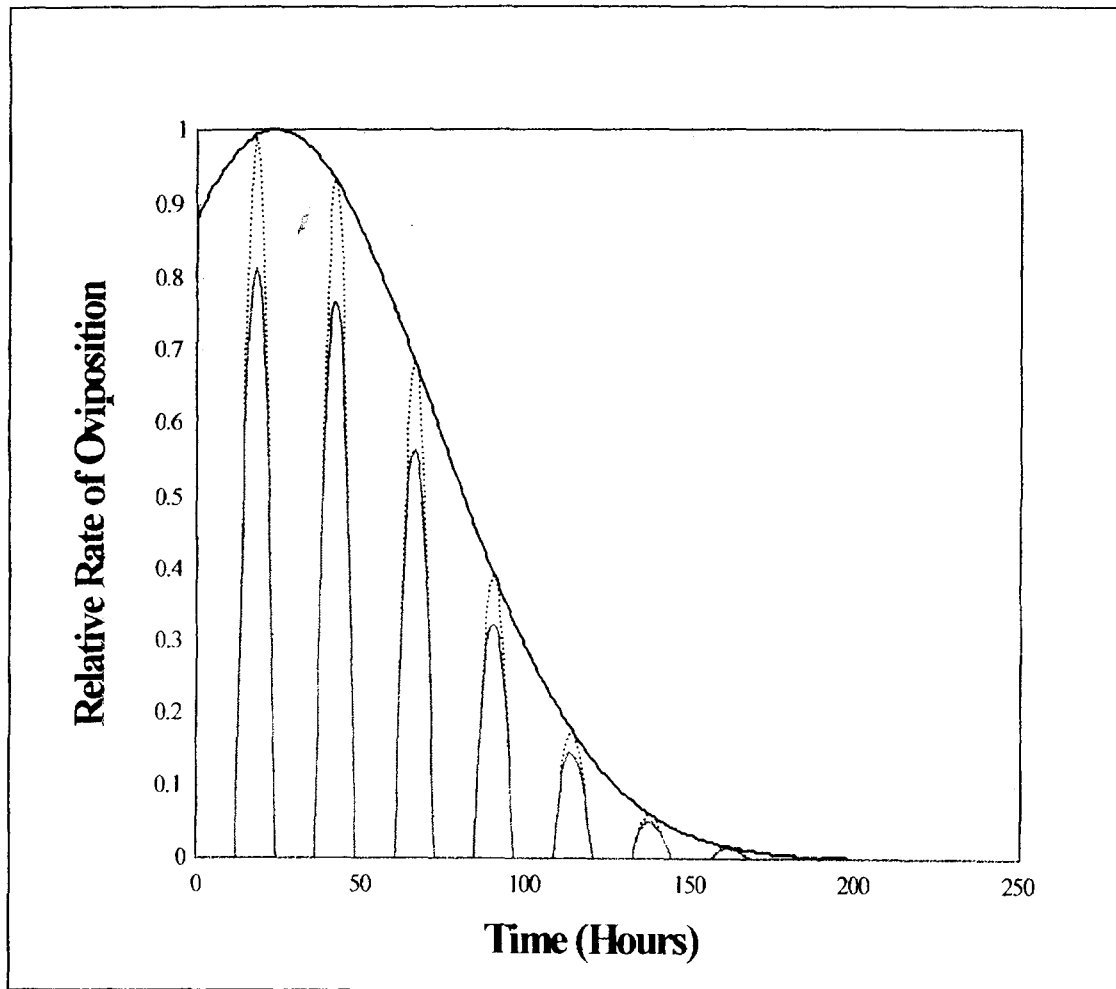


Figure 8. Simulation of oviposition using the oviposition submodel (Figures 5, 6, & 7) input to a cadaver deposited at dawn under a 24 hour cyclic temperature regime with mean = 25°C, amplitude = 5°C. This output is the product of Figures 6 and 7.

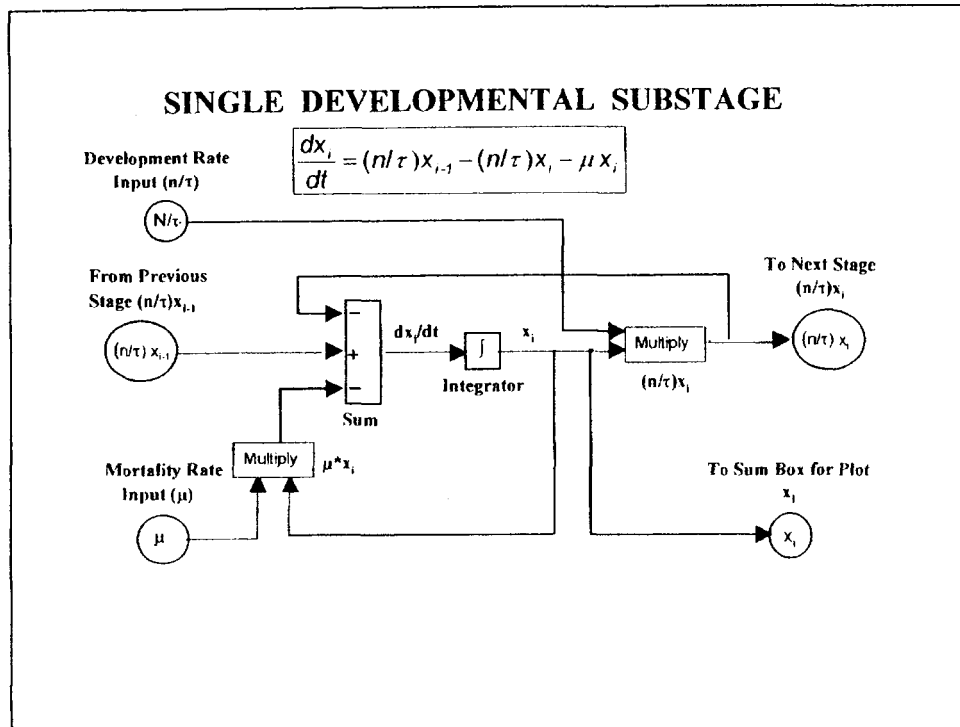


Figure 9. Simulink flow diagram of the basic substage model which can be replicated as necessary to duplicate the duration of an insect life stage.

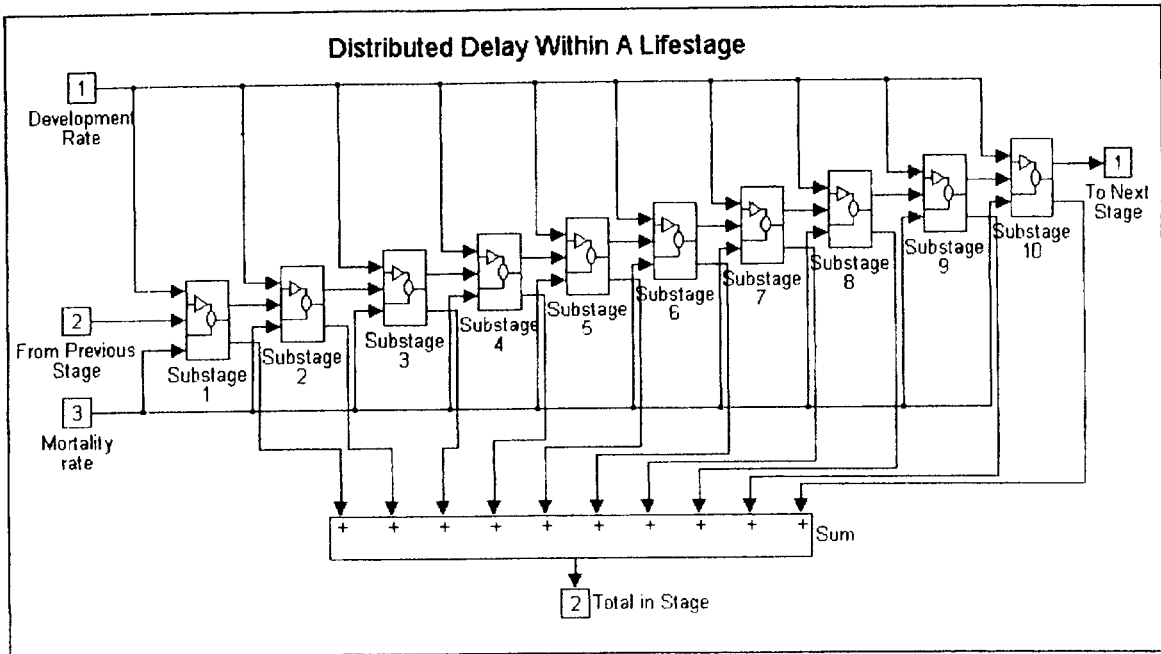


Figure 10. Substage flow within a life stage (each substage is a repetition of the diagram in Figure 39) this life stage submodel is 'grouped' to make the boxes representing egg, instar 1, 2, 3, and pupa in Figure 9.

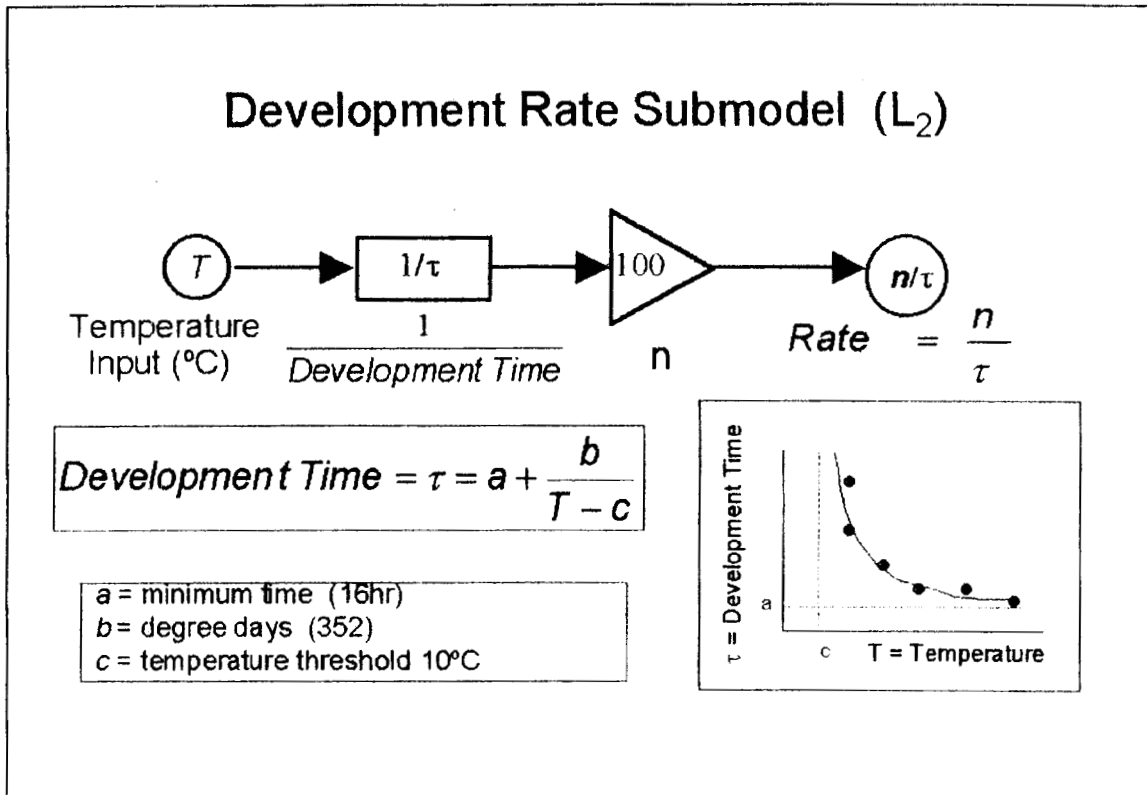


Figure 11. Simulink flow diagram of the model that introduces and combines the effect of temperature on insect development.

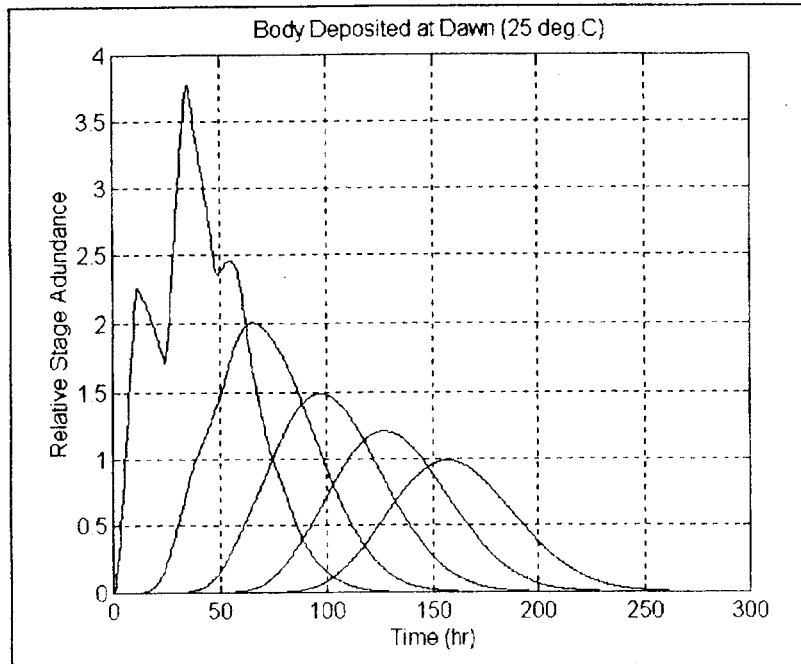


Figure 12. Proportion of each life stage over a 300 hour simulation period at 25°C.

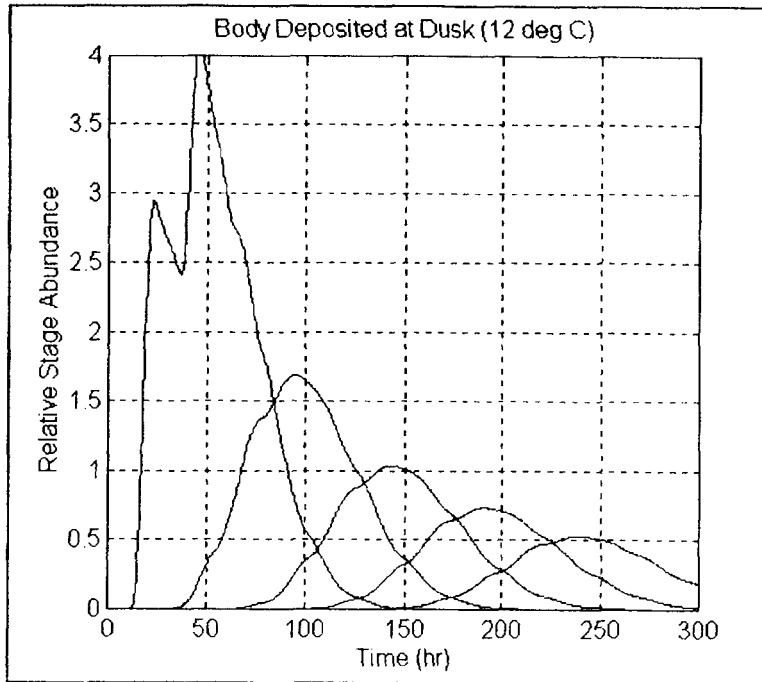


Figure 13. Proportion of each life stage over a 300 hour simulation period at 12°C.

Maggot Model Output (Dawn, 20°C)

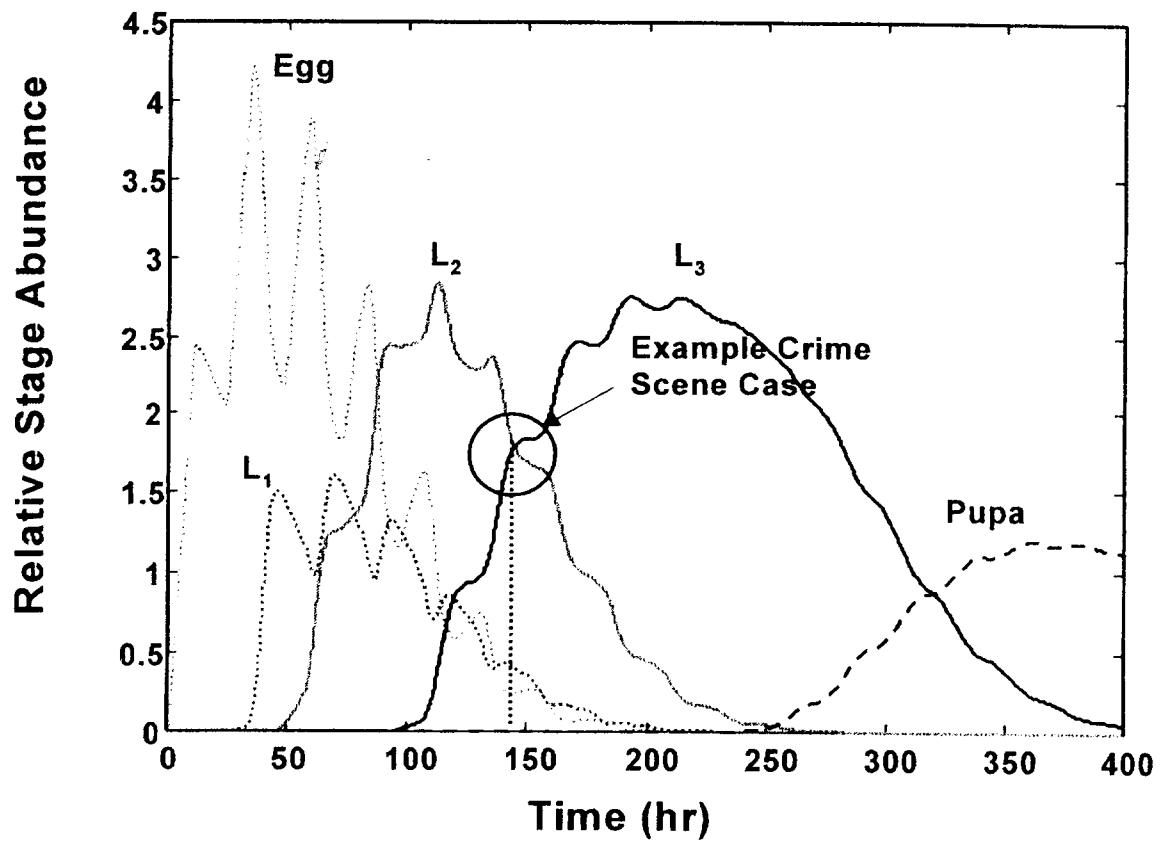


Figure 14. Computer simulation output with body assumed to be deposited at dawn.

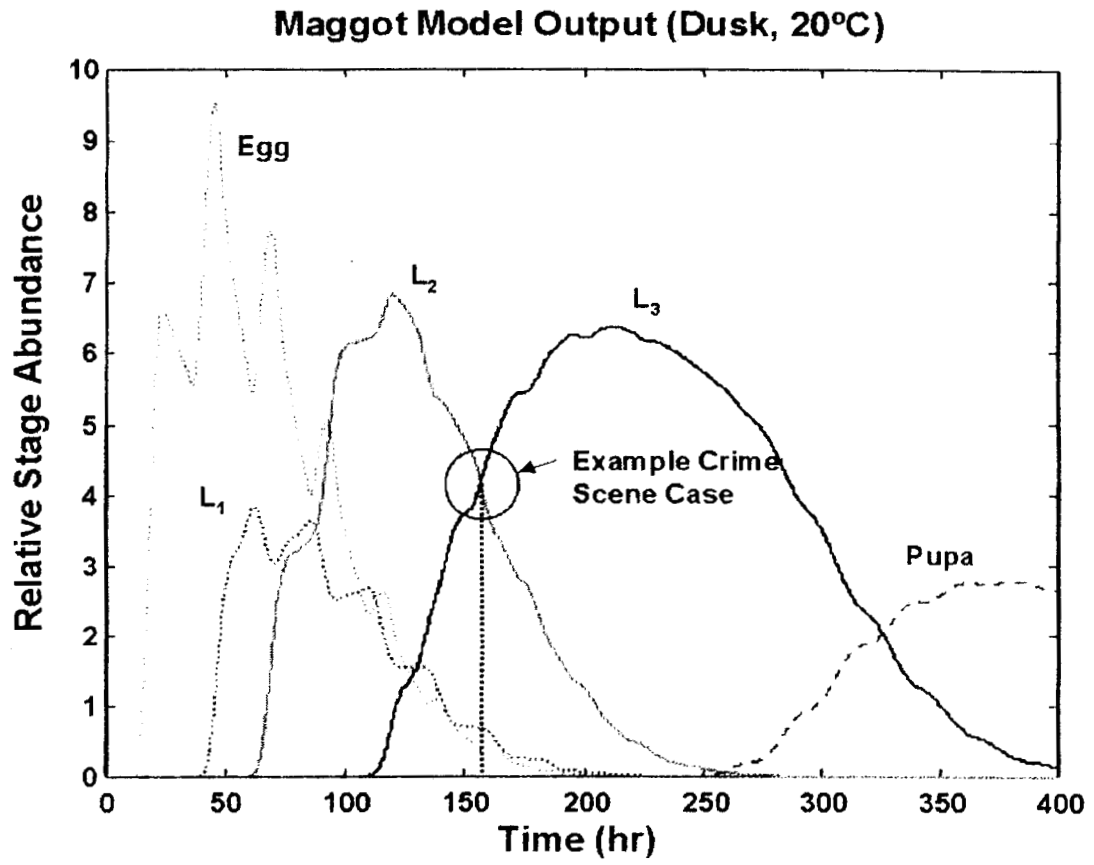


Figure 15. Computer simulation output with body assumed to be deposited at dusk.

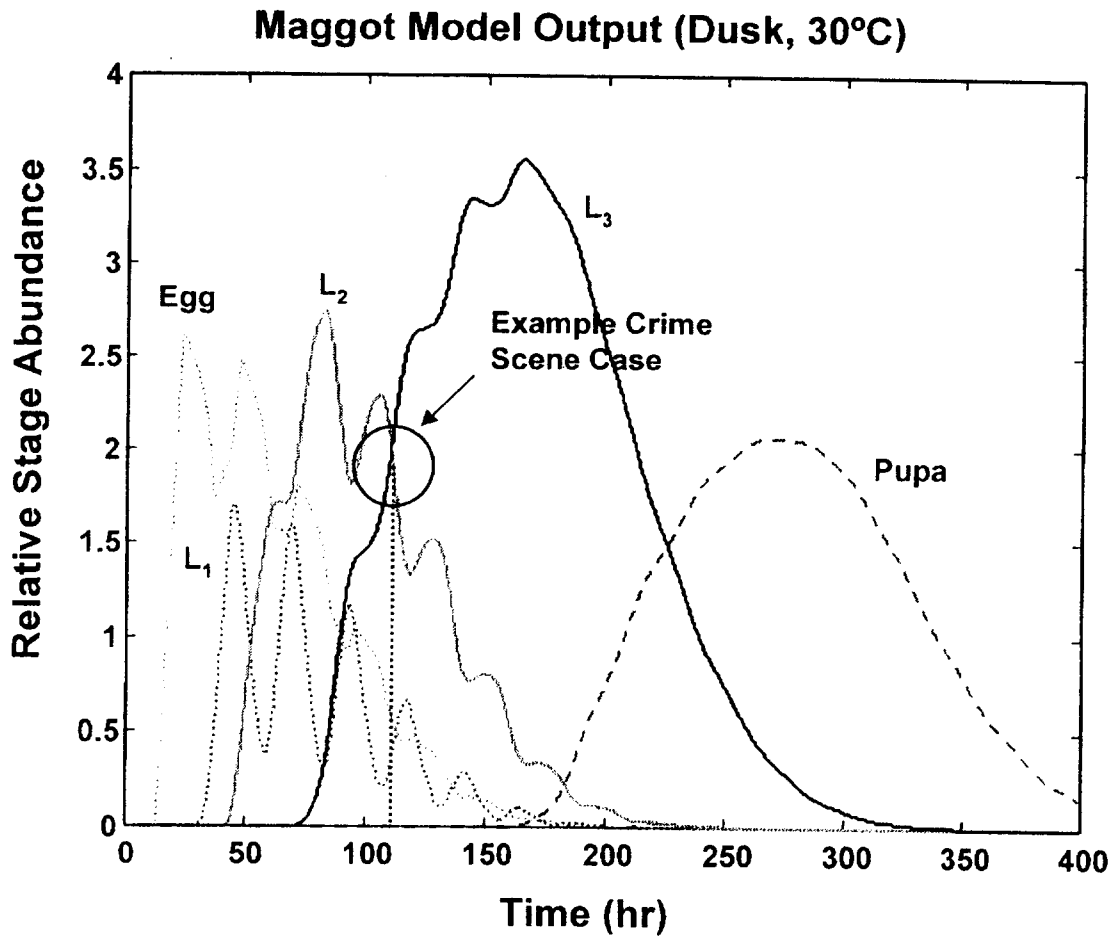


Figure 16. Computer simulation output with body assumed to be deposited at dusk.

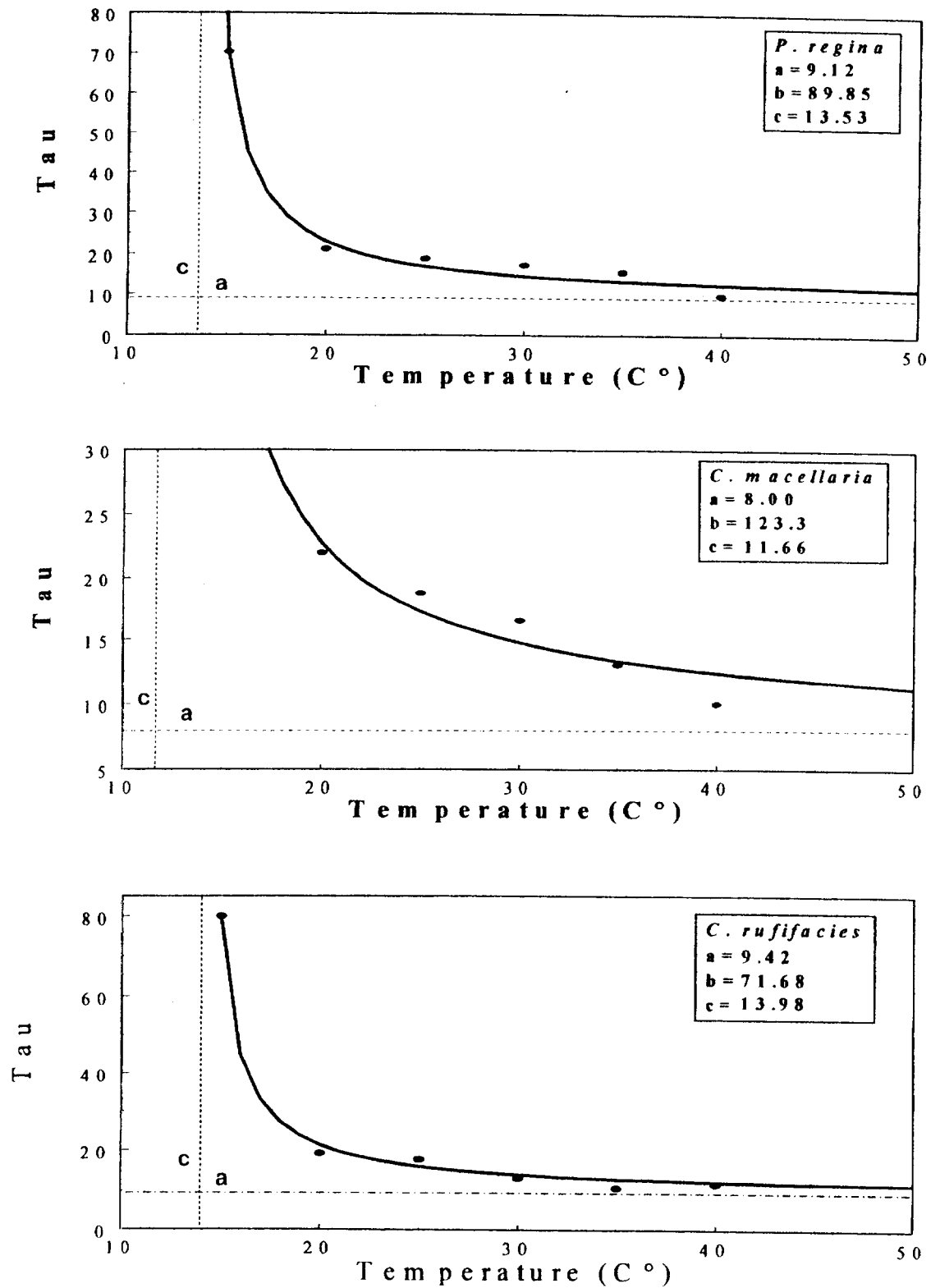


Figure 17. Curve fit of laboratory development data of the egg stage for three species of Calliphoridae (for a description of “a”, “b”, and “c” see Equation 4 or Figure 11).

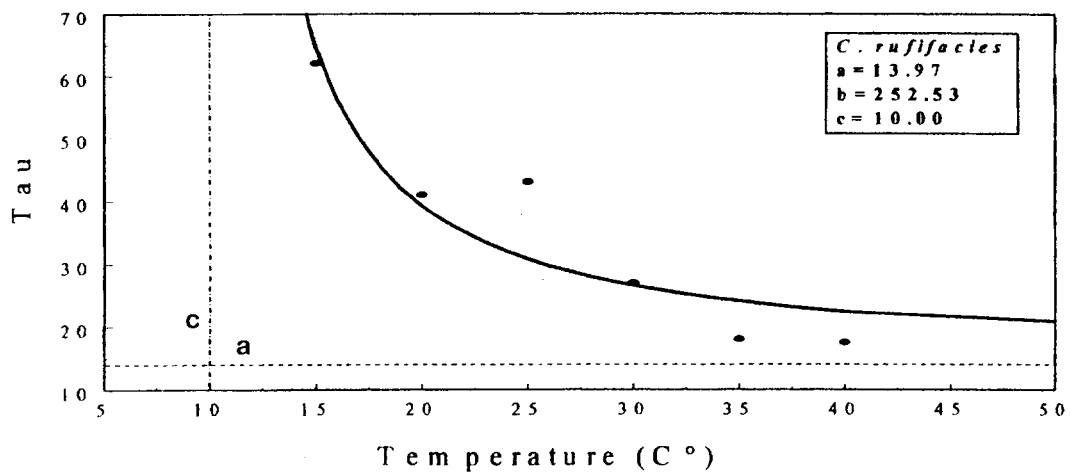
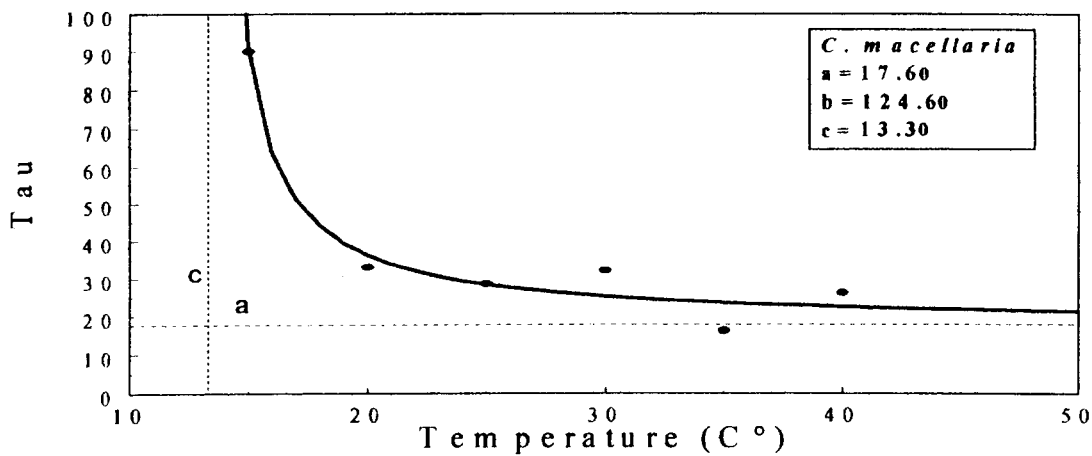
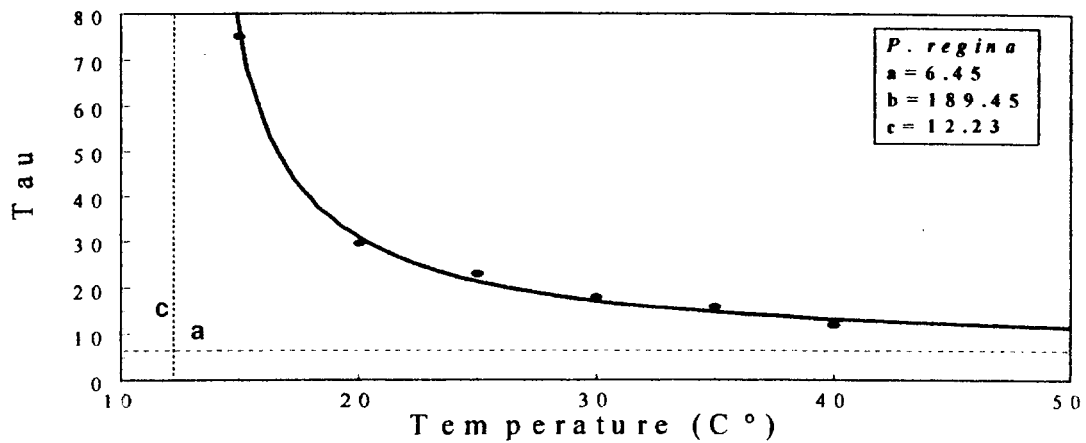


Figure 18. Curve fit of laboratory development data of the first instar for three species of Calliphoridae (for description of “a”, “b”, and “c” see Equation 4 or Figure 11)

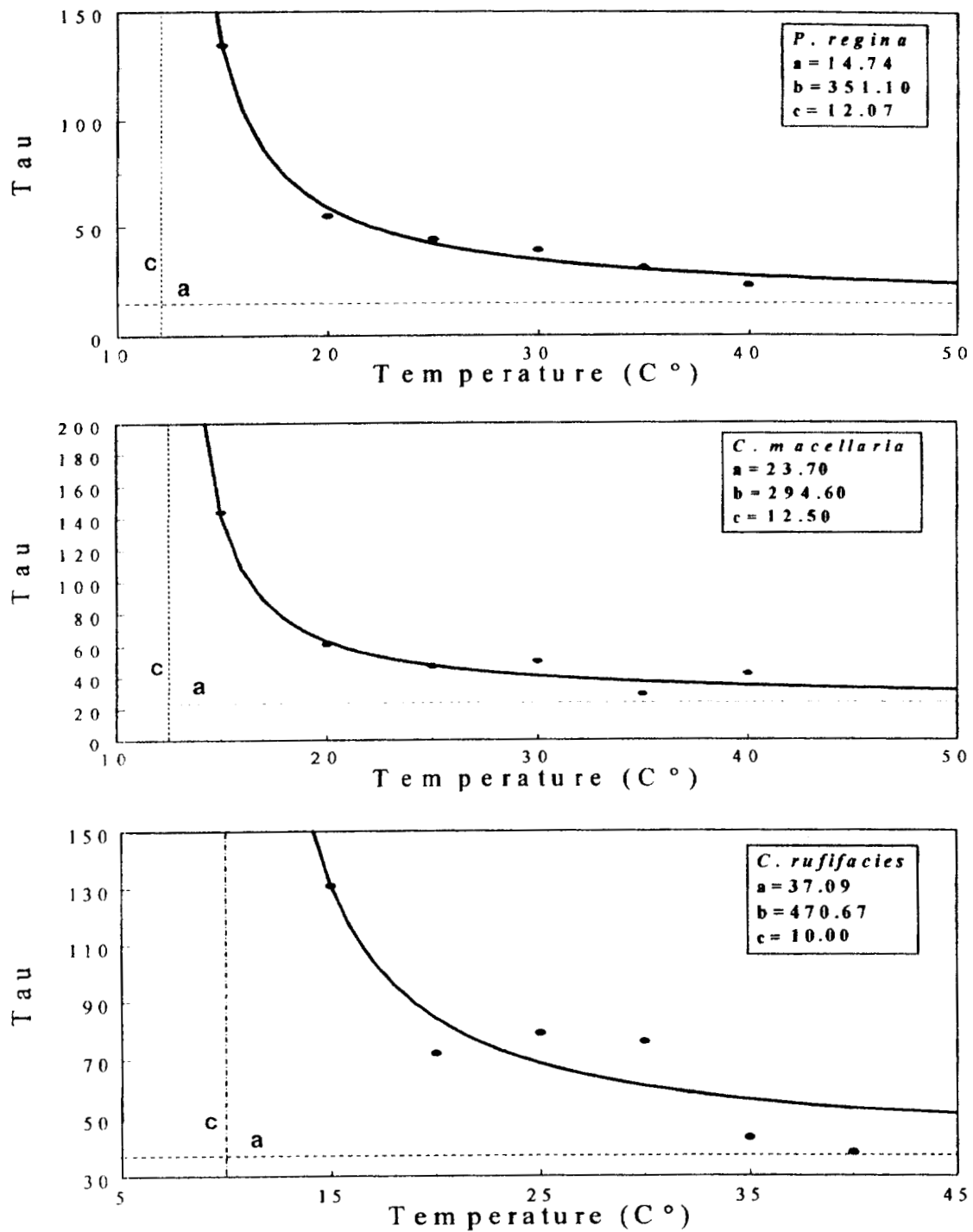


Figure 19. Curve fit of laboratory development data of the second instar for three species of Calliphoridae (for description of “a”, “b”, and “c” see Equation 4 or Figure 11).

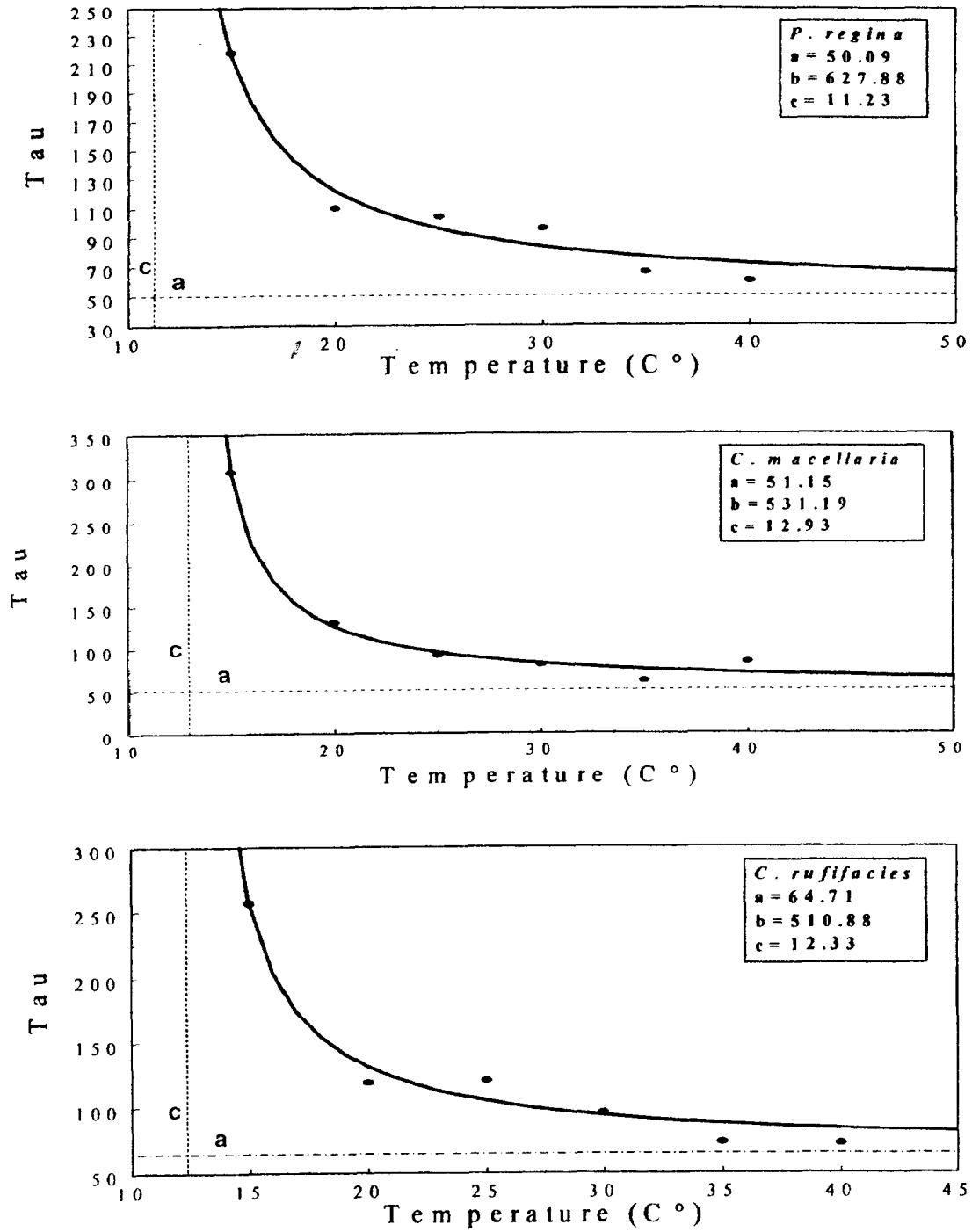


Figure 20. Curve fit of laboratory development data of the third instar for three species of Calliphoridae (for description of “a”, “b”, and “c” see Equation 4 or Figure 11).

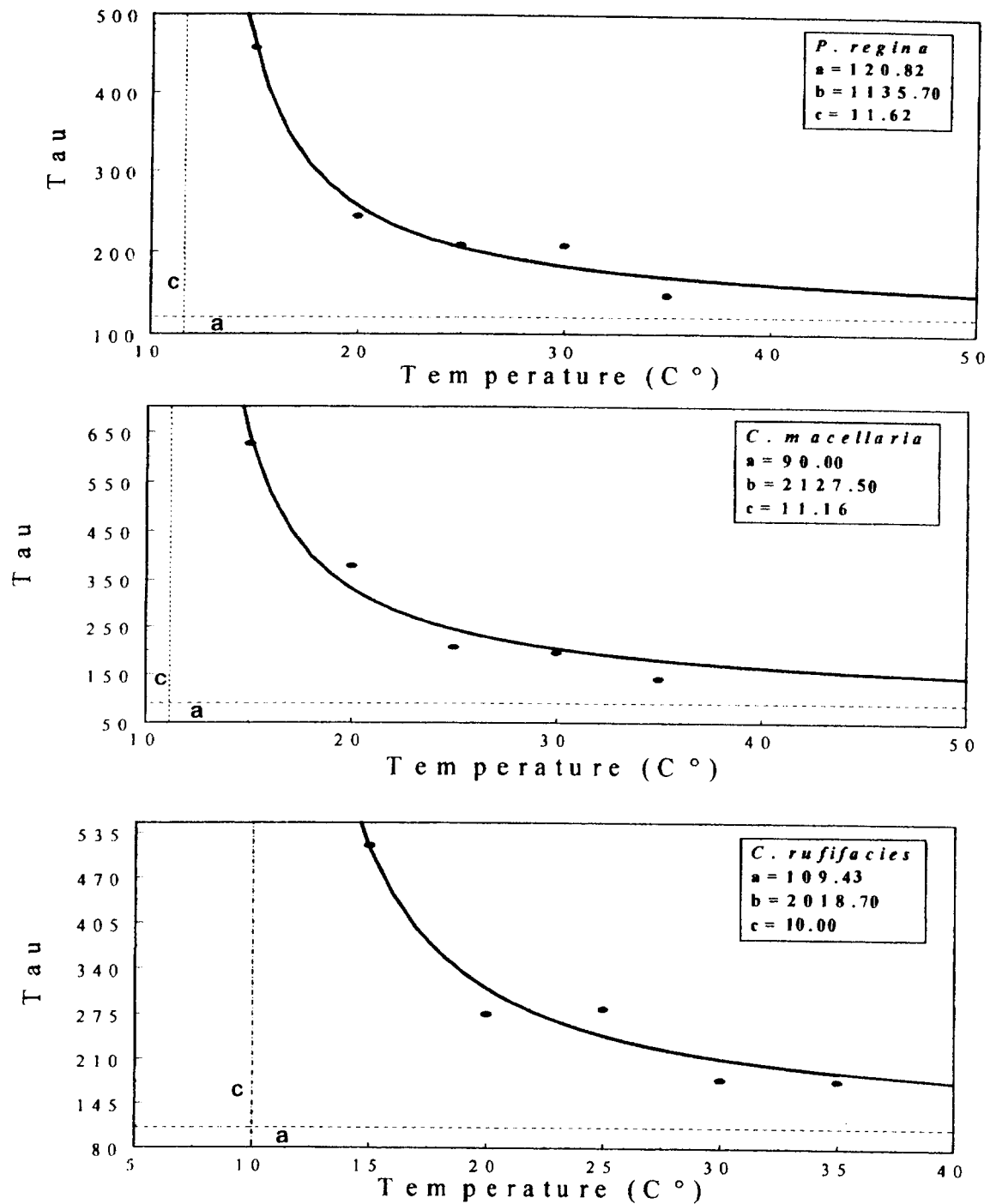


Figure 21. Curve fit of laboratory development data of the pupa for three species of Calliphoridae (for description of "a", "b", and "c" see Equation 4 or Figure 11).

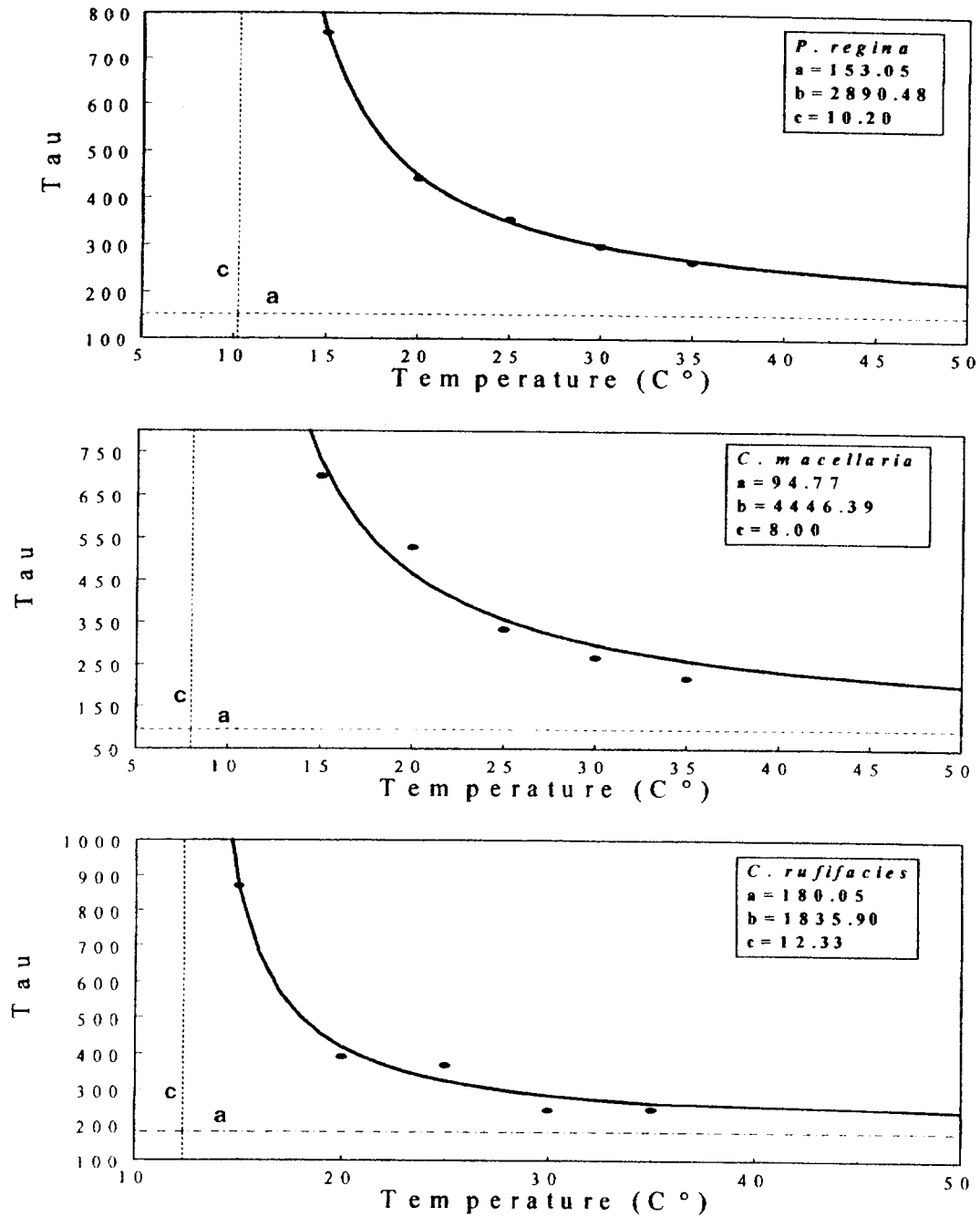


Figure 22. Curve fit of laboratory development data of the adult for three species of Calliphoridae (for description of “a”, “b”, and “c” see Equation 4 or Figure 11).

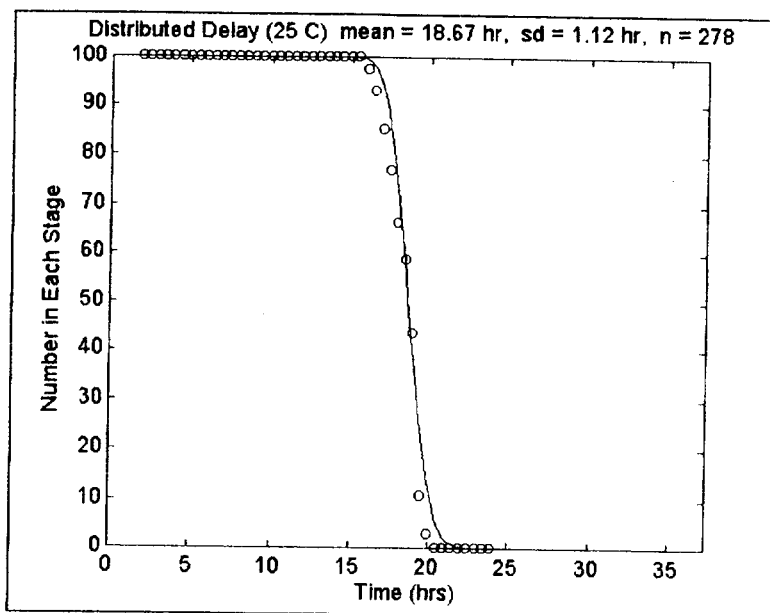


Figure 23. Comparison of computer model prediction and laboratory development data for number of eggs remaining unhatched at 25°C. (Line = distributed delay computer model prediction with mean time and SD taken from growth rate curves, and the points = observed laboratory development).

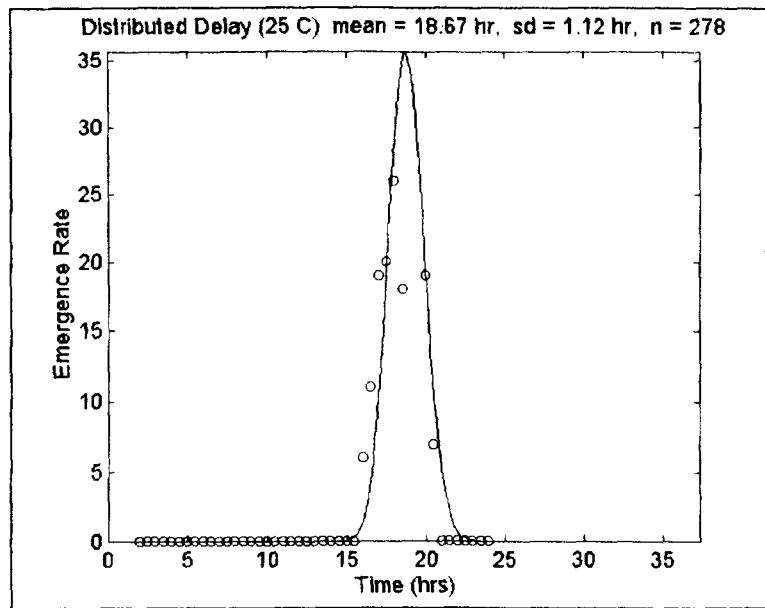


Figure 24. Comparison of computer model prediction and laboratory development data for rate of emergence (hatch) at 25°C. (Line = distributed delay computer model prediction with mean time and SD taken from growth rate curves, and the points = observed laboratory development).

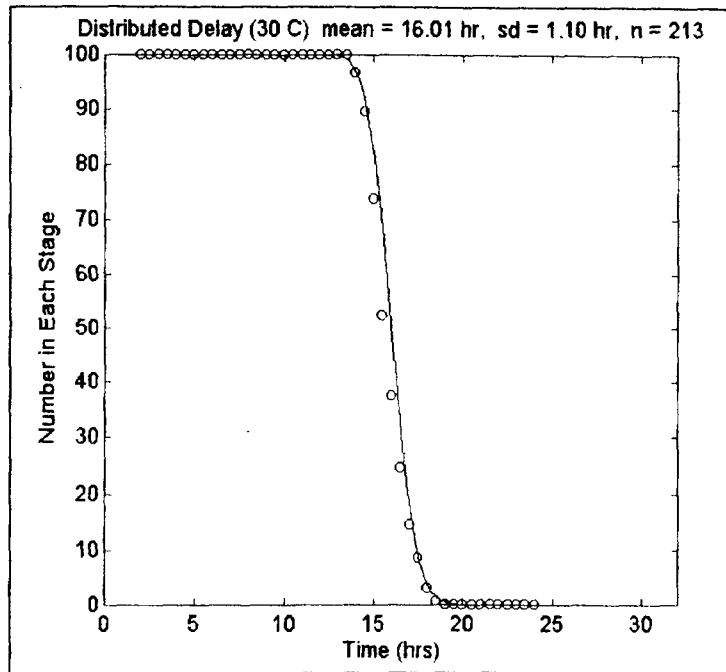


Figure 25. Comparison of computer model prediction and laboratory development data for number of eggs remaining unhatched at 30°C. (Line = distributed delay computer model prediction with mean time and SD taken from growth rate curves, and the points = observed laboratory development).

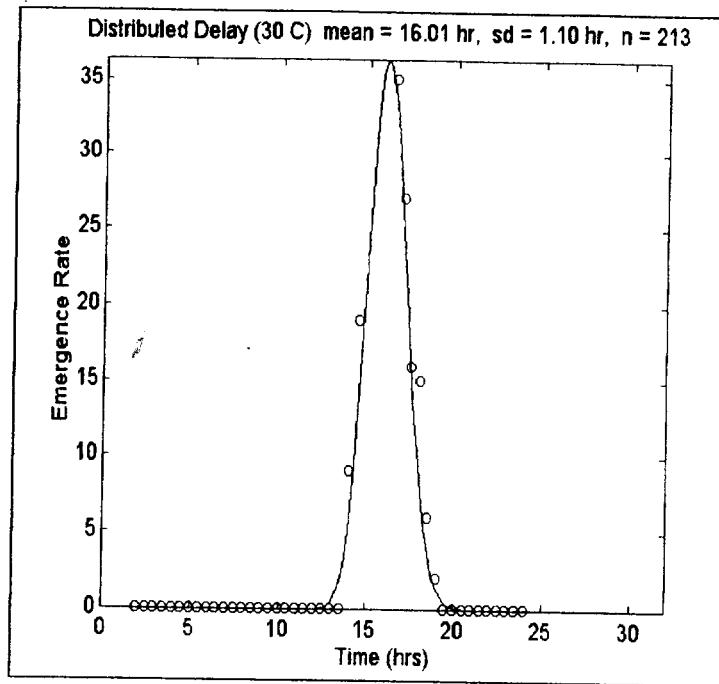


Figure 26. Comparison of computer model prediction and laboratory development data for rate of emergence (hatch) 30°C. (Line = distributed delay computer model prediction with mean time and SD taken from growth rate curves, and the points = observed laboratory development).

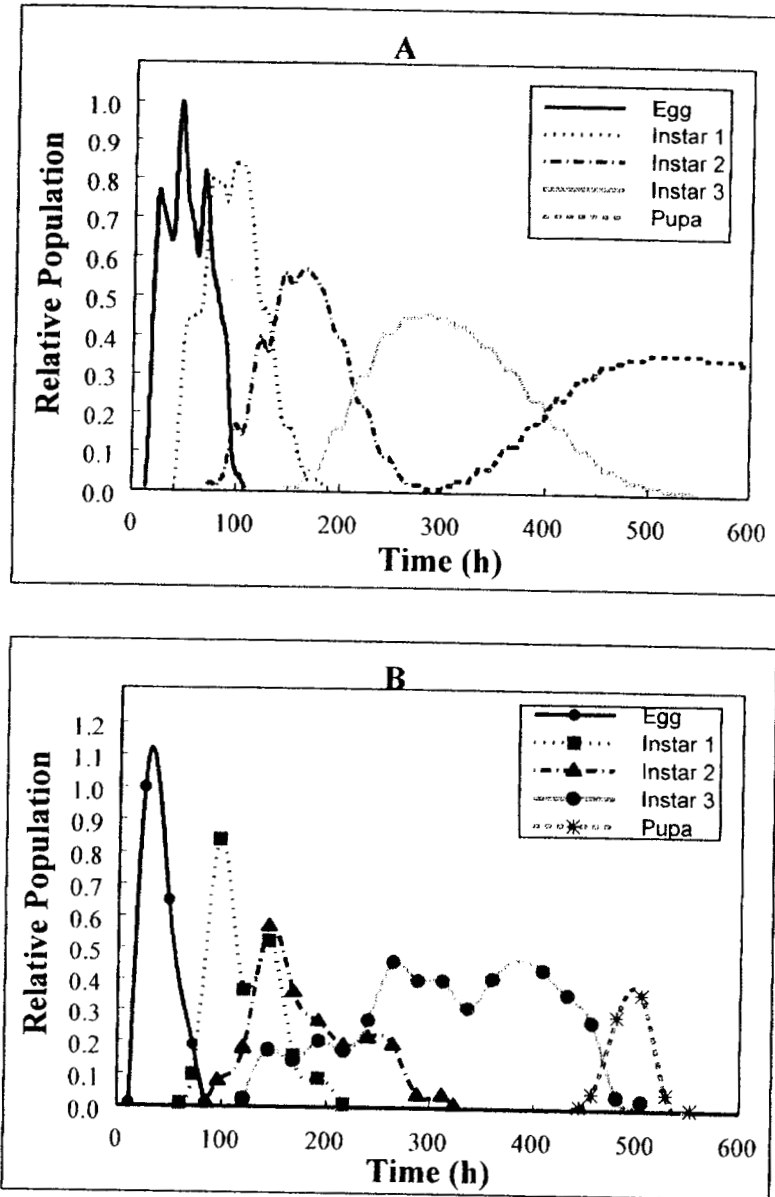


Figure 27. Development of immature stages of *C. macellaria*. (A.), computer model prediction; (B.), Development on *Sus scrofa* carcass in field conditions

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