

Predicting development times of six stored-product moth species (Lepidoptera: Pyralidae) in relation to temperature, relative humidity, and diet

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Abstract. A four-parameter nonlinear regression model was fitted to development data of six stored-product moth species (Lepidoptera: Pyralidae) reared at various constant temperatures, and at 60–80% relative humidity on wheat or wheat-based diets. The model provided new information and quantitative description for predicting egg, larval, pupal, and egg-to-adult (total) development times, and also was useful in comparing the influence of relative humidity and diet on development times. Averaged across the six moth species, about 8%, 77%, and 15% of total development time was spent in egg, larval, and pupal stages, respectively. Temperature had the greatest influence on egg-to-adult development time, followed by relative humidity and diet. The temperatures for maximum and minimum development rates (1/development time), and degree-days required for egg-to-adult development, varied with the species. Independently derived egg-to-adult development times ($n = 39$) for the moth species reared at fewer than five temperatures, and at 50–90% relative humidity on different diets, were compared with those predicted by the four-parameter model for the same species. Across all six species, in 64% of the cases, development times predicted by the model were within 3 days of the actual data. In 23% and 13% of the cases, model predictions were within 4–10 and >10 days, respectively, of the actual data.

INTRODUCTION

Development times of insects are influenced by temperature, relative humidity (RH), and diet. In other guilds, crowding or density is also a factor. For stored-product insects, extensive data are available on the effects of temperature on development times. Hagstrum & Milliken (1988), and Subramanyam & Hagstrum (1991) described the nonlinear relation between development time and temperature using a four-parameter regression model (Wagner et al., 1984) for several species and stages of stored-product beetles (Coleoptera). The nonlinear regression model fitted to data from each species facilitated quantitatively comparing differences in temperature-dependent development times among species, stages, relative humidities, and diets (Hagstrum & Milliken, 1988; Subramanyam & Hagstrum, 1991). Although extensive published data are available on egg-to-adult development times for several species of stored-product moths (Lepidoptera) reared at various temperatures, relative humidities, and on different diets, comparisons of differences among these species have not been made. Temperature, relative humidity, and diet influence population trends of insect species by affecting development times, survival, and fecundity. Quantitative analyses of environmental effects on insects help us in understanding, predicting or comparing population trends of insects living in the same or diverse habitats.

For example, development models will be valuable in accurately predicting phenological events in the insect's life cycle, such as time of egg hatch, pupation or adult emergence. In conjunction with age-specific fecundity and adult longevity data, these development models can be used to predict population trends of insect species (e.g. Hagstrum & Throne, 1989).

The present study quantitatively compares the influence of temperature, relative humidity and diet on development times of six stored-product moth species. Our objectives were: 1) to fit a nonlinear regression model to describe egg-to-adult development times of each moth species reared at constant temperatures and 60–80% RH; 2) to compare temperature-dependent development times among the species; 3) to determine the influence of humidity and diet on development times; 4) to estimate temperatures where development rates (1/development time) are maximum (T_{max}) and minimum (T_{min}); 5) to estimate degree-days above T_{min} required for completing development; 6) to calculate percentage of total development time spent in egg, larval, and pupal stages; and 7) to compare model predictions with less extensive independent data sets where development times were presented for moths reared at fewer than five temperatures and relative humidities, and on different diets.

MATERIALS AND METHODS

INFLUENCE OF TEMPERATURE ON DEVELOPMENT

Mean egg-to-adult development times for the following moths reared at constant temperatures and 60–80% RH were obtained from literature: rice moth, *Corcyra cephalonica* (Stainton) (Cox et al., 1981); carob moth, *Ephesia calidella* (Guenée) (Cox, 1974); almond moth, *Ephesia cautella* (Walker) (Burgess & Haskins, 1965; Tuli et al., 1966; Tzvetkov & Latif, 1987); raisin moth, *Ephesia figulilella* Gregson (Cox, 1974); Mediterranean flour moth, *Ephesia kuehniella* Zeller (Siddiqui & Barlow, 1973); and Indianmeal moth, *Plodia interpunctella* (Hübner) (Savov, 1973).

The nonlinear relation between egg-to-adult development time and temperature for each moth species was described by the following four-parameter nonlinear regression model (Wagner et al., 1984):

Development time =

$$\frac{1 + \text{EXP} [HH/1.987(1/TH - 1/T)]}{RHO25(T/298.15) \text{EXP}[HA/1.987(1/298.15 - 1/T)]} \quad (1)$$

where, T = temperature in Kelvin (K), $RHO25$ = development rate at 25°C (298.15 K), HA = enthalpy of activation of reaction that is catalyzed by a rate-controlling enzyme, HH = change in enthalpy associated with high-temperature inactivation of the enzyme, and TH = Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive. For each species, survival of eggs to the adult stage varied at the different temperatures. Therefore, regressions were weighted with number of survivors at each temperature. Regression equations and parameter values were generated by the Marquardt or derivative-free (DUD) least squares method using the SAS procedure PROC NLIN (SAS Institute Inc., 1988).

Because data for *E. cautella* were obtained from three separate studies, equation (1) was fitted to the data from each study. Significant differences ($P < 0.05$) in the temperature-dependent development among the studies were determined by comparing individual regression models to a pooled model (Draper & Smith, 1981). If individual models were not significantly different from one another, data were combined and equation (1) was fitted to the combined data. Similarly, significant differences in the temperature-dependent development between any two species were determined by the model comparison procedure (Draper & Smith, 1981).

INFLUENCE OF HUMIDITY ON DEVELOPMENT

Mean egg-to-adult development data at more than five constant temperatures and relative humidities (10, 20, 40, 60, 85, and 95% RH) were available only for *E. cautella* (Nawrot, 1979a). Equation (1) was fitted to the temperature-dependent development data at each relative humidity, and the model comparison procedure (Draper & Smith, 1981) was used to test for significant differences ($P < 0.05$) in development among humidities. If models were not significantly different from one another, the data were pooled and equation (1) was fitted to the pooled data.

INFLUENCE OF DIET ON DEVELOPMENT

Temperature-dependent development data on two distinctly different diets were available only for *E. cautella* and *E. kuehniella*. Equation (1) was fitted separately to development data of *E. cautella* reared on wheat or wheat-based diets (Burgess & Haskins, 1965; Tuli et al., 1966; Tzvetkov & Latif, 1987), and peanuts (Nawrot, 1979a). Differences ($P < 0.05$) in development on these two diets were compared using the model comparison procedure. Temperature-dependent development models for *E. kuehniella* reared on whole wheat flour (Siddiqui & Barlow, 1973), and white flour (Jacob & Cox, 1977) were compared similarly.

ESTIMATING TEMPERATURE FOR MAXIMUM DEVELOPMENT RATE (T_{max})

T_{max} for each species was estimated by the following four-parameter nonlinear regression model (Stinner et al., 1974):

$$R_T = A / \{ 1.0 + \text{EXP}[K1 + (K2 \times T'')] \} \quad (2)$$

where, R_T = development rate at temperature T (in °C); A = maximum R_T ; $\{ 1.0 + \text{EXP}[K1 + (K2 \times T'')] \}$; $K1$, $K2$ = empirical constants; and $T'' = T$ for $T < T_{max}$, or $T'' = [(2 \times T_{max}) - T]$ for $T > T_{max}$. Parameters A , $K1$, $K2$, and T_{max} were estimated by the DUD least squares method (SAS Institute Inc., 1988).

The influence of humidity on T_{max} was determined by fitting the temperature-dependent development data of *E. cautella* (Nawrot, 1979a) reared at 10, 20, 40, 60, 85, or 95% RH using equation (2). Development time ($1/R_T$) at T_{max} at each humidity was estimated using equation (2), and parameter estimates are given in Table 2. Estimated development times at T_{max} were regressed on corresponding humidities using the PROC REG procedure (SAS Institute Inc., 1988), to determine the change in development time with humidity. Intercept and slope estimates were tested for departure from zero (t -test; SAS Institute Inc., 1988).

ESTIMATING TEMPERATURE FOR MINIMUM DEVELOPMENT RATE (T_{min}), AND DEGREE-DAYS

For each species, a simple regression was fitted to development rates linearly related to temperature using the PROC REG procedure (SAS Institute Inc., 1988). The temperature where development rate is minimum (T_{min}), or assumed zero, was estimated by extrapolating the regression line to the x-axis (Campbell et al., 1974). Inverse of the regression slope value gave degree-days required for completing egg-to-adult development.

PERCENTAGE OF TOTAL DEVELOPMENT TIME SPENT IN IMMATURE STAGES

For all six species, data on development times of egg, larval, and pupal stages were insufficient to fit equation (1), because there were fewer than five data points. Therefore, percentage of total development time spent in immature stages was calculated. Based on these percentages, a mean and standard error (SE) for each species and stage was calculated.

CONTRIBUTION OF TEMPERATURE, RELATIVE HUMIDITY, AND DIET TO TOTAL DEVELOPMENT TIME

The greatest magnitude of difference in development time attributable to temperature, relative humidity or diet alone was calculated as the ratio of maximum and minimum development time. Maximum development times attributable to temperature for the six moth species were calculated using equation (1), and parameter estimates are given in Table 1. The development time at 15°C and T_{max} (Table 2) gave the maximum and minimum development times, respectively.

Imura (1981) reported egg-to-adult development times for *P. interpunctella*, *E. cautella* and *E. kuehniella* at 43.0–75.5%, 50.0–75.5% and 7.0–75.5% RH, respectively, and 25°C. For each species, the maximum and minimum development times within these humidity ranges were derived from the reported data. Similarly, maximum and minimum egg-to-adult development times due to diet alone at constant

temperatures and humidity levels for moth species reared on different diets were obtained from various sources (Williams, 1964; Abdel-Rahman et al., 1968; Bhattacharya et al., 1976; Nawrot, 1979b; Rathore et al., 1980; Mbata, 1989).

COMPARISON OF MODEL PREDICTIONS WITH INDEPENDENT DATA SETS

Independent mean egg-to-adult development times of moth species reared at fewer than five temperatures, 50–90% RH, and on different diets were compared with those predicted by equation (1) for the same species. The number of development times compared for *C. cephalonica* (Osman et al., 1984; Shazali & Smith, 1986), *P. interpunctella* (Abdel-Rahman, 1971; Bell, 1975; Mbata & Osuji, 1983), *E. figulilella* (Donohoe et al., 1949), *E. kuehniella* (Brindley, 1930; Ahmad, 1936; Bell, 1975), *E. cautella* (Bell, 1975), and *E. calidella* (Prevett, 1968) were 12, 15, 1, 7, 2 and 2, respectively. Difference in development times in these studies from those estimated by equation (1) were plotted against temperature to show departure from model predictions.

RESULTS

INFLUENCE OF TEMPERATURE ON DEVELOPMENT

The temperature-dependent egg-to-adult development times of the six moth species were satisfactorily described ($R^2 = 0.95–0.99$) by equation (1), and the parameter estimates are shown in Table 1. *E. cautella* data from the three separate studies were combined because individual development models were not significantly different from one another ($F = 2.38$; $df = 8, 10$; $P > 0.09$). In general, development times of each moth species decreased with an increase in temperature (Fig. 1), and the rate of decrease was faster between 15° and 24°C, and slower at > 24°C. Except for *E. kuehniella*, development times of the remaining species slightly increased at temperatures above 32°C. Temperature-dependent development times between the following species pairs were not significantly different from one another: *P. interpunctella* and *C. cephalonica* ($F = 2.92$; $df = 4, 8$; $P > 0.92$), *P. interpunctella* and *E. figulilella* ($F = 1.77$; $df = 4, 8$; $P > 0.22$), and *E. cautella* and *E. kuehniella* ($F = 1.34$; $df = 4, 22$; $P > 0.28$). Except for these three species pairs, all other species pair combinations were significantly different ($P < 0.05$) from one another.

TABLE 1. Parameter estimates (means) for the Wagner et al. (1984) model describing the nonlinear relation between mean egg-to-adult development time (in days) and temperature for six stored-product moth species.

Species	Temperature range (°C) ^a	<i>n</i> ^b	RHO25 ^c	HA ^c	HH ^c	TH ^c	<i>R</i> ²
<i>C. cephalonica</i>	17.5–35.0	8	0.147	70,608.81	69,761.91	293.86	0.99
<i>E. calidella</i>	15.0–35.0	8	0.039	28,804.90	61,040.99	301.88	0.99
<i>E. cautella</i> ^d	15.0–35.0	22	0.042	30,263.97	35,299.15	298.65	0.97
<i>E. figulilella</i>	17.5–35.0	8	0.018	18,230.72	56,136.47	306.41	0.95
<i>E. kuehniella</i>	20.0–30.0	8	0.023	14,888.81	66,188.79	305.87	0.99
<i>P. interpunctella</i>	18.0–34.0	8	0.024	28,786.48	62,929.03	303.45	0.99

^a For each species, the model described development within this temperature range.

^b *n*, number of observations.

^c See equation (1) for explanation.

^d Equation 1 was fitted to data combined from three separate studies, as described in text.

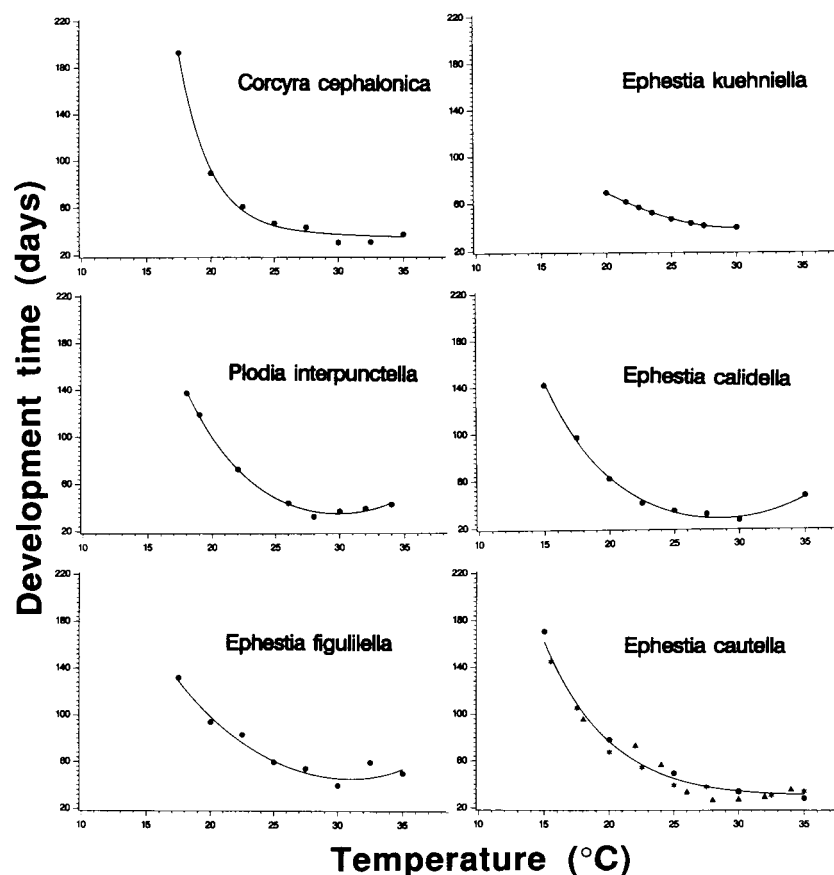


Fig. 1. Relation between mean egg-to-adult development times and temperature for each of the six stored-product moth species. The solid line represents development time predicted by the four-parameter model [equation (1) in text]. A single model explained *Ephestia cautella* data derived from Burges & Haskins (1965; $n = 9$), Tuli et al. (1966; $n = 5$), and Tzvetkov & Latif (1987; $n = 8$).

INFLUENCE OF HUMIDITY ON *E. CAUTELLA* DEVELOPMENT

Egg-to-adult development times were not significantly different ($F = 1.47$; $df = 12, 16$; $P > 0.23$) among 10, 20, 40, and 60% RH (Fig. 2). Egg-to-adult development times at 85 and 95% RH were also not significantly different from one another ($F = 0.55$; $df = 4, 10$; $P > 0.70$). However, development at higher humidities (85 and 95% RH) was significantly faster ($F = 6.57$; $df = 4, 42$; $P < 0.0004$) than at lower humidities (10, 20, 40, and 60% RH). At 85 and 95% RH, the insects developed about 1.2 times faster than at 10–60% RH, and this difference was consistent across temperatures (16 to 32°C). Development times among 60, 85, and 95% RH were not significantly different from one another ($F =$

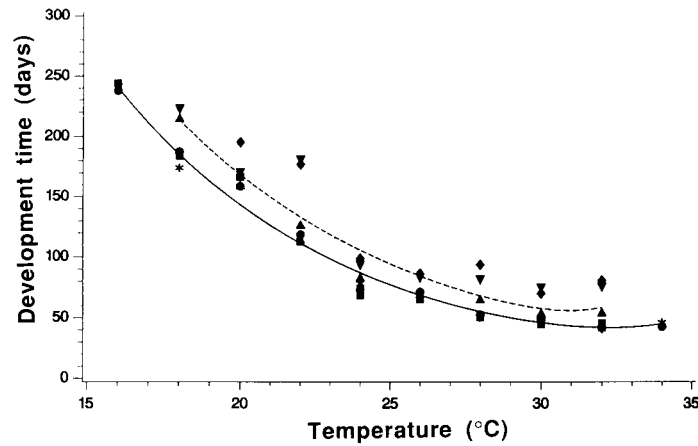


Fig. 2. Observed and predicted mean egg-to-adult development times for *Ephestia cautella* reared at constant temperatures and relative humidities. The temperature-dependent development at 85 + 95% RH (solid line; $n = 18$) was significantly faster ($P < 0.05$) than at 10 + 20 + 40 + 60% RH (dashed line; $n = 32$). Equation (1) parameters at 10–60% RH are: $RHO_{25} = 0.011$, $HA = 19577.01$, $HH = 146053.84$, $TH = 306.45$; parameters at 85 + 95% RH are: $RHO_{25} = 0.013$, $HA = 21173.47$, $HH = 89241.06$, $TH = 307.80$.

1.18; $df = 8, 15$; $P > 0.37$). However, differences in development at 10 and 60% RH were significant at the 10% significance level ($F = 3.35$; $df = 4, 8$; $P = 0.07$).

INFLUENCE OF DIET ON DEVELOPMENT

Egg-to-adult development times of *E. cautella* on wheat or wheat-based diets were significantly faster than on peanuts between 16 and 34°C (Fig. 3; $F = 104.48$; $df = 4, 41$; $P < 0.00001$). Development was 1.2 to 1.8 times faster on wheat than on peanuts, and the differences in development times between these two diets were greater at cooler than at warmer temperatures.

Egg-to-adult development of *E. kuehniella* was significantly faster on wheat flour than on white flour between 20 and 27.5°C (Fig. 3; $F = 44.88$; $df = 3, 6$; $P < 0.001$). The insects developed 1.6 to 1.9 times faster on wheat flour than on white flour, and these differences in development times were consistent across the temperatures compared.

ESTIMATED T_{MAX} , T_{MIN} , AND DEGREE-DAYS

T_{max} for the six species varied between 29.1 and 32.4°C (Table 2). T_{max} was highest for *E. cautella*; it was similar ($\approx 29^\circ\text{C}$) for *E. calidella*, *E. kuehniella*, and *P. interpunctella*.

T_{max} for egg-to-adult development of *E. cautella* at 10, 20, 40, 60, 85, and 95% RH was 30.0, 29.1, 31.0, 30.8, 32.8, and 32.14°C, respectively. Development times at T_{max} corresponding to these relative humidities were 74.2, 69.7, 58.4, 49.9, 40.8, and 41.2 days, respectively. The relation between development time at T_{max} (DTT_{max}) and humidity was described ($R^2 = 0.98$) by the regression equation

$$DTT_{max} = 76.76 - 0.41 \times RH \quad (3)$$

The y-intercept (76.76) and slope (-0.41) were significantly different ($P < 0.001$) from zero. The slope value indicated that development time at $T_{\max}$ decreased by 4.1 days for every 10% increase in humidity between 10 and 95% RH.

TABLE 2. Parameter estimates (mean $\pm$ SE) for the Stinner et al. (1974) model describing the nonlinear relation between mean egg-to-adult development rate and temperature for six stored-product moth species.

Species	$n^{a,b}$	$T_{\max}^c$	A^c	$K1^c$	$K2^c$	R^2
<i>C. cephalonica</i>	8	31.36 $\pm$ 0.26	0.05 $\pm$ 0.01	5.09 $\pm$ 0.53	-0.19 $\pm$ 0.04	0.97
<i>E. calidella</i>	8	29.19 $\pm$ 0.73	0.05 $\pm$ 0.01	5.15 $\pm$ 1.58	-0.23 $\pm$ 0.10	0.96
<i>E. cautella</i>	22	32.43 $\pm$ 0.70	0.04 $\pm$ 0.003	4.99 $\pm$ 0.65	-0.22 $\pm$ 0.04	0.93
<i>E. figulilella</i>	8	30.13 $\pm$ 0.95	0.11 $\pm$ 0.95	4.24 $\pm$ 6.49	-0.10 $\pm$ 0.14	0.92
<i>E. kuehniella</i>	8	29.11 $\pm$ 0.13	0.04 $\pm$ 0.003	3.64 $\pm$ 0.28	-0.16 $\pm$ 0.02	0.99
<i>P. interpunctella</i>	8	29.45 $\pm$ 0.51	0.03 $\pm$ 0.007	6.59 $\pm$ 1.72	-0.29 $\pm$ 0.10	0.96

^a n , number of observations.

^b Same temperature ranges as in Table 1.

^c See equation (2) for explanation.

$T_{\min}$ estimates (Table 3) were lowest for *E. kuehniella* (9.5°C) and highest for *P. interpunctella* (15.4°C). For the remaining species, $T_{\min}$ varied between 11.5 and 14.8°C. Degree-days required for egg-to-adult development of *C. cephalonica*, *E. calidella*, and *P. interpunctella* were essentially the same, and were lower than those required for the other species (Table 3). Degree-days required for egg-to-adult development of *E. cautella*, *E. figulilella* and *E. kuehniella* were also similar.

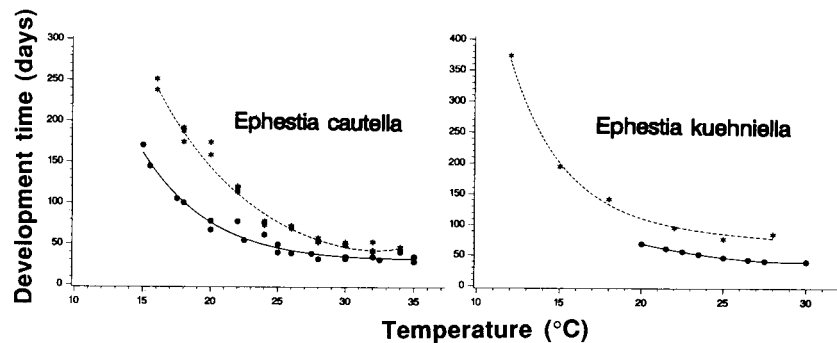


Fig. 3. Observed and predicted mean egg-to-adult development times for *Ephestia cautella* and *Ephestia kuehniella* reared at constant temperatures on different diets. Data on peanuts represents *E. cautella* development at 60 + 85 + 95% RH (Nawrot, 1979a). *E. cautella* development on wheat (solid line; $n = 22$) was significantly faster ($P < 0.05$) than on peanuts (dashed line; $n = 27$). Equation (1) parameters on wheat are: $RHO25 = 0.042$, $HA = 30265.32$, $HH = 35298.49$, $TH = 298.65$; parameters on peanuts are: $RHO25 = 0.013$, $HA = 20986.18$, $HH = 90260.83$, $TH = 307.77$. *E. kuehniella* development on wheat flour (solid line; $n = 8$) was significantly faster ($P < 0.05$) than on white flour (dashed line; $n = 6$). Equation (1) parameters on wheat flour are: $RHO25 = 0.023$, $HA = 14888.81$, $HH = 66188.79$, $TH = 305.87$; parameters on white flour are: $RHO25 = 0.202$, $HA = 50924.09$, $HH = 4791.76$, $TH = 288.20$.

TABLE 3. Estimates (mean $\pm$ SE) of temperature for minimum development rate (T_{min}), and degree-days (DD) above T_{min} required for egg-to-adult development of six stored-product moth species.

Species	Temperature range ($^{\circ}$ C) ^a	n^b	T_{min}	DD > T_{min}	R^2
<i>C. cephalonica</i>	17.5–30.0	6	14.75 $\pm$ 0.85	491.64 $\pm$ 41.72	0.97
<i>E. calidella</i>	15.0–30.0	7	11.95 $\pm$ 0.63	470.37 $\pm$ 25.31	0.99
<i>E. cautella</i>	15.0–35.0	19	11.52 $\pm$ 0.85	619.20 $\pm$ 37.65	0.94
<i>E. figulilella</i>	17.5–30.0	6	12.33 $\pm$ 1.30	758.73 $\pm$ 81.13	0.96
<i>E. kuehniella</i>	21.5–27.5	6	9.54 $\pm$ 0.42	724.11 $\pm$ 19.82	0.99
<i>P. interpunctella</i>	18.0–32.3	5	15.35 $\pm$ 0.76	435.73 $\pm$ 40.36	0.98

^a Development rates were linear within this temperature range.

^b n , number of observations.

PERCENTAGE OF TOTAL DEVELOPMENT TIME SPENT IN IMMATURE STAGES

Averaged across the six moth species (Table 4), about 7.9, 76.7, and 15.4% of total developmental time was spent in the egg, larval, and pupal stages, respectively. For all species, based on the percentage of time spent, the stages can be arranged as follows: larva > pupa > egg. Compared with similar life stages of the other species, *C. cephalonica* and *E. calidella* spent slightly more time in the egg and pupal stages, and less time in the larval stage.

TABLE 4. Percentage of total development time spent in egg, larval, and pupal stages for six stored-product moth species.

Species	n^a	Percent time in stage (mean $\pm$ SE)			Source
		Egg	Larval	Pupal	
<i>C. cephalonica</i>	2	11.8 $\pm$ 2.5	67.7 $\pm$ 6.2	20.5 $\pm$ 3.7	Rahman & Jahan (1979)
<i>E. calidella</i>	13	13.7 $\pm$ 0.6	60.7 $\pm$ 1.6	25.6 $\pm$ 1.1	Cox (1974)
<i>E. cautella</i>	78	6.8 $\pm$ 0.1	79.4 $\pm$ 0.7	13.9 $\pm$ 0.5	Takahashi (1961); Burges & Haskins (1965); Tuli et al. (1966); Nawrot (1979a)
<i>E. figulilella</i>	8	8.2 $\pm$ 0.4	75.2 $\pm$ 1.2	16.5 $\pm$ 1.0	Cox (1974)
<i>E. kuehniella</i>	31	6.8 $\pm$ 0.3	78.8 $\pm$ 0.9	14.4 $\pm$ 0.6	Brindley (1930); Ahmad (1936); Jacob & Cox (1977)
<i>P. interpunctella</i>	9	11.4 $\pm$ 0.5	72.7 $\pm$ 0.9	15.8 $\pm$ 0.9	Mbata & Osuji (1983)
Weighted mean		7.9	76.7	15.4	

^a n , number of observations.

CONTRIBUTION OF TEMPERATURE, RELATIVE HUMIDITY, AND DIET TO TOTAL DEVELOPMENT TIME

The greatest difference in development time due to temperature for the six moth species was 3.0 to 13.2-fold (Table 5). For three species of moths, humidity contributed only about 2-fold to differences in development time. For three moth species, diet alone contributed about 1.3 to 2.8-fold to differences in development time.

COMPARISON OF MODEL PREDICTIONS WITH INDEPENDENT DATA SETS

Independent development time data for the six moth species reared at fewer than five temperatures, 50–90% RH, and on different diets were often similar to those predicted by

TABLE 5. Magnitude of differences in mean egg-to-adult development times in relation to temperature, relative humidity, and diet for six stored-product moth species

Species	Development time (days)		Ratio ^a	Source
	minimum	maximum		
Temperature ^b				
<i>C. cephalonica</i>	36.6	483.0	13.2	Cox et al. (1981)
<i>E. calidella</i>	27.9	144.7	5.2	Cox (1974)
<i>E. cautella</i>	32.3	161.5	5.0	Burges & Haskins (1965); Tuli et al. (1966); Tzvetkow & Latif (1987)
<i>E. figulilella</i>	45.9	170.8	3.7	Cox (1974)
<i>E. kuehniella</i>	36.4	108.7	3.0	Siddiqui & Barlow (1973)
<i>P. interpunctella</i>	34.9	233.2	6.7	Savov (1973)
Relative humidity				
<i>E. cautella</i>	35.5	82.0	2.3	Imura (1981)
<i>E. kuehniella</i>	42.1	93.3	2.2	Imura (1981)
<i>P. interpunctella</i>	29.2	70.5	2.4	Imura (1981)
Diet				
<i>C. cephalonica</i>	37.6	56.3	1.5	Mbata (1989)
<i>E. cautella</i>	22.0	61.0	2.8	Bhattacharya et al. (1976)
<i>E. cautella</i>	32.0	41.3	1.3	Rathore et al. (1980)
<i>E. cautella</i> ^c	40.7	87.0	2.1	Nawrot (1979b)
<i>P. interpunctella</i>	38.0	65.9	1.7	Williams (1964)
<i>P. interpunctella</i>	35.4	45.9	1.3	Abdel-Rahman et al. (1968)

^a Maximum development time / minimum development time.

^b Minimum development time was calculated from equation (2) in text and parameter estimates are given in Table 2. Maximum development time was calculated at 15°C using equation (1) in text and parameter estimates are given in Table 1.

^c Larval development time only.

equation (1) between 18 and 35°C (Fig. 4). Only 5 out of 39 development times (12.8%) varied by > 10 days from model predictions. Of the remaining 34 development times, 25 varied by < 3 days, and 9 varied between 4 and 10 days.

DISCUSSION

The nonlinear relation between egg-to-adult development time and temperature at 60–80% RH for the six moth species was adequately described by equation (1). The magnitude of differences in development times among species was 1.4, 1.9, 1.6 and 1.9-fold at 20, 25, 30 and 35°C, respectively. The development times predicted by equation (1) for the six species averaged 83.2, 46.4, 36.7 and 46.1 days at 20, 25, 30 and 35°C, respectively. Predicted development times of *E. figulilella* were longer than average at all temperatures. *E. cautella* and *C. cephalonica* developed more rapidly than the other species at 35°C. At 25 and 30°C, *E. calidella* developed more rapidly than the other species. Differences in development times among the species were smaller at cooler temperatures than at warmer temperatures.

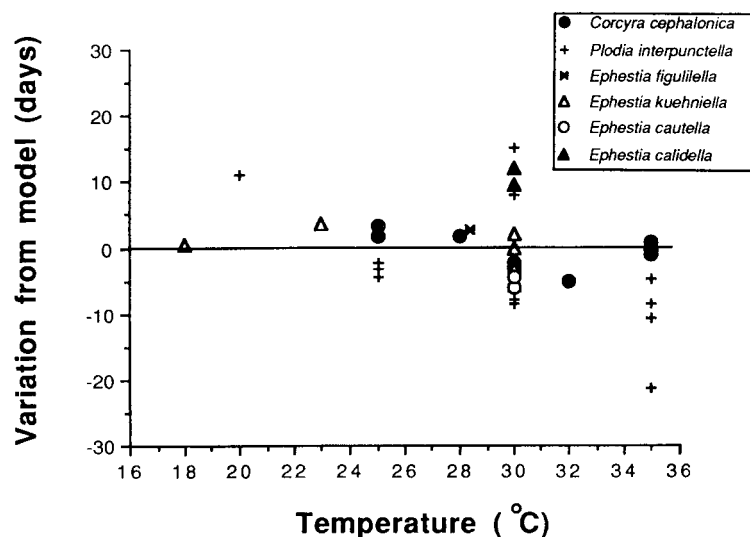


Fig. 4. Departure of independent mean egg-to-adult development times ($n = 39$) from development times predicted by equation (1) for six stored-product moth species.

Differences in egg-to-adult development times for the moth species among relative humidities (2.2 to 2.4-fold) and diets (1.3 to 2.8-fold) were smaller than those due to temperatures (3.0 to 13.2-fold). This indicated that temperature had the greatest influence on development times, followed by relative humidity, and diet. Similar results were reported for several species of stored-product beetles (Hagstrum & Milliken, 1988).

Temperature-dependent development of *E. cautella* was faster at $> 60\%$ RH, and on wheat or wheat-based diets. For *E. cautella*, differences in development time among humidities were consistent across temperatures (Fig. 2). This view is indirectly supported by the fact that the estimated $T_{\max}$ was similar at 10, 20, 40, 60, 85, and 95% RH. Therefore, the 4.1-day decrease in development time at $T_{\max}$ for every 10% increase in relative humidity (equation 3) is also applicable to other temperatures. Differences in development time with humidity are attributable to differences only in larval development time, because humidity has no significant effect on development of eggs or pupae of stored-product moths (Imura, 1981; Mbata, 1989). Humidity directly affects metabolism (e.g. respiration) of actively feeding larvae, and indirectly affects the palatability or physical condition of the diet by altering the diet moisture content. Development of *E. kuehniella* was faster on wheat flour than on white flour (Fig. 3). However, unlike *E. cautella*, differences in development time between the diets were consistent across temperatures. Because data were derived from two independent studies for comparing development on different diets, it is plausible that differences observed here, in part, may be attributable to variation in development between insect strains.

$T_{\max}$ for the six species ranged between 29.1 and 32.4°C, and $T_{\min}$ between 9.5 and 15.4°C. Howe (1965) reported 28–32°C as the optimum temperature range for egg-to-adult

development and population increase of *C. cephalonica*, *E. cautella*, and *P. interpunctella*. Our estimated T_{max} for these species was well within this temperature range. For *E. calidella* and *E. kuehniella*, Howe (1965) reported 25–29°C and 24–27°C, respectively, as the optimum temperature range. Our estimated T_{max} for these two species was above the upper limit of Howe's temperature ranges. T_{max} for the moth species was 4–6°C lower than T_{max} estimates for six species of beetles (Subramanyam et al., 1991). Except for *E. kuehniella*, T_{min} estimates for *C. cephalonica*, *E. cautella*, *P. interpunctella*, and *E. calidella* were respectively 3, 5, 3, and 2°C lower than those reported by Howe (1965). For *E. kuehniella* the minimum temperature reported by Howe (1965) was similar to T_{min} (10°C). Our T_{min} values were lower than Howe's (1965) because T_{min} in our study was estimated by extrapolating the regression line to the x-axis whereas his were based on data derived by rearing insects at constant temperatures. T_{min} estimates for the six moth species were generally 2–4°C lower than those for the beetles (Subramanyam et al., 1991).

For stored-product insects, egg-to-adult development time changes with temperature (Fig. 1). However, the percentage of time spent in the egg, larval, and pupal stages is generally similar across temperatures (Hagstrum & Milliken, 1988; Subramanyam & Hagstrum, 1991). Therefore, time spent in egg, larval, and pupal stages for the six moth species at any temperature can be calculated from the percentage of time spent in the immature stages (Table 4), and from parameter estimates for equation (1) given in Table 1. Averaged across the six moth species, about 8%, 77%, and 15% of the total development time was spent in egg, larval, and pupal stages, respectively. In contrast, averaged across six species of beetles (Hagstrum & Milliken, 1988), about 15%, 66%, and 19% of total development time was spent in egg, larval, and pupal stages, respectively.

There are noteworthy differences in the predicted egg-to-adult development times between moths and beetles (Hagstrum & Milliken, 1988). Average development times of the six moth species were longer than those for beetles at 20 (83.2 vs 67.2 days), 25 (46.4 vs 40.0 days), 30 (36.7 vs 27.1 days), and 35°C (46.1 vs 22.9). Moths and beetles have similar assimilation efficiencies (Demianyk & Sinha, 1988). Therefore, this longer development time is a consequence, in part, of moth larvae acquiring food for producing eggs in contrast to beetle adults acquiring food for producing eggs. Hence, much of the increase in development time of moths compared with beetles is in the feeding larval stage. The greater developmental time required for moths compared with beetles is also reflected in more degree-days (DD) required for completing development [436–758 DD for moths and 273–686 DD for beetles (Subramanyam et al., 1991)]. This difference is not attributable to differences in T_{min} , because T_{min} estimates for moths and beetles (see Subramanyam et al., 1991) are similar.

CONCLUSIONS

Fitting linear and nonlinear regression models to the temperature-dependent egg-to-adult development data of six stored-product moth species allowed us to quantify the effects of temperature, relative humidity, and diet on development times. These models were also useful in comparing differences in development times, and temperature thresholds (e.g. T_{max} & T_{min}) among the species. Comparison of model predictions with independent data, and a quantitative reanalysis of published data on the response of these six moth species to different environmental conditions, indicated that temperature greatly

influenced development times, followed by relative humidity, and diet. Differences among the six species in the temperature-dependent development at 60–80% RH on optimal diets were smaller at cooler temperatures than at warmer temperatures. The development time differences among the six species, in part, could be due to strain differences, because different strains of an insect species have different development times at the same temperature (Campbell et al., 1974). However, lack of significant differences between the three studies for *E. cautella* indicates that the effect of strain and study methods on development times may be small. The small effect of diet, humidity, strain and study methods in contrast to the large effect of temperature indicates that regression models may be useful in predicting development times of these moth species in many storage environments. The three cases in which data are available over the full temperature range for more than one humidity or diet indicate that these factors simply shift the temperature-dependent development curve up or down on that axis. Data collected at two or three temperatures at a different humidity or on a new diet would be sufficient to establish the magnitude of this shift. These regression models, therefore, can reduce the labor required to establish the effects of different (new) environments on moth development. $T_{\min}$ and $T_{\max}$ estimates could be used for calculating degree-days (see Subramanyam & Hagstrum, 1991; Subramanyam et al., 1991) to forecast egg-to-adult development of these six moth species in the field.

The percentage of total development time spent in egg, larval, and pupal stages can be used to predict the duration of each stage from total development time predicted by equation (1). In addition, the effect of change in environmental conditions on the change in duration of immature stages can be predicted similarly.

The quantitative analyses presented in this paper shows the magnitude of differences in development times of six stored-product moth species attributable to temperature, relative humidity, and diet. The analyses (models) and summaries presented here should make development data of these moths more readily available and useful to researchers. In conjunction with age-specific fecundity and adult longevity data collected at various temperatures, relative humidities, and on different diets, these development models will be valuable in predicting population trends of the six moth species in many storage environments.

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