Life history data for *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) in farm-stored corn and the importance of sub-optimal environmental conditions in insect population modelling for bulk commodities

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Abstract

Life history data for a strain of the Angoumois grain moth collected in South Carolina, USA in 1992 are compared to published data. The survival of the South Carolina strain was much higher than that reported in the literature and development was slower. Models simulating growth of Angoumois grain moth populations under actual storage conditions were prepared for the two data sets and compared. The literature-based model underestimated population size, probably because data for conditions below 20°C were unavailable.

To further investigate the importance of sub-optimal temperature, we bounded our model at 20°C, as per our literature-based model. This model performed very poorly compared to both the complete model and compared to the literature model. Underestimates were extreme because of the slower development of this strain. A final model was prepared using our data for only the linear portion of increase in development rate (20°C–30°C) and extrapolating to known limits of development and survival (10°C and 40°C). This model performed quite differently, with frequent large overestimates of population size, particularly early in storage under cool conditions.

It was concluded that accurate, useful models can be ensured only from complete life histories appropriate to the species biotype being studied. Accurate models may be generated using existing information but this is not a consistently reliable approach.

Introduction

The development of advanced computing technology has made it possible to create population models that can be used to predict population growth as a function of a wide array of deterministic variables (Throne 1994). Variables such as adequate food resources and protection from localised weather, which produce a favourable environment for stored-product insect pest population growth, may be readily described as a function of temperature and moisture content (relative humidity) (e.g. Hardman 1978). Published accounts of insect life histories for certain cosmopolitan stored-product pests have been used to prepare computer models simulating population growth, most of which have not been validated (Throne 1994). Certain models have been used in the preparation of commodity-based expert systems.

Life history data for stored-product insects often do not include information on the 'slow' or 'poor' biology, i.e., the conditions where growth is quite protracted or where survival is quite low and often these two responses are linked. In addition, properly stored commodities may seldom reach optimal conditions for insect growth. This may result in a situation where a model is being used to estimate growth for a considerable length of time under conditions for which little or no data were collected. This causes concern because simulation studies (Throne 1989) have indicated that small changes in development or survival can have a large impact on the size of subsequent populations. In addition, using published life histories to model population growth for a potentially different biotype of the pest species may be prone to fallibility (McFarlane et al. 1993). The current assumptions are that sub-optimal biology has little impact on resulting population size and that commerce-induced gene-flow across populations reduces the probability of marked biotypic differences in insect population development. These assumptions will be critically assessed by comparing our data to another published life history study for *Sitotroga cerealella* on stored maize in India (Grewal and Atwal 1967). This publication supplies a considerable amount of life history data for this species on stored maize, although in Grewal and Atwal (1967) the maize kernels were mixed with flour.

Materials and Methods

Life history data

Angoumois grain moths were collected from farm-stored maize at two sites in south-central South Carolina, USA in late winter and early spring, 1992. A laboratory population was established at 25°C, 65% r.h. on 'Pioneer 3320' maize from the 1991 crop using the pooled collections of moths. Newly-emerged F_2 adults were confined in a 237 mL mason jar containing an 8 cm × 30 cm piece of black construction paper that had been folded eleven times and stapled in the centre to yield a tight 'accordion-like' oviposition substrate that was 8 cm × 2.5 cm wide (Ellington 1930). After confinement at culture conditions for 12 hours the adults were removed and the papers unfolded. Cohorts of approximately 50 eggs were cut from the paper strips and placed in 237 mL mason jars with screen and filter-paper-lined lids in a sealed salt box containing equilibrated salt solutions at temperatures ranging from 10 to 40°C by 5°C increments. Salts used were KCl, NaCl, NaBr and K_2CO_3, which produce environments ranging from 43 to 87% r.h. across this temperature range (Greenspan 1977). Cohorts were observed daily until hatch ceased.

For development from hatch through adult emergence, newly-hatched F_3 larvae (collected as described above) were

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placed in 12 mL translucent polyethylene vials (2.7 cm high × 2.2 cm internal diameter) containing two equilibrated kernels of 'Pioneer 3320' maize. The vials were modified with fine mesh nylon screening fixed in the lid and base to facilitate respiration. Twenty-five larvae were prepared, as described, for each environmental condition and observations were made daily until all adults had emerged.

Simulation models

First, response surface equations were fitted to the South Carolina data and to the data of Grewal and Atwal (1967) using a curve-fitting procedure to relate developmental period to temperature and relative humidity. Fit was assessed by viewing the response surface and evaluating the r^2 value and the regression *F* statistic. All response surfaces selected were biologically plausible. Variation in development rate was then simulated using a time-varying distributed delay (Manetsch 1976) as described in Throne (1989). Standard deviations for the data of Grewal and Atwal (1967) and for the emergence of single individuals in the current study were calculated using the method of Shaffer (1983). Next, response surfaces were fitted to the developmental mortality data for the current study and for the data of Grewal and Atwal (1967) and fit was assessed as above. Fecundity and female longevity data from Grewal and Atwal (1967) were fitted with response surfaces as above, with Shaffer's (1983) method used to calculate standard deviations on longevity for use in the distributed delay. Four models were prepared.

Model 1

This model used all the data from the current study for development and the adult data from Grewal and Atwal (1967) to simulate population growth. Oviposition below 10°C and above 40°C was set at 0. Oviposition and survival were extrapolated to these extremes using the fitted response surfaces. For adults, maximal longevity below 10°C was set at 50 days based on our experience, and maximal longevity above 40°C was set at 4 days (D. K. Weaver and J. E. Throne, unpublished data). This model includes data that adequately describe the entire range of immature development.

Model 2

For this model we used the data and fitted equations for Grewal and Atwal (1967) which did not include any data below 20°C: thus development below this temperature was set at 0 and mortality for these conditions followed a time-varying distributed delay based on the maximal survival duration from our current study. Adult data are treated as for the first model, except for oviposition, which is set at zero above 35°C and below 20°C. This model is based on published data for stored maize and will allow for a comparison with the model that includes our data for the immature stages. Note that the adult stages are based on common data. The sole difference between the two models for this stage is extrapolation of the fitted equations for adults from 35 to 40°C and from 20 to 10°C in the first model.

This second model could not assess the role of sub-optimal biology in a comparison with the first because all the reported data for immature development and survival differ markedly from our findings (Tables 1 and 2). Therefore, two additional models were prepared.

Model 3

This model uses the fitted equations from model one, but with development at temperatures below 20°C and above 35°C set at 0 as in the second model. Adult data were treated as in the second model. This model is an approximation of conducting our study only at temperatures of 20°C and above and includes curvilinearity at the high temperature.

Model 4

The fourth model uses linear equations fitted to the data for the immature stages from our current study for the linear portion of development and survival curves, which was from 20 to 30°C. These equations were then extrapolated to extremes of 10 and 40°C as in the first model. Adult data were treated as in the first model. This allows us to test the importance of exact data for both sub-optimal and supra-optimal temperatures, by comparing this model with the first one.

Simulations

All models were run with actual environmental data for a bin at one of the collection sites for the moth population from South Carolina, as reported in Throne (1989). The temperature varied significantly during this time, but maize moisture content did not vary significantly. Therefore, the simulations are run using 75%r.h.. Models were started with 5 newly-emerged adult pairs on the first day of the storage season. This is realistic, based on our experience, because eggs and newly-hatched larvae are destroyed at harvest and relatively low numbers of newly-emerged adults are observed immediately after harvest. For simplicity, no subsequent recruitment was included in these models.

Results and Discussion

The life history data collected differed greatly from those reported in Grewal and Atwal (1967). Survival during both the egg stage and through immature development was much greater for the South Carolina strain we collected than for the strain collected in India (Tables 1 and 2). Duration of development was also much longer for the South Carolina strain (Tables 1 and 2). Note that the differences between the strains are least significant near optimal conditions (25–30°C, 56–84% r.h.). This similarly appears to indicate that the assumption that biotypic differences are unimportant is contingent upon environmental conditions. The assumption is most correct where development occurs rapidly and survival is high. The assumption is least correct at both sub-optimal and supra-optimal conditions.

We believe this finding has important ramifications for insect population modelling in stored-products and have thus produced several models to illustrate its effect. The models compare the impact of different data sets for immature development and survival only; the adult data are common and were obtained from Grewal and Atwal (1967). Model 1 contains all of the information from our first replicate of a development rate study using South Carolina moths. Model 2 uses information for all stages that was obtained from Grewal and Atwal (1967). Figure 1 illustrates that Model 1 gives much higher population numbers during the cool storage months (see graph at bottom of Fig. 1). At the end of the simulation, the lines appear to start to converge as temperature begins to increase towards the optimal and as population size increases, so that on a log scale there is only a nine-fold difference at 270 storage days (Fig. 1 and Table 3). However, this simulated difference is nearly 10 million individuals. This indicates the

Table 1. Duration of egg stage and percentage survival at constant temperatures and relative humidities for Angoumois grain moths collected in South Carolina, USA in 1992 and for those reported in Grewal and Atwal (1967).

Temperature (°C)	Relative humidity[a] (%)	Current study	Literature
		Days in stage (S.D.) [% survival]	Days in stage (S.D.)[b] [% survival]
10	43, 62, 76, 87	— [0]	Not measured
15	43	25.5 (1.4) [80]	Not measured
	61	26.4 (0.9) [80]	
	76	29.6 (1.9) [88]	
	86	29.1 (0.9) [98]	
20	43 / 40	14.2 (0.9) [95]	9.2 (1.1) [47]
	60 / 60	14.1 (0.4) [96]	8.7 (1.0) [64]
	75	14.1 (0.6) [86]	
	80		8.5 (1.0) [65]
	85	13.6 (0.9) [94]	
25	43 / 40	8.8 (0.7) [82]	6.9 (0.9) [60]
	58 / 60	8.5 (0.8) [83]	5.6 (0.7) [80]
	75	8.8 (1.4) [92]	
	80		5.5 (0.7) [82]
	84	8.3 (0.7) [92]	
30	43 / 40	6.5 (0.8) [82]	4.2 (0.6) [71]
	56 / 60	6.6 (0.5) [83]	4.1 (0.6) [73]
	75	6.5 (0.9) [93]	
	80		4.0 (0.6) [77]
	84	6.0 (0.5) [97]	
35	43 / 40	6.7 (0.6) [63]	4.8 (0.7) [29]
	55 / 60	6.5 (0.6) [74]	4.6 (0.6) [44]
	75	6.3 (0.8) [70]	
	80		4.4 (0.6) [55]
	83	5.8 (0.5) [81]	
40	43, 53, 75, 82 /40, 60, 80	— [0]	— [0]

[a]For 10 and 15°C, relative humidities available for the current study only. Percent humidities following '/' are from the literature and are paired with the nearest condition from the current study. In the case of the literature data for 80% r.h., these values have been offset for comparison to either of the two highest relative humidities from the current study.
[b]Standard deviations for the literature means were calculated using: S.D. = $0.209(\text{MEAN})^{0.73}$ (Shaffer 1983).

importance of collecting 'biotypic' life history data to ensure a that model developed for practical usage is as accurate as possible. Our literature-based model for Angoumois grain moths probably would not be very accurate for storage environments where grain temperatures routinely drop below 20°C or exceed 35°C, such as in the U.S.

Our results suggest in addition that collecting the non-optimal data is very important, especially given the range of grain temperatures typical of a relatively warm area such as South Carolina, USA, where grain temperatures may be below 20°C for nearly half of the storage year (Fig. 1). However, since the life history data from Grewal and Atwal (1967) differ so greatly from those we found, we chose to treat our data in two different ways. First, we bounded our data and fitted equations to resemble those collected in the literature study, with no development below 20°C (Fig.2, Model 3). Secondly, we deleted all data above 30°C and below 20°C from our data set and fitted linear temperature functions to the data. These were then extrapolated to 10 and 40°C and used to develop Model 4 (Fig. 2). Model 3 (Fig. 2) performed even more poorly than Model 2 (Fig. 1). This is a function of the slower development of the South Carolina strain and results in estimates that are almost totally inaccurate. Even late in the storage season this model was only 0.04% accurate compared with Model 1 (Table 3, 270 days). When plotted on a log scale Model 4 appears to be most similar to Model 1 and total numbers of individuals become quite close at certain times (Fig. 2). However, for most of the storage season, Model 4 systematically overestimated insect numbers, which is economically meaningful. For example, at 270 days of storage, total insect numbers are 140 million greater for Model 4 than for Model 1. Early, inaccurate predictions of high insect numbers could force a sale of maize during the cooler months when its market value is typically lower than in the spring and summer. This inaccuracy is quite evident at 180 days when numbers for Model 4 are eight-fold greater than for Model 1 (Table 3). This illustrates that it is very important to have complete biotypic life history data for modelling stored-product insect population growth, at least in regions where seasonality produces pronounced changes in temperature in a stored commodity.

In this paper we have made numerous extrapolations on equations and modifications to our data set and to those reported in the literature (the equations are listed in an appendix). Extrapolation and modification were carefully studied and when an equation generated a biologically unsound estimate it was bounded to the nearest known limit from our current life history study or from our experience

Table 2. Duration of larval through adult emergence for male and female Angoumois grain moths at constant temperatures and relative humidities for a population collected in South Carolina, USA in 1992. Pooled percent survival for both sexes is also reported for this population. Duration of larval through adult emergence for unsexed Angoumois grain moths and percent survival are also reported from Grewal and Atwal (1967).

Temperature (°C)	Relative humidity[a] (%)	Current study	Literature
		Days in stage female (S.D.)[b] / male (S.D.)[b] [% survival]	Days in stage[c] (S.D.)[b] [% survival]
10	43, 62, 76, 87	—[0]	Not measured
15	43	254.0 (11.9)[b] / 199.0 (45.8) [20]	Not measured
	61	166.1 (22.7) / 184.0 (40.1) [64]	
	76	133.8 (10.0) / 153.6 (39.3) [80]	
	86	136.9 (11.2) / 166.7 (35.4) [56]	
20	43 / 40	69.3 (3.8) / 73.8 (6.0) [68]	38.7 (3.0) [15]
	60 / 60	69.8 (4.4) / 73.7 (13.8) [68]	35.9 (2.9) [30]
	75	63.5 (19.1) / 64.7 (8.4) [88]	
	80		33.7 (2.7) [32]
	85	62.4 (13.0) / 68.6 (16.1) [84]	
25	43 / 40	54.4 (21.1) / 43.4 (3.3) [52]	31.0 (2.6) [38]
	58 / 60	41.4 (12.0) / 38.4 (3.5) [76]	29.2 (2.5) [41]
	75	35.2 (2.9) / 36.7 (6.3) [76]	
	80		27.8 (2.4) [44]
	84	45.2 (3.4) / 48.9 (16.7) [80]	
30	43 / 40	35.1 (5.7) / 36.4 (4.1) [56]	27.5 (2.3) [26]
	56 / 60	31.4 (4.5) / 33.8 (13.1) [48]	26.2 (2.3) [39]
	75	36.7 (18.0) / 29.6 (6.5) [76]	
	80		24.1 (2.1) [49]
	84	35.0 (7.4) / 50.6 (15.4) [52]	
35	43 / 40	—/— [0]	36.8 (2.9) [4]
	55 / 60	47.0 (3.5)[b] / 57.0 (4.0)[b] [8]	34.1 (2.7) [10]
	75	39.2 (4.5) / 36.0 (2.9) [28]	
	80		32.6 (2.7) [13]
	83	—/ 81.0 (5.2)[b] [4]	
40	43, 53, 75, 82 /40, 60, 80	— [0]	— [0]

[a]For 10 and 15°C, relative humidities available for the current study only. Percent humidities following '/' are from the literature and are paired with the nearest condition from the current study. In the case of the literature data for 80% r.h., these values have been offset for comparison to either of the two highest relative humidities from the current study.

[b]Standard deviations for the current study when one individual emerged and for the literature means were calculated using: S.D. = $0.209(\text{MEAN})^{0.73}$ (Shaffer 1983).

[c]These data were calculated by combining the larval and pupal data from this study.

Table 3. A comparison of the total number of individuals (all stages) produced by the four models at three-month storage intervals. These numbers help to illustrate the large differences between the model estimates, which are plotted on Figures 1 and 2 with a log scale.

Simulation model	Days of storage in South Carolina, USA		
	90	180	270
1	640	23000	1.1×10^7
2	210	290	1.3×10^6
3	66	5	4600
4	7900	160000	1.5×10^8

based on ongoing experiments. We emphasise that we have done so to illustrate that the keys to accurate modelling are sound data that are biologically relevant for the particular biotype of the species studied, and to show that little may be gained from extrapolation. Data that are available in the literature, no matter how well they were collected, may be of little value to regions other than where they were collected. There is simply no way to predict whether or not this is true for all given situations. The other point is that the assumption that low temperature biology contributes little to population growth may be erroneous for certain situations. The maize temperature was effectively below 20°C for 150 days in the data used for this study, which were collected in one of the warmest regions of the U.S. (Figs 1 and 2). The mean duration of development for immature Angoumois grain moths from this region at 15°C is about 150 days (Table 2). Thus, larvae that hatched early in the winter emerge as adults as the temperature exceeds 20°C in the spring. This affects population growth tremendously. We suggest that accurate data for bulk

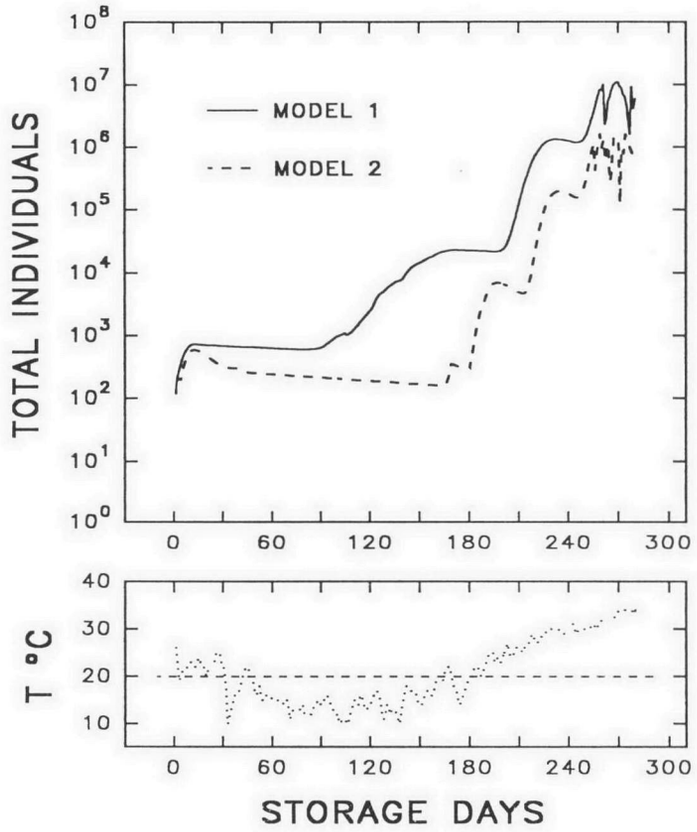

Fig. 1. Comparison of Model 1 and Model 2. Note the effect of storage temperature in creating deviation between the models.

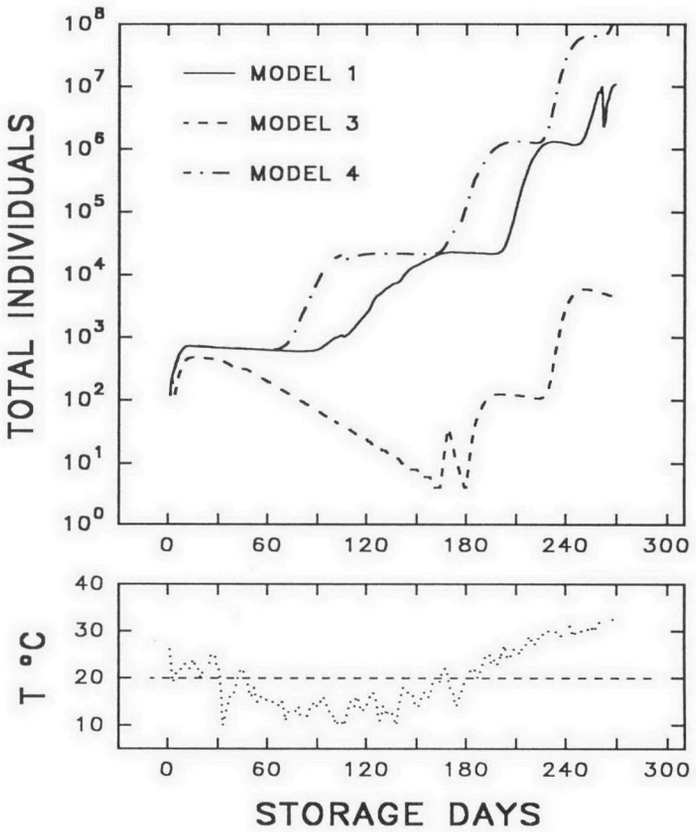

Fig. 2. Comparison of Model 1, Model 3 and Model 4. Note the effect of low storage temperature on deviation among models.

grain temperature over a long period (years) in a particular geographic region be carefully considered before using published life history data from other temperatures to create predictive models. Moreover, since models are typically validated in small quantities of stored products, we recommend that validations be conducted at temperatures representative of bulk grain storage in that particular region. The thermal inertia of small quantities of grain is insufficient to remain constant, and insolation alone, under cool ambient conditions, may be sufficient to keep mean temperatures near optimal, where they are not representative of actual storage temperatures for many areas where commodities are stored.

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Appendix

Equations used in the simulation models

Eggs laid = 123.499 + [0.227614* (Temp** 2.5)]–[0.0364930*(Temp**3)]–[810.663/(r.h.**0.5)]. Based on data from Grewal and Atwal (1967). Used in all models. Oviposition was bounded at a lower extreme of 0 eggs per day. Extrapolated to 10 and 40°C for Model 1. For Model 2 and Model 3 oviposition outside of the temperature range from 20 to 35°C was set at 0.

Egg development 1 = –6.71886 + [0.00156779*(Temp**2)* Log (Temp)] + [7544.88/ (Temp**2)]. Based on the data from the current study. Used in Model 1 and Model 3. In Model 3, outside of the range from 20–35°C no eggs hatched.

Immature male development 1 = 276.9914193–(9176 .77643/Temp) + [131132.6881/ (Temp**2)]–(2.390 + 11533*r.h.)+[0.017623645*(r.h.**2)]. Based on data from the current study. Used in Model 1 and Model 3. In Model 3, outside of the range from 20 to 35°C no adult males emerged.

Immature female development1= 35.4599 + {24211596* [TEMP** (–4.6904)]} –(140811* (r.h.**(–2.49998))) + ((5.62911E11* (TEMP** (–4.69042)))* (r.h.**(–2.49998))). Based on data from the current study. Used in Model 1 and Model 3. In Model 3, outside of the range from 20 to 35°C no adult females emerged.

Adult longevity= 37917.3– (3745.37*LOG(TEMP))– (103284/ LOG(TEMP)) + (155711/TEMP) + (0.5880* (r.h.**0.5)). Based on data for female longevity from Grewal and Atwal (1967). Used in all models, but output for temperatures outside of the range from 15 to 35°C was set at the output for 15 and 35°C in Model 1 and Model 4. For Model 2 and Model 3 adults died gradually over 4 days above 35°C and died gradually over 50 days below 20°C.

Egg survival1= 3.81885–(0.0869475* (Temp**2) *Log (Temp)) + (0.0737847* (TEMP**2.5))–(0.00370284* (TEMP**3)) – (151.263*LOG(TEMP)/(TEMP**2)) + (1.5 + 1942E-7* (r.h.**3)). Based on data from the current study. Used in Model 1 and Model 3. Survival was set at 0 for temperatures above 35°C and below 10°C.

Immature survival= -0.535799 + 1.43836*EXP((–EXP(– (TEMP–21.3047) / 10.2681)) –((TEMP–21.3047) / 10.2681) +1)*(EXP(–EXP(–((r.h.–73.1316)/50.6698))–((r.h.-73.1316) /50.6698)+1)). Based on data from the current study. Used in Model 1 and Model 3. Survival was set at O above 35°C and minimal survival was set at 0.

Egg development2= –35672.3+(3533.30*LOG(TEMP)) + (96945.9/ (LOG (TEMP))) –(145253/(TEMP)) –(0.163966 *LOG(r.h.**2)). Based on data from Grewal and Atwal (1967). Used in Model 2. Outside of the range from 20 to 35°C no eggs hatched.

Larval development = 27770.4 –(214333/ LOG(TEMP)) + (189924/ (TEMP **0.5) + (532968/ (TEMP**2))– 0.000 400287 * (r.h.**2)). Based on data from Grewal and Atwal (1967). Used in Model 2. Outside of the range from 20 to 35°C no larvae pupated.

Pupal development=26.6734– (.030824* (TEMP**2.5)) + (.00479741* (TEMP**3))+(164.529/r.h.). Based on data from Grewal and Atwal (1967). Used in Model 2. Outside of the range from 20 to 35°C no adults emerged.

Egg survival2=-0.0184696+(0.00125312*(TEMP**2.5))– (0.000199538*(TEMP**3)) – (2.75224E16*EXP(-r.h.)). Based on data from Grewal and Atwal (1967). Used in Model 2.

Larval survival= –0.415739 + (0.00409703*(TEMP**2)) –(.000101845 *(TEMP**3))–(276.222/(r.h.**2)). Based on data from Grewal and Atwal (1967). Used in Model 2.

Pupal survival = (0.250285–(.0636112*LOG(TEMP)) –(0.00372889 * LOG(r.h.)))/(1–(.497083*LOG(TEMP)) +(0.0647804*(LOG(TEMP)**2))–(0.00924077*LOG(r.h.)))Based on data from Grewal and Atwal (1967). Used in Model 2.

Egg development 3 = 29.3036– (0.769002 *Temp) – (0.00645732 *r.h.). Based on data from the current study. Used in Model 4. Output for temperatures greater than 30°C were set at that for 30°C. If temperatures exceeded 35°C no eggs hatched.

Immature male development 2=269.521– (2.27820* TEMP) – (5.76098*r.h.)+(0.0479332*(r.h.**2)). Used in Model 4. Output for temperatures greater than 30°C were set at that for 30°C.

Immature female development 2 = 138.895– (3.23713 *TEMP) – (0.160336*r.h.). Used in Model 4. Output for temperatures greater than 30°C were set at that for 30°C.

Egg sururvival 3 = 0.868486– (0.00370715 *TEMP) +(0.00189414*r.h.). Used in Model 4. Survival was set at 0 for temperatures below 10°C and above 35°C.

Immature survival 2 = 0.867359– (0.0184638 *TEMP) +(0.00431522*r.h.) Used in Model 4. Survival was set at 0 for temperatures below 10°C and above 35°C.

Note: All models had r.h. bounded at an upper limit of 80% and a lower limit of 40%. All simulations run in this study, however, had a constant relative humidity of 75% because the grain moisture content did not vary over the storage interval.