Quantitative Analysis of Temperature, Moisture, and Diet Factors Affecting Insect Development

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FORUM: Ann. Entomol. Soc. Am. 81(4): 539–546 (1988)

ABSTRACT Extensive published data on the developmental times of nine species of stored-product Coleoptera in relation to temperature, moisture, and diet were described by regression equations. At most temperatures, the order of relative influence of these factors on development was temperature > moisture > diet. However, moisture and diet influenced larval development more than temperature near the optimal temperature for development of each species. Egg, larval, and pupal stage durations at 27°C averaged 15, 66, and 19% of the total developmental time, respectively, at moistures above 12%, and 12, 72, and 15% of total developmental time at moistures below 12%. Similar percentages were found at other temperatures between 20 and 35°C.

KEY WORDS Insecta, stored-product Coleoptera, age structure, modeling

DEVELOPMENTAL TIMES of many species of poikilotherms as a function of temperature have been described by regression equations (Wagner et al. 1984). Such regression equations can provide a simple means of calculating developmental times in insect population models or can be used for quantitative comparisons of the effect of temperature on the developmental times of different stages and species of insects. Because temperature affects population trends through its effects on developmental time, fecundity, and survival, such comparisons are extremely important in understanding and predicting differences in the population trends of different species in the same habitat. While extensive published data are available for developmental times of stored-grain insects reared under different temperatures, moistures and diets, for only a few of these studies have regression equations been fitted or have data from different studies been compared. The object of this study was to compare comprehensively the results of these many studies using regression analysis as a means of determining the relative importance and potential interaction of temperature, moisture, and diet as factors influencing insect developmental times for a complex of species occupying a common habitat. Our analysis included egg, larval, and pupal stages of nine species of Coleoptera.

Materials and Methods

Data for the mean developmental times of different stages of nine species of stored-product Coleoptera obtained under a variety of temperatures, moisture conditions, and diets were compiled from the published literature listed in Table 1. A polynomial model, $d = t + t^2$, in which d is developmental time and t is centigrade temperature, and the nonlinear model

$$\text{Developmental time} = \frac{1 + \exp\left[\frac{\text{HH}}{1.987}\left(\frac{1}{\text{TH}} - \frac{1}{\text{T}}\right)\right]}{\text{RHO25}\frac{\text{T}}{298.15}\exp\left[\frac{\text{HA}}{1.987}\left(\frac{1}{298.15} - \frac{1}{\text{T}}\right)\right]} \quad (1)$$

from Wagner et al. (1984) were fitted to these data. In Equation 1, T is Kelvin temperature and RHO25, HA, HH, and TH are fitted parameters. The statistical analysis system (SAS Institute 1982) was used to fit these regression equations, to calculate 95% confidence limits, and to plot graphs. Models were compared using the model comparison procedure of Draper & Smith (1981). The influence of moisture on development was evaluated by fitting temperature–development equation (1) to data collected at two moisture levels. High and low moisture levels included data collected at >12% and <12% moistures, respectively, and represent upper and lower halves of the moisture range for which data are available. Because diet is a discrete variable and not continuous like temperature and moisture, and because so many different diets were used, diet was considered only as part of the residual variance not explained in the regression models by differences in temperature or moisture. The width of the confidence intervals is a measure of the maximum influence diet could have had on developmental time.

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Table 1. Sources of data on the effects of temperature, moisture, and diet on the developmental time of stored-grain insect pests

Family and species	Stage[a]	Diet[b]	Source of data
Bostrichidae			
Rhyzopertha dominica (F.)	E, L, P, T	WC	Bains 1971
	E, L, P, T	W, WF, C, R	Begum et al. 1974
	E	W	Birch 1945
	E, L, P, T	W, WF	Howe 1950
Cucujidae			
Cryptolestes ferrugineus (Stephens)	E, L, P, T	WC	Bishop 1959
	L, P	WC	Rilett 1949
	E, L, P, T	W+	Smith 1965
Cryptolestes pusillus (Schonherr)	E, L, P	W+	Ashby 1961
	E, L, P, T	WC	Bishop 1959
	E, L, P, T	WF	Currie 1967
	E, L, P, T	WF	Davies 1949
	T	W, WF, C	Williams 1954
Cryptolestes turcicus (Grouvelle)	E	WC	Bishop 1959
	E	WF	Lefkovitch 1962
Oryzaephilus surinamensis (L.)	T	O+	Arbogast 1976
	E, L, P, T	O+	Curtis 1974
	L	WF	Hafez & Wakid 1967
	L	WF	Howe 1956a
	E, L, P, T	W+	Komson & Stewart 1968
	E, L, P, T	OR	Lergenmueller 1958
	E, L, P, T	W+	Nigam et al. 1969
	E, L, P, T	OR	Thomas 1940
Curculionidae			
Sitophilus oryzae (L.)	E	W	Birch 1944
	E, T	W	Birch 1945
	E	W	Birch & Snowball 1945
	T	W, C, R	Kiritani 1965
	T	W	Reddy 1950
	E, T	W	Sharifi & Mills 1971
Dermestidae			
Trogoderma inclusum LeConte	E	MA	Hadaway 1956
	E	BR	Strong 1975
Tenebrionidae			
Tribolium castaneum (Herbst)	E, L, P	W+	Gray 1948
	E, L, P, T	WF	Howe 1956b
	E, L, P, T	W+	Kennington 1953
	L	CC, W+	LeCato & Flaherty 1973
	E, L, P, T	W+	Park & Frank 1948
	T	Ml	Roorda et al. 1982
	T	W+	Soliman & Lints 1982
	E, L, P, T	WF	Uniyal et al. 1972
	T	W	White 1982
Tribolium confusum Duval	E	WF	Al-Rawy 1958
	E, L, P, T	WF	Brindley 1930
	E, L, P, T	WF	Chapman & Baird 1934
	E, L, P	W+	Gray 1948
	E, L, P	WF	Hardman 1976
	E, L, P, T	WF	Holdaway 1932
	E, L, P, T	WF	Howe 1960
	E, L, P, T	W+	Kennington 1953
	T	B	Lamb & Loschiavo 1981
	E	WF	Lin et al. 1954
	E, L, P, T	W+	Park & Frank 1948
	E, L, P, T	WF	Stanley 1946

[a] The egg, larval, pupal, and total developmental times are indicated by E, L, P, and T, respectively.
[b] Diets included whole wheat (W), cracked wheat (WC), wheat flour (WF), wheat flour plus yeast, other fungi, oats, freeze-killed egg or adult moths or wheat germ (W+), rolled oats (OR), rolled oats plus yeast (O+), corn (C), cracked corn (CC), Brewer's malt (MA), millet (Ml), barley (B), rolled barley (BR), and rice (R).

Results and Discussion

The relationship between temperature and developmental times of different stages and species of stored-product insects often found together in the same stored-grain environment was initially modeled using two types of regression equations. Parameters for one of these equations are listed in Table 2. The nonlinear model consistently fit the

Table 2. Parameters for equation describing relationship between temperature and development time (days) for 9 species of stored-product Coleoptera

Species	Stage	Moisture	*N*	RHO25	HA	HH	TH	r^2
C. turcicus	Egg	High	12	0.674	40,014	39,341	294.2	0.9969
O. surinamensis	Egg	High	15	0.552	37,492	34,088	294.5	0.9442
S. oryzae	Egg	High	9	0.333	30,611	52,961	301.3	0.9949
T. confusum	Egg	High	31	0.274	40,062	44,426	297.2	0.9989
C. ferrugineus, C. pusillus, T. castaneum[a]	Egg	High	38	0.187	25,739	40,926	305.2	0.9640
R. dominica	Egg	High	13	0.182	40,271	41,848	299.0	0.9977
T. castaneum, T. confusum[b]	Pupa	High	37	0.141	34,661	37,073	302.1	0.9575
O. surinamensis	Pupa	High	14	0.127	26,192	43,003	306.5	0.9916
C. ferrugineus, C. pusillus, R. dominica[c]	Pupa	High	29	0.124	19,134	60,708	311.4	0.9551
T. inclusum	Egg	High	7	0.110	16,773	79,859	311.9	0.9989
C. ferrugineus, T. castaneum, T. confusum[d]	Larva	High	43	0.088	60,047	60,191	296.8	0.9554
R. dominica	Larva	High	4	0.052	59,499	58,739	297.1	0.9655
C. ferrugineus	Total	High	8	0.050	41,578	42,052	298.7	0.9774
T. castaneum	Larva	Low	7	0.049	64,895	63,734	297.6	0.9975
O. surinamensis	Larva	High	13	0.045	16,469	78,169	309.3	0.8876
T. confusum	Larva	Low	9	0.034	36,334	53,369	302.2	0.9759
C. pusillus	Larva	High	9	0.031	12,701	55,742	314.3	0.9502
O. surinamensis	Larva	Low	7	0.031	11,996	214,954	309.3	0.8959
S. oryzae	Total	High	8	0.029	13,915	57,050	308.6	0.9631
O. surinamensis	Total	High	12	0.028	20,324	71,719	308.7	0.9823
T. castaneum, T. confusum[e]	Total	High	27	0.023	14,739	77,851	311.9	0.7747
C. pusillus	Total	High	9	0.022	10,814	117,859	313.5	0.9607
O. surinamensis	Total	Low	4	0.022	20,028	525,140	309.0	0.9823
T. castaneum, T. confusum[f]	Total	Low	15	0.020	7,339	617,007	311.3	0.7750
C. ferrugineus	Larva	Low	3	0.019	23,372	65,217	307.7	—
C. ferrugineus	Total	Low	3	0.018	24,656	57,450	307.0	—
R. dominica	Total	High	4	0.017	11,172	952,361	309.4	0.9982

[a] Equations for these three species were not significantly different with the model comparison procedure ($F = 1.71$; df = 8, 26; $P > 0.1$).
[b] Equations for these two species were not significantly different with the model comparison procedure ($F = 1.44$; df = 4, 29; $P = 0.25$).
[c] Equations for these three species were not significantly different with the model comparison procedure ($F = 0.43$; df = 8, 17; $P > 0.25$).
[d] Equations for these three species were not significantly different with the model comparison procedure ($F = 1.23$; df = 8, 31; $P > 0.25$).
[e] Equations for these two species were not significantly different with the model comparison procedure ($F = 0.43$; df = 4, 19; $P > 0.25$).
[f] Equations for these two species were not significantly different with the model comparison procedure ($F = 0.97$; df = 4, 7; $P > 0.25$).

data better than the polynomial model and was used for the analyses. Typical differences between the two models are shown for *Tribolium confusum* Duval in Fig. 1. Note that as temperatures increased, the polynomial model alternated twice between under- and overestimating developmental times, whereas the nonlinear model predicted more accurately the developmental times over the entire range of temperatures. A single equation is given for more than one species when equations for individual species were not significantly different (Table 2). Combining data for more than one species reduced the number of equations from 36 to 27. In both the egg and larval stages, the data for three species were combined into one equation, and in the pupal stage, the data for two species were described by one equation and the data for three species by another. Thus, fewer equations were required to describe the development of the pupal stage than any other stage. The model parameter RHO25—the developmental rate (1/developmental time) at 25°C—was generally highest for eggs, intermediate for pupae, and lowest for larvae (Table 2).

The predicted and actual mean developmental times with 95% confidence limits are shown for eggs (Fig. 1), larvae (Fig. 2), pupae (Fig. 3), and total development (Fig. 4). Careful study of the graphs reveals many similarities and differences between species or stages of insects too numerous to mention individually. In general, the rate of decrease in developmental time decreased with increasing temperature. However, at high temperatures, the developmental times of some of the stages and species increased again. For example, high temperatures increased the developmental times of *Sitophilus oryzae* (L.) eggs (Fig. 1) and *Oryzaephilus surinamensis* (L.) larvae (Fig. 2). High temperatures also increased larval developmental times for *T. confusum* and *Cryptolestes ferrugineus* (Stephens) (Fig. 2) at low, but not high, moistures. In fact, the tendency for moisture to affect the development of larvae, but not eggs or pupae (Thomas 1940, Howe 1956a,b, 1960), indicates that moisture may be important in altering either the rate of feeding or the efficiency with which feeding larvae can assimilate and convert their diet. Overall, the duration of the larval stage

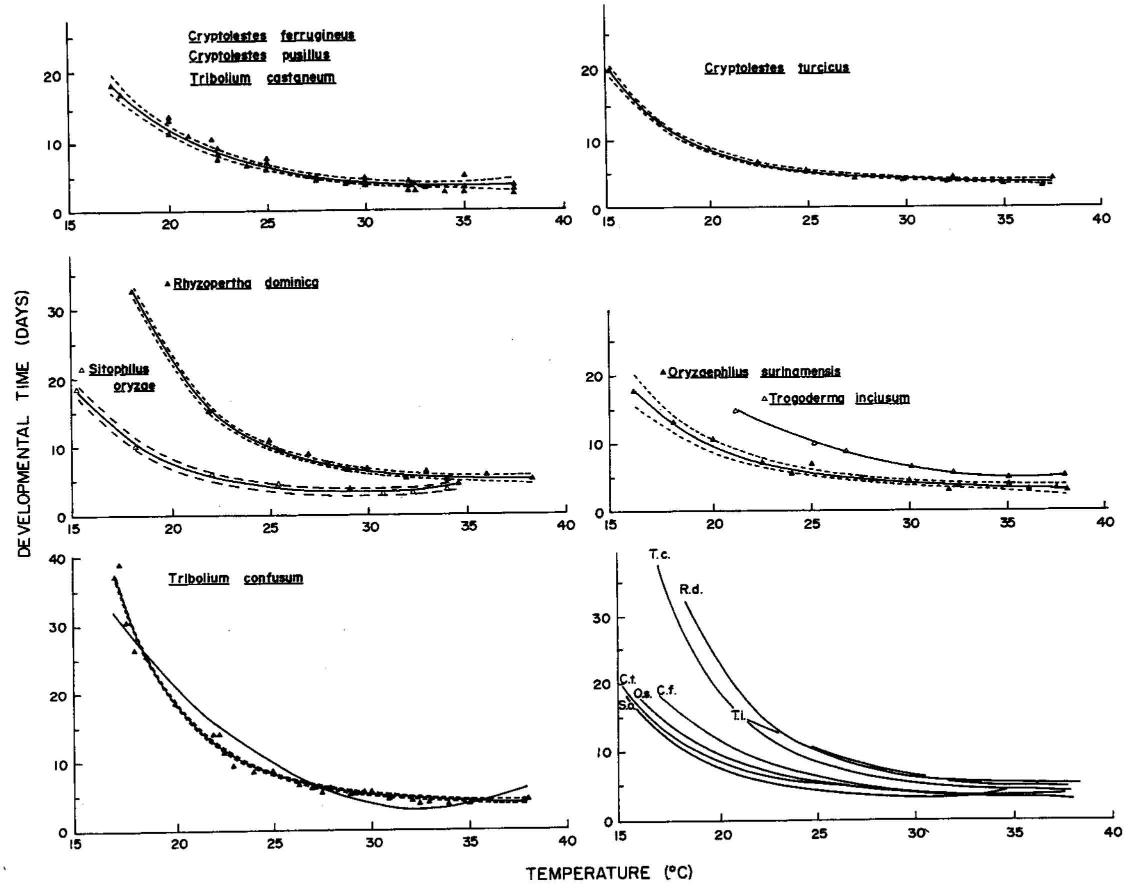

Fig. 1. Predicted (——) and actual (symbols) mean developmental times (d) of the egg stage as a function of temperature (t) for nine species of stored-product Coleoptera with 95% confidence limits (- - -). The polynomial model, $d = 128 - 7.7t + 0.12t^2$, with $r^2 = 0.9559$ and df = 25 is also shown for *T. confusum* without confidence limits. Curves for all species are overlayed in the lower right of the figure and labeled with first letters of genus and species names. The curve representing three species is labeled with C.f.

(Fig. 2) represents a larger proportion of the total developmental time (Fig. 4) than do the other stages (Fig. 1 and 3).

The 95% confidence limits include the variation in developmental times attributable to factors other than temperature and moisture. Diet is probably one of the most important factors contributing to this variation. The extent to which the feeding stage (larvae) has wider confidence limits than the nonfeeding stages (eggs and pupae) is an indication of how much diet contributes to developmental times. At most temperatures considered, the relative importance of factors influencing developmental time would be temperature > moisture > diet. However, near each species' optimal developmental temperature, changes in moisture and diet seem to influence their development more than changes in temperature.

Among different species, a developmental stage represented similar percentages of the total developmental time (Table 3). Averaged over all species, the duration of egg, larval, and pupal stages at 27°C were 15, 66, and 19% of the total developmental times, respectively, at moistures above 12%, and 12, 72, and 15% of total developmental times at moistures below 12%. Similar percentages were found at other temperatures. Lowering the moisture tended to increase the percentage of the total developmental time represented by the larval stage.

Our synthesis based on data from 45 published studies representing over 50 years of work provides an understanding of the relationship between environment and insect development that is important to anyone interested in insects. Many of our conclusions would not have been evident without the extensive quantitative analysis we conducted. This is perhaps the most comprehensive analysis that has been done for such a large group of species commonly found together in the same habitat. From the analysis, one now can see clearly how different environmental factors can have a dominant influence when they are combined in different ways,

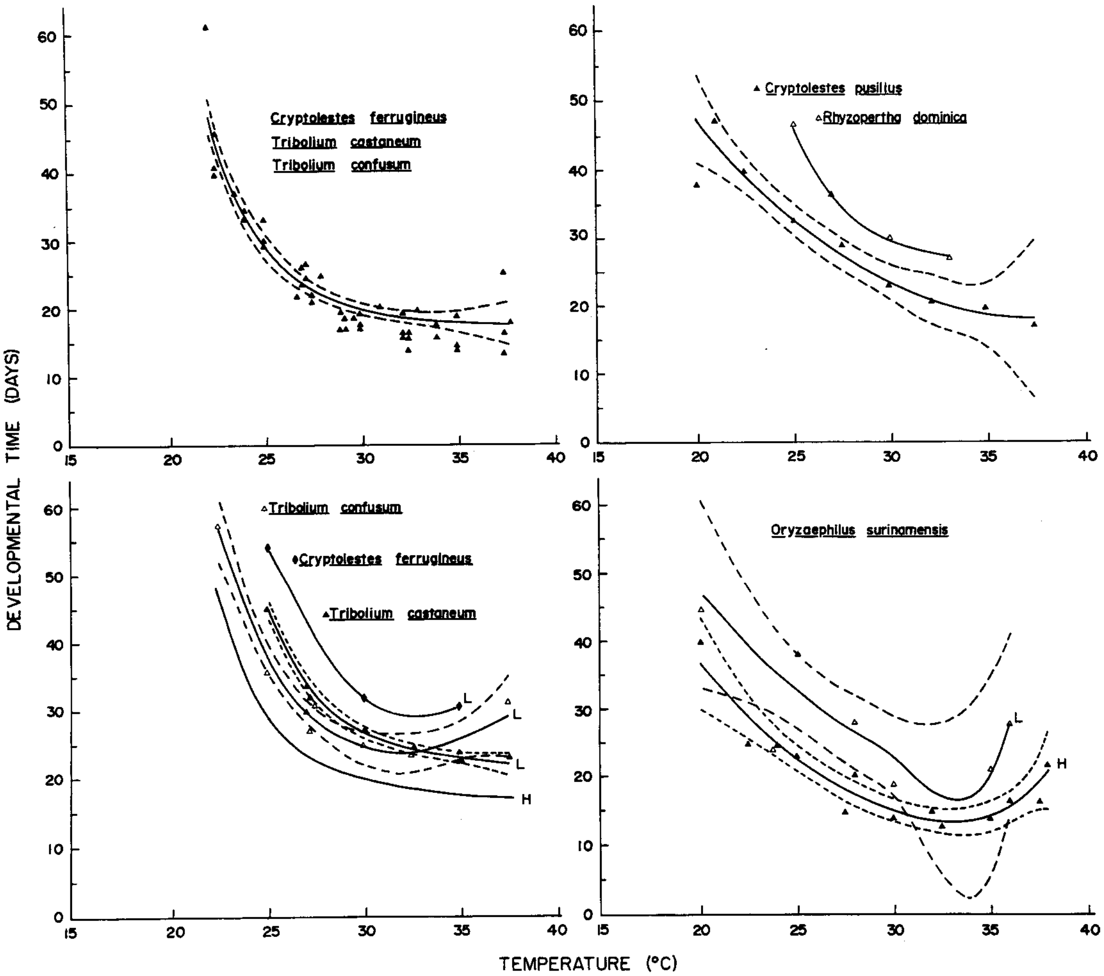

Fig. 2. Predicted (——) and actual (symbols) mean developmental times of the larval stage as a function of temperature and moisture for six species of stored-product Coleoptera with 95% confidence limits (- - -). Data are grouped as moisture >12% (H) or <12% (L).

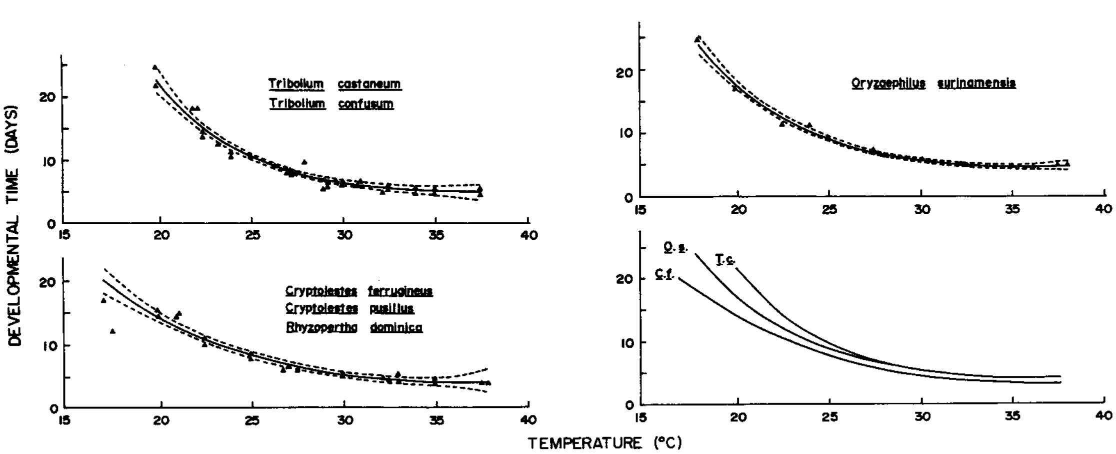

Fig. 3. Predicted (——) and actual (symbols) mean developmental times of the pupal stage as a function of temperature for six species of stored-product Coleoptera with 95% confidence limits (- - -). At the bottom left of figure, curves for all species are overlayed and labeled with the first letters of genus and species names.

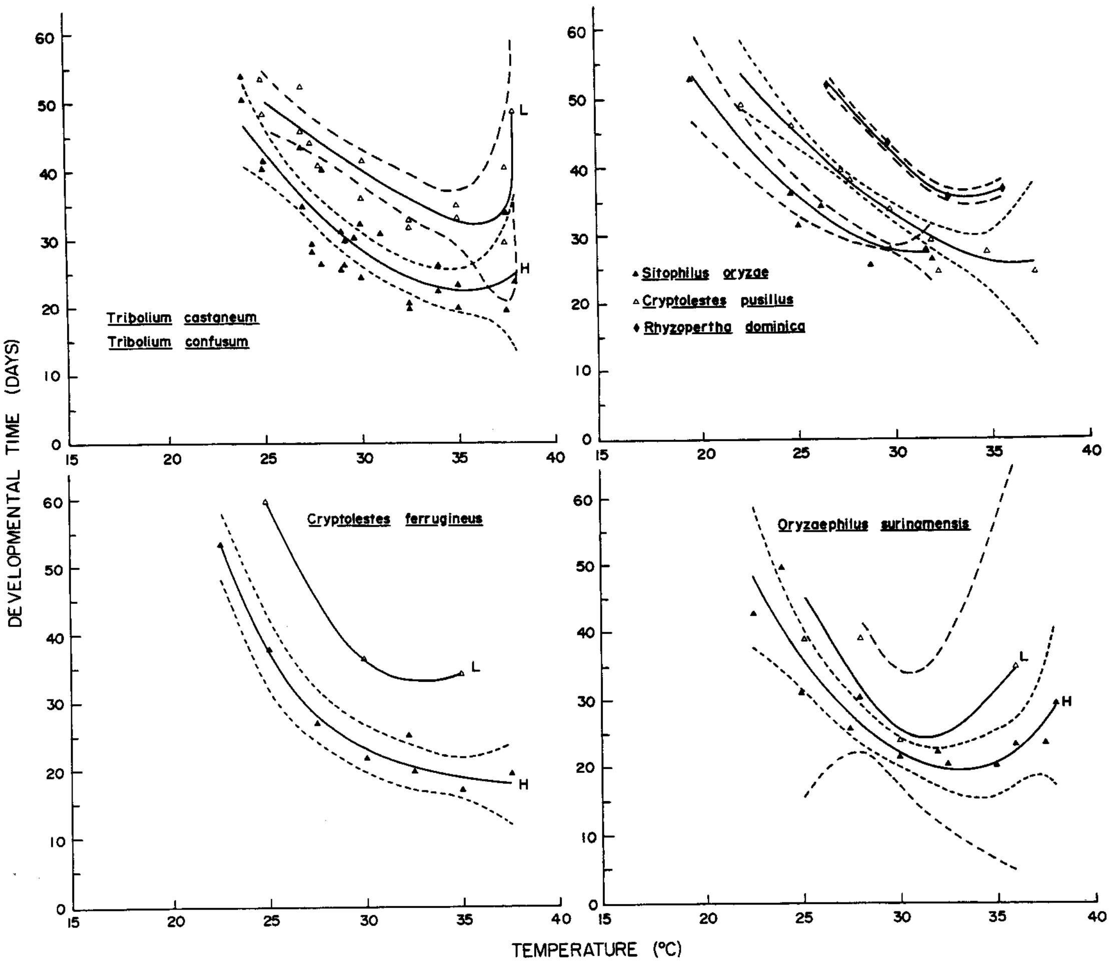

Fig. 4. Predicted (——) and actual (symbols) mean total developmental times as a function of temperature and moisture for seven species of stored-product Coleoptera with 95% confidence limits (- - -). Data are grouped as moisture >12% (H) or <12% (L).

Table 3. Predicted percentage of total developmental time spent in each of three development stages for six species of stored-grain Coleoptera at two moisture levels

Species	Percentage of development in stage					
	Egg		Larval		Pupal	
	A	B	A	B	A	B
			>12% moisture			
T. confusum	17	15–17	61	61–68	21	17–22
R. dominica	16	11–16	72	70–72	12	12–19
C. ferrugineus	16	14–17	65	65–70	19	16–19
O. surinamensis	15	15–16	62	57–65	23	20–28
T. castaneum	15	13–15	66	65–66	19	19–22
C. pusillus	13	13–16	70	65–71	17	15–19
Avg	15		66		19	
			<12% moisture			
T. confusum	15	12–15	67	61–73	18	14–26
O. surinamensis	12	11–13	70	63–73	18	16–24
T. castaneum	11	7–11	74	73–81	15	12–15
C. ferrugineus	11	9–11	78	77–81	11	10–12
Avg	12		72		15	

For each stage, the percentage at 27°C (A) and the range of percentages (B) over a range of temperatures (20, 22, 25, 27, 30, 32, and 35°C) are calculated using the fitted equations in Table 2.

and how the developmental times of different species and stages of insects can differ even in the same environment.

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Received for publication 14 July 1987; accepted 6 November 1987.