

near door and windows recorded minimum temperature. The humidity was found to be higher in ventilated areas than interior part.

Tab. 1 Population strength of insects with respect to temperature, humidity and time

Time	Temperature (°C)		Relative Humidity (%)		Insect Count at T ₁			Insect count at T _{avg}		
	T ₁	T _{avg}	T ₁	T _{avg}	B	M	U	B	M	U
10.00 am	25.8±0.5	26.8±0.7	73.4±3.3	73.2±2.2	1±0	2±1	2±1	1±0	1±1	4±1
12.00 noon	26.7±0.2	27.8±2.0	72.5±3.3	69.9±2.3	1±1	0±1	4±2	1±1	0±1	6±3
2.00 pm	26.7±0.3	28.9±1.0	70.9±3.8	68.0±5.0	2±1	2±2	9±3	1±2	3±3	13±7
4.00 pm	27.0±0.5	28.5±0.9	70.0±3.9	68.5±5.0	5±3	6±3	14±4	2±2	4±1	17±11

T₁ – Near the ventilation area; T_{avg} – Far from ventilation; B – Bottom of stack; M – Middle of stack; U – Upper portion of stock

It was observed that five fold increase in insect population at the top of stack during day time and about seven fold increase in insect population after 4.00 pm. The results are in line with the report of Rajan *et al.* (2018) who reported that vast numbers of *T. castaneum* take flight inside godowns in the late afternoon. The results of the present study will help to design an advanced scientific grain storage godown for safe storage of grains in gunny bags for longer duration. It will also help develop effective management tactics to reduce the severity of infestations caused by stored product insects.

5. Future Progress

Effect of temperature, humidity and ventilation on insect population was studied for short duration. To establish the efficient pest management practices, the influence of all the above said factors on microbial growth and chemical analysis has to be studied. Further pest management by integrating the different methods based on the results of the study in large scale godown has to be studied.

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Modelling of population dynamics of insects in any ecosystem with several distributions of insect development: A Review

Fuji Jian ^{1*}, Digvir S. Jayas ¹, Paul G. Fields ², Noel D.G. White ²

¹ Department of Biosystems Engineering, University of Manitoba, Winnipeg, MB, R3T 5V6 Canada.

² Morden Research and Development Centre, Agriculture and Agri-Food Canada, c/o: Department of Biosystems Engineering, University of Manitoba, Winnipeg, MB, R3T 5V6 Canada.

*Corresponding author, Email: Fuji.Jian@umanitoba.ca

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Abstract

Predicting the occurrence of insects with a high accuracy requires the estimation of insect development time and the variation among individuals for each life stage and species under different environmental conditions such as fluctuating temperature, variation of relative humidity, different body sizes and stages of the insects, levels of crowding, and food supply. This review summarized the modeling methods of population dynamics of

insects with several distributions of insect development, assumption and prediction accuracy of these developed models, and disadvantages and advantages of these modelling methods. These modeling methods include degree day model, nonlinear model, and distribution delay models. The structure of most common models are cohort, Leslie matrix, simulation, and individual based. The relationships among the modeling assumptions, effects of temperature, and other environmental factors, and structures of the developed models were examined. A new modelling approach such as physiological-biological time scale and chaos theory was suggested.

Key words: Degree day, nonlinear model, distribution delay, Leslie model, chaos.

Introduction

Predicting the occurrence of insects in an ecosystem with a high accuracy is essential for conducting integrated pest management. These predictions require the estimation of insect development time and the variation among individuals for each life stage and species under different environmental conditions such as fluctuating temperature, variation of relative humidity, different body sizes and stages of the insects, food sources, and levels of crowding. This adds another level of complexity to models already complicated by accounting for the variable time of development (Stinner et al. 1974, Wagner et al. 1984 a and b, Briere et al. 1999, Gramig et al. 2015), variations under different temperatures (Anderson et al. 1982, Worner 1992, Regniere et al. 2012, Damos and Savopoulou-Soultani 2012, Moore and Remais 2014), variations among different growth stages and ages, and discrepancies under constant and fluctuating temperatures (Hagstrum and Milliken 1991, Nachman and Gotoh 2015). However, complexity does not assure more accuracy in all cases. Therefore, the right mathematical approach and theoretical assumptions should be developed to model population dynamics of insects with several distributions of development time. This review outlines the basic modelling methods, the disadvantages and advantages of the methods, reasons for the low accuracy of these developed models from their applications, and suggestions for future model development.

Temperature effect and modelling

Temperature is the only considered factor in almost all, if not all, of these published models in the literature (Damos and Savopoulou-Soultani 2012) because temperature is the most critical factor affecting insect development. Damos and Savopoulou-Soultani (2012) reviewed the temperature-driven models for insect development. Empirical and semi-theoretical mathematical models have been developed. Even though none of these models is based on accepted biophysical laws such as Eyring's absolute reaction rate theory, temperature effect on enzymes has been recognized by the empirical equations of Van't Hoff's law and Arrhenius (Schoolfield et al. 1981). The basic assumption of the enzymes was used for most model development such as degree day and nonlinear models. To calculate the temperature effect, three general types of models are developed: degree-day summation, non-linear temperature inhibition, and distribution delay. These empirical or semi-theoretical equations predicting average development rates are in exponential or logistic format and explain the thermodynamics of complex biological processes by the laws of chemical reactions. This provides biologists with a greater understanding of the temperature-dependent and developmental responses for a given insect species. With this approach, developed models could be extended beyond the range of temperatures specified by model theory or beyond the range of temperatures measured. However, these empirical and semi-theoretical models are not valid for most practical cases because exponential or logistic increase is observable on a limited range and not throughout all temperature regimes. Therefore, different researchers modified these empirical equations (Sharp and DeMichele 1977). However, these modified equations have limited application because of their limited fit to laboratory data, and usually these developed models have not been validated with field data because it is difficult to collect field data; there are inherent variations in the field data; and predictions from models are uncertain.

There are three issues with the modelling temperature response of insects: development rates, development times at temperatures near thresholds (extremes) where excessive mortality or

developmental abnormalities can occur, and individual variation from the average developmental rates and reproductive responses. These three issues are handled in the models of degree day, nonlinear, and distribution delay differently.

Degree day models

To model the effect of temperature, the development of an organism is viewed as a biological clock that measures time thermal units, and it is often referred to as thermal time. Although physiological time accelerates or slows under different temperature fluctuations, the thermal time unit to complete a particular developmental event under both field and laboratory conditions is assumed to be the same by modellers because thermal requirement is the basis for insect development. This is the basic assumption of the degree day model. Degree-day models were initially developed for agricultural applications and have been widely used since the 1730s in many research areas related to farming (Moore and Remais 2014). The degree-day model, without considering the individual variation from the average developmental times or rates and reproductive responses, is a simplistic representation of a potentially complex developmental process (Moore et al. 2012).

Degree day model is the most widely used mathematical format to estimate insect development time because it requires minimal data for formulation, calculations are easy and applications are simple, and often yields approximately correct values. Most of degree day models only estimate the average development time, and do not consider the individual variation from the average developmental times or rates and reproductive responses. This simple format of degree day model is widely used in many agricultural areas. Recently, Nachman and Gotoh (2015) developed a biological age model with the consideration of the individual variation from the average developmental rates and reproductive responses. This newly developed model used probability distribution to estimate the individual variation and this probability distribution was related to temperature effect and development time mathematically. This mathematical relationship among development probability distribution and temperature effect and development time is the modification of the degree day model. Therefore, this new developed model combined the degree day model with distribution delay model. This modeling framework was successfully used to model several insect species (Skovgard and Nachman 2017).

Even though different researchers used different mathematical equations to calculate the degree days (Moore and Remais 2014), and used different assumptions to quantify the relationship between the sum of degree days and the insect development, the developed degree day models have a low prediction accuracy. A degree day model developed under constant temperature cannot be used to predict insect population under fluctuating temperature (Hagstrum and Milliken 1991, Jian et al. 2017). Developmental times of many species under constant temperature differ from these under fluctuating temperatures with the same mean (Hagstrum and Milliken 1991) because short periods of colder or warmer temperatures under fluctuating temperatures may have an overriding influence on development rate when compared to the mean temperature over a longer period of time (Hagstrum and Milliken 1991). Low prediction accuracy of the degree day model under fluctuating temperature will have a large drawback because most life tables studied are conducted at constant temperature under laboratory conditions. The development differences between constant and fluctuating temperatures could not only increase the complexity of the degree day model, but also make the degree day model unsuitable. Researchers have shown that these differences could be resolved by integration of temperature developmental times over the fluctuating temperature cycle to predict development times at fluctuating temperatures (Dallwitz 1984, Hagstrum and Milliken 1991). Therefore, combination of the degree day model with other mathematical tools might be one of the choices to improve prediction accuracy. However, deciding the integration interval is part of arts and science, and different researchers used different assumptions

The main reason causing this low prediction accuracy of degree day models might be the basic assumption of the degree day model. The basic assumption of the degree day model is that: the

completion of a given stage in development requires an accumulation of a definite amount of heat energy, thus, degree day models apply the accumulated temperatures as the heat energy to establish the relationship between the development and the environmental conditions without considering the additive effect of the accumulated energy and morphological change of the organisms. Insects might have a mixture of linear and non-linear development. It is difficult to find the right equation because both linear and non-linear models generally cannot represent the complete effects of temperature on an organism. Nonlinear indicates that the whole becomes something greater than the mere sum of its individual parts or linear parts due to the interaction effects between factors. Moore and Remais (2014) found the difference between linear and non-linear predictions of *Nephus bisignatus* (Bohrman) (Coleoptera: Coccinellidae) emergence can be up to a week, which is not trivial and have important implications for the use of degree-day models in ecological applications. It is common that temperature not only influences the rate of chemical reactions, but also induces conformational changes in biological systems. For any degree day model, the most challenging task is to find the base temperature. Insects under fluctuating temperature may not have a distinct low temperature development threshold, and development rates become asymptotically smaller as temperature decreases (Eubank et al. 1973). The organism's response to high and low temperatures, as well as to the specific methods used to estimate accumulated degree-days, can lead to markedly divergent model predictions. Therefore, prediction of the degree day model is very sensitive to the tailored system, region, and time scale. This requires development of models that are tailored to the specific system, region, and time scale under a good fit. Therefore, a new modeling framework to cater these effects on insect development should be developed.

Nonlinear models

The initial objective for most of the nonlinear regression models is to describe developmental rate of insects over the full range of temperatures. This modeling procedure can be easily generated using several different software if the developed models are only used to predict the average developmental time or rate (reverse of the average development time, lifespan, or LT50). Most of these developed models considered the maximum and minimum development temperatures. These maximum and minimum development temperatures correspond to the assumption that there is no growth below the minimum temperature threshold, while developmental rate increases to reach a maximum at optimal temperature, and then declines rapidly approaching zero at the maximum temperature threshold that is often considered as the lethal temperature. To include the prediction of the distribution of the development time delay, this developed nonlinear model becomes complex because probability and/or likelihood estimation must be used.

One type of nonlinear temperature inhibition models is the biophysical model. Biophysical models are developed based on Van't Hoff's law which states that the rate of chemical reactions increases between two- and three-fold for each 10°C rise. The Arrhenius equation relates the chemical reaction rate to temperature and the activation energy of the reaction in an exponential equation. However, these models usually have a large prediction error because exponential increase is observable in a limited temperature range and not throughout all temperature regimes, and temperature affects not only the rate of chemical reactions, but also induces morphological changes in biological systems (Schoolfield et al. 1981, Sharpe and DeMichele 1977, Briere et al. 1999). Nonlinear models predicting average development rate with considering minimum and maximum development temperatures are usually complex (most have more than four thermodynamic parameters) and can only be used for the insects for which the model was initially developed (Schoolfield et al. 1981, Wagner et al. 1984 a and b, Wang and Engel 1998, Briere et al. 1999, Hansen et al. 2011, Regniere et al. 2012). These thermodynamic parameters were found to be highly correlated (Schoolfield et al. 1981, Briere et al. 1999). To eliminate this correlation, different researchers (Schoolfield et al. 1981, Briere et al. 1999) re-parameterized these models, and some researchers just used different mathematical equations to best fit the data which cover the entire

insect development temperature (Jian et al. 2007). This parameterization in turn results in a nonlinear model with no or few biophysical assumptions.

Distribution delay models

Life history studies usually require to determine recruitment (actual number), duration, and survivorship for each life stage. The most used methods to model this life history are Leslie matrix format, distribution delay model (referred to as distributed maturation models or variable development rate models), and combination of both. In a Leslie matrix format, the organism's life cycle is divided into sub-stages with a length equal to the length of the shortest stage. At each time step, all individuals in the population are advanced to the next sub-stage and the time step is usually set as the sub-stage length. All individuals in a cohort can advance in age at the same rate (development index model) or change from one stage to the next at the same age (sojourn time models). Mathematically, the development index model is a special case of the sojourn time model (Schaalje and Vaart 1989). The Leslie matrix model has been of limited use in ecology because it models exponential population growth. One format of the modified Leslie matrix is the distribution delay. In the distribution delay format of the Leslie matrix model, advance of an individual from one stage to the next is not only based on the mean length of development time, but also the variability among individuals. The advance of an individual can be calculated from a probability distribution based on the mean and standard deviation or is assigned a predetermined probability (Schneider and Ferris 1986). Survivorship of an individual can also use the same method as that used for the advance of an individual or use mathematical equations describing the survivorship pattern. Weibull function is mostly used to describe this probability distribution (Schneider and Ferris 1986). Erlang probability distribution can be used to describe the asymmetric and positively skewed development rates within the population (Wegner et al. 1984 a and b, Schneider and Ferris 1986). These asymmetric and positively skewed development rates are assumed as the effect of temperature and enzyme concentration (Curry et al. 1978, Sharpe and DeMichele 1977). The stochastic treatment of the Leslie matrix model can include the insect density effect and stochastic process on the survivorship and development rate by making the elements of the projection matrix vary with the age distribution or density (Leslie 1959, Vansickle 1977, Desharnais and Cohen 1986, Desharnais and Liu 1987, Liu and Cohen 1987). More complex models could be formulated to allow for time delays, but the above are commonly used. During the model development of a Leslie matrix, the temperature effect is usually implicit because it is difficult to combine the effect of fluctuating temperatures in each time step when the Leslie matrix is advanced to the next time step. For example, if temperature is changed every hour and this fluctuating temperature effect will influence the Leslie matrix, then the Leslie matrix should be calculated every hour. This will increase the difficulty of parameter estimation for the Leslie model calculation. There is no model developed in this way because the use of the Leslie matrix formulation allows the overall model to be stated concisely and this small time step will downgrade this advantage. Because the fecundity and death rate may change abruptly as an individual matures from one stage to the next, the Leslie, Von Foerster (Longstaff 1988) and related models are implicitly formulated in terms of growth stages. Cuff and Hardman (1980) calculated the fecundity and survival rate by considering the effect of temperature, moisture content, weight of free water, weevil density, and oxygen concentration. These calculated fecundity and survival rates were the basic components of the Leslie matrix in each time step. Other environmental factors such as respiration of insects, feeding, and egestion activities were also considered by modifying the Leslie matrix in each time step. Because these environmental factors influence the insect development rate, Cuff and Hardman (1980) used both physiological and chronological time scale to track insect age in each sub-stage and advance the sub-stage, respectively. This increases the complexity of the Leslie matrix model. This might be one of the reason few Leslie matrix models with distribution delay were developed after the 1990s.

Models that predict this stochastic development distribution usually involve application of probability distributions and likelihood estimation. These developed models are similar except they use different 1) variables, such as mean or median development time (Wagner et al. 1984 a and b,

Gramig et al. 2015) or development rate; 2) forms of frequency distribution, such as probability or cumulative density function; 3) types of probability distribution such as normal quadratic and beta; and 4) equations, such as Erlang probability distribution function, Weibull function (Wagner et al. 1984b), nonlinear functions with different assumptions (Gramin et al. 2015, Nachman and Gotoh 2015). The most commonly used model strategies are distributed delays (Nisbet and Gurney 1982, Wagner et al. 1984 a and b, Schneider and Ferris 1986), cohort-based (Sharpe and DeMichele 1977, Nachman and Gotoh 2015, Skovgard and Nachman 2017), Leslie model based (Longstaff and Cuff 1984, Henson 1999), simulation based (Longstaff 1988, Maggi et al. 2013), and individual-based (Regniere et al. 2012). The parameter values estimated from these developed models are usually not comparable even for the same stage of an insect species under different environmental conditions because the chronological time is used as the time scale and these factors are changing with time. The distribution of development time and the variation in the chronological time scale is different under different temperatures.

Other environmental factors

The major constraint of most developed models is directly related to temperature and do not take into account other climatic variables such as photoperiod, humidity, nutrition, as well as crowding and competition at different density levels and in different patch sizes. Incorporating more factors in the equations, temperature-driven models have the potential to describe the general ecological behaviour, abundance, distribution, and outbreaks of insects on a regional or even global scale, with important practical applications. Nachman and Gotoh (2015) claimed their developed model framework could simulate the growth of an insect population in a variable environment by modifying the response variable y in the equation (y was a product of limiting factors) with the assumption of a multiplicative relationship between the environmental factors. Nisbet and Gurney (1982) considered the quantity of food. Cuff and Hardman (1980) considered other environmental factors. However, this modelling approach has not been verified. This modelling approach increases the complexity and the y in Nachman and Gotoh's model has no basic biological meaning. Therefore, a new modeling approach should be developed to effectively predict the effect of these environmental factors with sound biological meaning.

Future model development

Physiological or biological time is intuitively obvious to some extent, but has been explicated in various ways in the literature. It is referred to as heat units and is measured in degree-days and development accumulation as the basis of physiological time scale in model development. Physiological age as a life-history event are sometime related to cyclic event such as biological rhythmicity. Nachman and Gotoh (2015) used biological age as a measure of the cumulated day-degrees an individual has achieved while in a given stage. From the view of an insect body, ageing might be the result of physiological and biological advance in the chronological time scale. Therefore, a physiological-biological time scale which can normalize the distribution of the development time and the variation should be developed.

The time delays, cyclical patterns of insect populations (periodic forcing), and nonlinearities in population models are the typical characteristics that lead to chaos in the natural ecological world (Logan and Allen 1992, Boeing 2016). Even though whether the insect populations have the chaos is still in debate, this debate has largely been carried out on theoretical grounds, and chaos occurring in the time series of forest insect pests have been proven (Turchin 1990, Turchin and Tylor 1992). Analysis of insect-population data collected inside lab or controlled field conditions for the signature of chaos presents significant limitations because: 1) chaos analysis is unrealistically data intensive; 2) data collected under lab and/or controlled field conditions usually reduce the dimensionality such as that interactions between species or among species and food sources are usually simplified and completely sampling of the entire population is usually difficult or impossible, and this simplification will rarely occur in nature; 3) chaos characteristics usually show after a few

generations of insect populations (Turchin and Tylor 1992), and collation of the lab or field data are usually interrupted before chaos shows; and 4) analysis of a complex ecological system in reduced dimensionality will tend to obscure complex dynamics and ignore the chaos (Logan and Allen 1992). Therefore, study of chaos in a real system by using mathematical modelling is critical. To analyze the chaos of population dynamics, this developed model should be a reasonable representation of the natural system and parameter values should be in a realistic range. This requires complex models which represent the reality in nature and the developed model should also be validated.

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High Quality Genomic Resources for Stored Product Insects

Erin D. Scully^{1*}, Scott M. Geib², Sheina B. Sim²

¹Stored Product Insect and Engineering Research Unit, USDA-ARS-Center for Grain and Animal Health Research, Manhattan, KS 66502, USA.

²Tropical Crop and Commodity Protection Research Unit, USDA-ARS-Daniel K. Inouye U.S. Pacific Basin Agricultural Research Center, Hilo, HI 96720, USA.

*Corresponding author: Erin.Scully@ars.usda.gov

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Abstract

The expansion of genomic resources for stored product insects has largely been hampered by cost, time required for inbreeding, and technical issues that can arise during genome assembly from pooling multiple individuals together for DNA isolation and library preparation. However, newer library methods, such as 10X Chromium libraries, largely overcome these issues in that sufficient DNA can be recovered from a single individual for library prep and allelic variants are assembled as separate phase blocks, eliminating the need for inbreeding. Using 10X Chromium libraries coupled with 150 x 150 bp HiSeqX sequencing to a depth of at least 60X coverage, we are developing high quality draft genome assemblies for eight different stored product insect species, including Dermestidae (*Trogoderma variabile*, *Trogoderma granarium*, and *Dermestes maculatus*), Tenebrionidae (*Tribolium confusum*), Anobiidae (*Lasioderma serricorne* and *Stegobium paniceum*), Bostrichidae (*Prostephanus truncatus*), and Pyralidae (*Plodia interpunctella*). Overall, BUSCO (Benchmarking Using Single Copy Orthologs) scores exceeded 95% in all assemblies with few fragmented or duplicated genes, suggesting a high quality assembly of the gene space. Further, scaffold N50s exceeded 1 Mb in many cases and further