Modeling Differences in Insect Developmental Times between Constant and Fluctuating Temperatures

DAVID W. HAGSTRUM AND GEORGE A. MILLIKEN[1]

USDA-ARS, U.S. Grain Marketing Research Laboratory,
Manhattan, Kansas 66502

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ABSTRACT Developmental time data collected at constant temperatures poorly predicted developmental times of red flour beetle, *Tribolium castaneum* (Herbst), and 16 other species at fluctuating temperatures over a broad range of mean temperatures or amplitudes of fluctuating temperatures. Developmental times at constant temperatures tended to be shorter above 25–30°C temperature range and longer below this range, than at fluctuating temperatures with the same means. Differences between developmental times at constant temperatures and those at fluctuating temperatures also tended to increase with the amplitude of fluctuating temperatures. Different methods were compared for predicting insect developmental times at fluctuating temperatures. One method made predictions by integrating constant temperature developmental time data over the 24-h fluctuating temperature cycle. This adjusts for the nonlinear relationship between temperature and developmental time. After making this adjustment, predictions were >40% closer on average to observed developmental times at fluctuating temperatures. With developmental time data collected at fluctuating temperatures, temperature–development equations can be fitted over a broader range of temperatures above and below those favorable for survival of insects at constant temperatures. When these equations were used to do integration, predictions of developmental times at fluctuating temperatures were even better, improving by ≈70%. Improvement may be a result partially of consideration of both the means and amplitudes of fluctuating temperatures in predicting developmental times. These methods provide an alternative to degree-day accumulation method for prediction of developmental times at fluctuating temperatures in the field.

KEY WORDS Insecta, degree-day, developmental threshold, thermoperiod

DAILY TEMPERATURE CYCLES that occur in the field are generally not considered by the degree-day method, which uses data collected at constant temperatures in the laboratory to predict developmental times in the field (Higley et al. 1986). Developmental times of many species are known to differ between constant and fluctuating temperatures with the same mean (Hagstrum & Hagstrum 1970, Hagstrum & Leach 1973). Developmental time data collected at constant temperatures in the laboratory can only be expected to provide rough estimates of developmental times in the field at fluctuating temperatures. Several investigators have shown that differences between developmental times at constant temperatures and those at fluctuating temperatures can be partially resolved by integration of constant temperature developmental times over the fluctuating temperature cycle to predict developmental times at fluctuating temperatures (Eubank et al. 1973, Butler & Watson 1974, Stinner et al. 1974, Ables et al. 1976, Butler et al. 1976, Hilbert & Logan 1983, Dallwitz 1984). This integration adjusts for the nonlinear relationship between temperature and developmental time. Lamb (1961) demonstrated that differences between developmental rates at constant temperatures and those at fluctuating temperatures can also be reduced by using oxygen uptake as a weighting factor. Weighting resulted in a reduced contribution of developmental rates at low temperatures compared with high temperatures to developmental times.

In addition to using developmental time data collected at constant temperatures, the degree-day method also assumes that development does not occur at temperatures below the developmental threshold. The developmental threshold is generally estimated by fitting a linear regression equation to developmental times at several constant temperatures and calculating the temperature at which developmental time equals zero. Messenger & Flitters (1959) proposed that development at temperatures below the low temperature developmental threshold for constant temperatures was one explanation for differences between developmental times at constant temperatures and those at fluctuating temperatures. Eubank et al. (1973) suggested that developmental rates of insects at

[1] Department of Statistics, Kansas State University, Manhattan, Kans. 66506.

Table 1. Species for which duration of developmental time has been determined under constant and fluctuating temperatures

Acarina	
Damaeus onustus Koch	Lebrun 1977
Tetranychus mcdanieli McGregor	Tanigoshi et al. 1976
Coleoptera	
Anthonomus grandis Boheman	Cole & Adkisson 1981
Epilachna varivestis Mulsant	Mellors & Allegro 1984
Sitophilus oryzae (L.)	Hagstrum & Leach 1973
Tribolium confusum Duval	Al Rawy 1958
Trogoderma inclusum (LeConte)	Hagstrum & Leach 1973
Diptera	
Hypoderma lineatum (de Villers)	Pfadt et al. 1975
Hypoderma bovis (L.)	Pfadt et al. 1975
Musca autumnalis De Geer	Moon 1983
Hemiptera	
Anasa tristis De Geer	Fielding & Ruesink 1988
Lygus hesperus Knight	Butler & Watson 1974
Sigara alternata (Say)	Sweeney 1977
Homoptera	
Diuraphis noxia (Mordvilko)	Kieckhefer & Elliott 1989
Empoasca fabae (Harris)	Hogg 1985
Macrosiphum avenae (F.)	Kieckhefer et al. 1989
Rhopalosiphum maidis (Fitch)	Elliott et al. 1988
Rhopalosiphum padi (L.)	Elliott & Kieckhefer 1989
Schizaphis graminum (Rondani)	Walgenbach et al. 1988
Hymenoptera	
Aphidius sonchi Marshall	Liu Shu-sheng & Hughes 1984
Encarsia tricolor (Westwood)	Avilla & Copland 1988
Muscidifurax raptor Girault	Ables et al. 1976
Spalangia endius Walker	Ables et al. 1976
Telenomus podisi Ashmead	Yeargan 1980
Lepidoptera	
Agrotis ipsilon (Hufnagel)	Kaster 1983
Heliothis armiger (Hübner)	Foley 1981
Ostrinia nubilalis (Hübner)	Beck 1982
Pieris brassicae L.	Neumann & Heimbach 1975
Spodoptera litura F.	Miyashita 1971
Trichoplusia ni (Hübner)	Butler et al. 1976
Orthoptera	
Gryllus bimaculatus de Geer	Behrens et al. 1983

fluctuating temperatures may not have a distinct low temperature developmental threshold, but that developmental rates become asymptotically smaller as temperature decreases. Dallwitz (1984) provided a method for calculating hourly developmental rates from developmental times of insects held at fluctuating temperatures. This allowed developmental rates to be determined for temperatures above and below the range favorable for survival of insects at constant temperatures.

Differences between developmental times at constant temperatures and those at fluctuating temperatures with similar means have been reported for >79 species (Hagstrum & Hagstrum 1970, Hagstrum & Leach 1973 and Tables 1 and 2). These studies included 2 acarines, 1 aranean, 10 coleopteran, 16 dipteran, 4 heteropteran, 12 homopteran, 1 neuropteran, 1 thysanopteran, 10 hymenopteran, 18 lepidopteran, and 4 orthopteran species. Nine of these studies were published before 1930, 20 between 1930 and 1960, and the remaining 53 were published after 1960. Most of these studies were on economically important species and many of these studies were aimed at evaluation and improvement of the degree-day accumulation method for prediction of insect developmental times. Fluctuating temperatures can also affect insect behavior (Hagstrum & Tomblin 1973, Beck 1983), but we limit our discussion to their effects on developmental times.

We describe here differences between developmental times of *Tribolium castaneum* Herbst at constant temperatures and those at fluctuating temperatures. The differences observed with this species are compared with those for 16 other species reported in the literature. For three species, two developmental stages are considered. Another objective is to provide a simpler program than that provided by Dallwitz (1984) for calculation of developmental times as a function of temperature from developmental times at fluctuating temperatures. Programs are provided for these calculations and for predicting developmental times at fluctuating temperatures from temperature–development equations. For 17 species, four methods of predicting developmental times at fluctuating temperatures are compared.

Materials and Methods

The developmental times of *T. castaneum* were determined at six constant temperatures and six sinusoidal fluctuating temperatures with the same means. Temperatures were controlled within ±0.1°C and relative humidity was maintained at 70 ± 1%. All six fluctuating temperatures had 24-h periods and ±5°C amplitudes. Developmental times from egg to adult were determined by placing 50 eggs that were less than 12-h-old on 50 g of wheat flour with 5% yeast and recording adult emergence at 12-h intervals. The wheat flour was spread in a thin layer evenly over a plastic box (13 by 13 by 3 cm deep) covered with a screen top for ventilation.

Data for mean development times of 17 different species at constant and fluctuating temperatures were compiled from the published literature listed in Table 2. These studies include those that used at least 5 constant temperatures and 5 fluctuating temperatures with a symmetrical 24-h sinusoidal or square wave cycle. In Table 2, the range of constant temperatures is also compared with that of fluctuating temperatures used for each species and the amplitudes of fluctuating temperatures are shown. The nonlinear model used here is one developed by Sharpe & DeMichele (1977) to describe developmental time at constant temperature,

Table 2. Sources and ranges of data on effects of constant and fluctuating temperatures on the developmental times of different species and stages of insects

Species	Stage	Temperature ranges, °C		Fluctuation amplitude, °C	Source
		Constant	Fluctuating		
Coleoptera					
Tribolium castaneum	Total	22.5–35.0	17.5–40.0	5	present study
T. confusum	Egg	17.5–40.0[a]	15.0–35.0	2.5, 5, 7.5	Mikulski 1936
T. confusum	Pupa	20.0–40.0[a]	17.5–35.0	2.5, 5, 7.5	Mikulski 1936
Diptera					
Anopheles quadrimaculatus	Hatch–adult	19.0–34.6	15.7–32.5	3, 4, 7, 8	Huffaker 1944
Ceratitis capitata	Egg	11.6–35.5	3.0–37.7	2.8, 5.5, 8.3	Messenger & Flitters 1958, 1959
Dacus cucurbitae	Egg	11.4–36.3	2.9–41.8	2.8, 5.5, 8.3	Messenger & Flitters 1958, 1959
D. dorsalis	Egg	12.7–36.3	2.9–39.2	2.8, 5.5, 8.3	Messenger & Flitters 1958, 1959
Drosophila melanogaster	Total	15.0–27.5	12.5–26.0	2.5, 5.0, 7.5	Siddiqui & Barlow 1972
Lucilia cuprina	Pupa	15.0–35.0	−2.6–42.1	8, 9, 10, 11, 12, 13	Dallwitz 1984
Homoptera					
Acyrthosiphon pisum	Total	5.0–25.0	5.0–30.0	2.5, 5.0, 7.5, 10.0	Siddiqui et al. 1973
Circulifer tenellus	Egg	15.5–40.5	4.4–37.7	1, 3, 4, 5, 7, 8, 10, 15, 17	Harries & Douglass 1948
C. tenellus	Nymph	15.5–40.5	4.4–37.7	1, 3, 4, 5, 7, 8, 10, 15, 17	Harries & Douglass 1948
Therioaphis maculata	Total	11.0–35.0	2.5–37.7	5.5	Messenger 1964
Hymenoptera					
Trichogramma pretiosum	Total	15.0–34.0	10.0–37.85	8.35	Butler & Lopez 1980
Lepidoptera					
Anagasta kuhniella	Total	20.0–27.5	12.5–27.5	2.5, 5.0, 7.5	Siddiqui & Barlow 1973
Heliothis zea	Egg	21.0–35.0	10.0–40.5	2.7, 5.5, 11, 13.9	Eubank et al. 1973
Pectinophora gossypiella	Total	18.0–34.0	14.0–30.0	4.0	Welbers 1975
Platynota idaeusalis	Larva–pupa	13.0–27.0	6.0–36.0	3, 4, 6, 8, 9, 12	Rock 1985
Pseudaletia unipuncta	Egg	10.0–31.0	5.0–29.0	4, 7, 8, 12	Guppy 1969
Pseudaletia unipuncta	Larva	10.0–31.0	5.0–29.0	4, 7, 8, 12	Guppy 1969

[a] Because developmental time over only a narrow range of constant temperatures was reported by Mikulski (1936), constant temperature data from several studies as in Hagstrum & Milliken (1988) were used.

Developmental time

$$= \frac{1 + \exp\left[\frac{HH}{1.987}\left(\frac{1}{TH} - \frac{1}{K}\right)\right]}{RHO25\frac{T}{298.15}\exp\left[\frac{HA}{1.987}\left(\frac{1}{298.15} - \frac{1}{K}\right)\right]} = F(T, \theta), \qquad (1)$$

and used by Hagstrum & Milliken (1988) and Wagner et al. (1984) to compare developmental times of different stages and species of insects. In equation (1), K is Kelvin temperature and RH025, HA, HH, and TH are fitted parameters. The statistical analysis system (SAS Institute 1982) was used to calculate these temperature–development regression equations for constant and fluctuating temperatures. Fig. 1 contains a listing of the SAS program used to calculate temperature–development equations from developmental times at fluctuating temperatures. The input variables were mean temperature (MEANTEMP), amplitude of temperature fluctuation above or below the mean (AMPL), and mean developmental time in hours or days (MEANDEVT). Equations were fitted to developmental times at constant temperatures (C), to developmental times at fluctuating temperatures (F), and to weighted developmental times at fluctuating temperatures (W). Developmental times at fluctuating temperatures could be predicted with four methods. Methods 1 and 2 used types C and F equations, respectively, to integrate over fluctuating temperature cycle. Methods 3 and 4 used types C and W equations, respectively, and a developmental weighting factor, WT = (1/DEVTIME)$^{\mathrm{WEIGHT}}$, during integration. For each species and stage, the SAS program in Fig. 1 was run with WEIGHT values ranging from 0.75 to 1.05 in 0.5 increments and the weighting factor that provided the best fit of the temperature–developmental time equation was used.

For fluctuating temperatures, it was necessary to integrate equation (1) over the range of temperature fluctuations by considering the amount of time that insects are exposed to each temperature. The model for a mean temperature ± amplitude of fluctuation is

Developmental time (temperature)

$$= \int_{\mathrm{Temperature-AMPL}}^{\mathrm{Temperature+AMPL}} h(T)F(T, \theta)\, dT + e \qquad (2)$$

```
01 FILENAME FTEMP 'FTEMP.DAT';
02 DATA FTEMP; INFILE FTEMP;
03 INPUT MEANTEMP AMPL MEANDEVT; WEIGHT=0.90;
04 PROC NLIN METHOD=MARQUARDT ITER=250 CONVERGENCE=.00001;
05 PARMS RHO25=0.03 HA=45000 HH=50000 TH=300;
06 DEVTIME=0; DRHO25=0; DHA=0; DHH=0; DTH=0; IWT=0;
07 TP1=MEANTEMP;
08 DO TIME=1 to 24 by 1;
09   TP2=MEANTEMP+AMPL*SIN(TIME*3.14159/12);
10   TMN=(TP1+TP2)/2;
11   TP1=TP2;
12  *IF TIME LT 12 THEN TMN=MEANTEMP+AMPL;
13  *IF TIME=12 or TIME=24 THEN TMN=MEANTEMP;
14  *IF TIME GT 12 AND TIME LT 24 THEN TMN=MEANTEMP-AMPL;
15   XM=1/(TMN+273.15);
16   ARGA=((1/298.15)-XM)*HA/1.987;
17   ARGH=((1/TH)-XM)*HH/1.987;
18   ARRAY ARGS (I) ARGA ARGH;
19   DO OVER ARGS;
20       IF ARGS < -150 THEN ARGS = -150;
21       IF ARGS >= 150 THEN ARGS=150;
22   END;
23   EXPONA=EXP(ARGA);
24   EXPONH=EXP(ARGH);
25   NUMER=1+EXPONH;
26   DENOM=RHO25*EXPONA/(298.15*Xm);
27   YHAT=NUMER/DENOM;
28   WT=1/YHAT**WEIGHT;
29   IWT=IWT+WT;
30   DEVTIME=DEVTIME+YHAT*WT;
31   DRHO25=DRHO25-(YHAT/RHO25)*WT;
32   DHA=DHA-(YHAT*ARGA/HA)*WT;
33   DHH=DHH+(ARGH*EXPONH/(HH*DENOM))*WT;
34   DTH=DTH-(EXPONH*HH/(1.987*TH*TH*DENOM))*WT;
35  *YHAT=DENOM/NUMER;
36  *DEVRATE=DEVRATE+YHAT;
37  *DRHO25=DRHO25+YHAT/RHO25;
38  *DHA=DHA+YHAT*ARGA/HA;
39  *DHH=DHH-ARGH*EXPONH*DENOM/(HH*NUMER**2);
40  *DTH=DTH+YHAT*HH*ARGH/(1.987*TH*TH*NUMER);
41 END;
42 DEVTIME=DEVTIME/IWT;
43 DRHO25=DRHO25/IWT;
44 DHA=DHA/IWT;
45 DHH=DHH/IWT;
46 DTH=DTH/IWT;
47 *DEVTIME=1/(DEVRATE/24);
48 *DRHO25=DRHO25/24;
49 *DHA=DHA/24;
50 *DHH=DHH/24;
51 *DTH=DTH/24;
52 MODEL MEANDEVT=DEVTIME;
53 DER.RHO25=DRHO25;
54 DER.HA=DHA;
55 DER.HH=DHH;
56 DER.TH=DTH;
57 QUIT;
```

Fig. 1. Statistical Analysis Systems program for calculating nonlinear temperature–development equations from developmental times at fluctuating temperatures. See text for definition of variables and explanation of program. The line numbers are provided only for the purpose of explaining the program and should be omitted when entering the program.

where h(T) is a temporal weight function denoting the amount of time that insects are exposed to temperature T, AMPL is the amplitude of fluctuation above and below mean temperature, and e is the error in fitting regression. For example, if the temperature is constant, then h(T) is 1 for that constant temperature. If the insects are subjected to T + AMPL for 12 h and T − AMPL for 12 h, then h(T + AMPL) = 0.5 and h(T − AMPL) = 0.5. For the sinusoidal fluctuating temperature curve, h(T) was approximated by breaking the 24-h period into 24 one-hour intervals and computing the average temperature during each interval as the mean of the temperatures at times t and t + 1. In this case, the temporal weight function is 1/24. Developmental time (temperature) is the sum of development completed during the 24 one-hour increments of the temperature cycle. Because temperature is a function of time, the integral in (2) was reexpressed as an integral over time,

$$\text{Developmental time (time)} = \int_0^{24} F[T\ (\text{time}), \theta]\ d\text{time} + e, \qquad (3)$$

where T (time) is the temperature at a given time interval of the fluctuating temperature cycle. This integral is approximated using Simpson's rule with 1-h increments, where T (time) is the average temperature during that one hour. The development time curve is evaluated at the temperature during this time increment, weighted by 1/24, and the incremental developmental times are accumulated over the 24-h day. In Fig. 1, lines 8–41 in the SAS program numerically integrate developmental times during each iteration of the regression, fitting the predicted developmental times over a 24-h fluctuating temperature cycle. Lines 7–11 calculate hourly temperatures during a daily sinusoidal temperature curve. In line 7, TP1 is set to mean temperature at TIME = 0. In line 9, TP2 is the calculated temperature at TIME + 1. TMN in line 10 is the mean temperature for the interval TIME to TIME + 1. Then, in line 11, the temperature at TIME + 1 becomes the temperature for TIME = 1, TIME is incremented by 1 h in line 8 and a new temperature (TP2) is calculated for TIME = 2 in line 9. Substitution of lines 12–14 for lines 9–11 allows integration of a square wave with 11 h at high temperature, 1 h of declining temperature, 11 h at low temperature, and 1 h of rising temperature. With each pass through the program, the developmental time (DEVTIME) is calculated in lines 15–27, and added to previous accumulated developmental time in line 30. This accumulation of the hourly increments of developmental times over the 24-h period represents the integration process. During the first pass, the regression parameters in line 5 are used, but these are modified in line 52 before each additional pass. Lines 31–34, 37–40, 43–46, 48–51, and 53–56 are derivatives required for the Marquardt method of fitting nonlinear models. During the modeling of developmental times at fluctuating temperatures, the models predicted longer than expected developmental times for low temperatures and shorter than expected developmental times for high temperatures. The developmental weighting factor in line 28, WT = $(1/\text{DEVTIME})^{\text{WEIGHT}}$, was used during the accumulation process to adjust for this bias. Substituting lines 35–40 for lines 27–34, and lines 47–51 for lines 42–46 switches from weighted to unweighted regression. In the unweighted regression, integration of developmental rate (DEVRATE) worked better than integration of developmental

```
01  DATA FTEMP;
02  RHO25=0.03224;
03  HA=43035.43747;
04  HH=52680.78027;
05  TH=302.01935;
06  MEANTEMP=30;
07  AMPL=5;
08  WEIGHT=0.9;
09  DEVTIME=0; IWT=0;
10  TP1=MEANTEMP;
11  DO TIME=1 to 24 by 1;
12     TP2=MEANTEMP+AMPL*SIN(TIME*3.14159/12);
13     TMN=(TP1+TP2)/2;
14     TP1=TP2;
15    *IF TIME LT 12 THEN TMN=MEANTEMP+AMPL;
16    *IF TIME=12 or TIME=24 THEN TMN=MEANTEMP;
17    *IF TIME GT 12 AND TIME LT 24 THEN TMN=MEANTEMP-AMPL;
18     XM=1/(TMN+273.15);
19     ARGA=((1 /298.15)-XM)*HA/1.987;
20     ARGH=((1/TH)-XM)*HH/1.987;
21     EXPONA=EXP(ARGA);
22     EXPONH=EXP(ARGH);
23     NUMER=1+EXPONH;
24     DENOM=RHO25*EXPONA/(298.15*XM);
25     YHAT=NUMER/DENOM;
26     WT=1/YHAT**WEIGHT;
27     IWT=IWT+WT;
28     DEVTIME=DEVTIME+YHAT*WT;
29    *YHAT=DENOM/NUMER;
30    *DEVRATE=DEVRATE+YHAT;
31  END;
32  DEVTIME=DEVTIME/IWT;
33 *DEVTIME=1/(DEVRATE/24);
34  OUTPUT;
35  PROC PRINT; VAR MEANTEMP AMPL DEVTIME;
36  QUIT;
```

Fig. 2. Statistical Analysis Systems program for predicting developmental times at fluctuating temperatures using a symmetrical 24-h sinusoidal or square wave temperature cycle and nonlinear temperature–development equations. Definition of variables is as in Fig. 1. The line numbers are provided only for the purpose of explaining the program and should be omitted when entering the program.

time. The weighting as in Lamb (1961) resulted in a reduced contribution of developmental times at low temperatures compared with high temperatures. Figure 2 shows the program used to calculate predicted developmental times from temperature–development equations. As in Fig. 1, switching lines 15–17 for 11–14 allows integration of square wave instead of sinusoidal wave, and switching lines 29–30 for lines 26–28 and line 33 for 32 gives unweighted instead of weighted predictions. No voucher specimens are available.

Results

Developmental times of *T. castaneum* were significantly longer at constant 22.5, 25, and 27°C temperatures and significantly shorter at constant 32.5 and 35°C temperatures than at fluctuating temperatures with similar means (Table 3). At 30°C, developmental times were the same for constant and fluctuating temperatures. For 17 species, differences between developmental times at constant temperatures and those at fluctuating temperatures are shown in Fig. 3A and 3B as the percent deviation of developmental times at constant temperatures from those at fluctuating temperatures. The percent deviation tended to be less for temperature

Table 3. Developmental times of *Tribolium castaneum* at constant and fluctuating temperatures

Temperature, °C	Constant			Fluctuating			Student's t
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	
22.5	575	66.4	0.18	614	61.6	0.17	19.453
25.0	391	41.9	0.13	342	38.2	0.10	22.617
27.5	171	28.2	0.08	168	27.5	0.09	5.829
30.0	85	24.3	0.11	85	24.3	0.13	0.000
32.5	174	19.7	0.08	342	21.4	0.06	−16.597
35.0	1,041	18.8	0.04	945	20.8	0.04	−35.650

fluctuations of <7°C amplitude (Fig. 3A) than for those of larger amplitudes (Fig. 3B). Over a range of 8–36°C, correlations between percent deviation and temperature were highly significant ($P <$ 0.0001) (see Fig. 3 for r^2 and df). The percent deviation decreased from 8 to 25 or 28°C and then again increased with further increases in temperature beyond 25 or 28°C. Developmental times at constant temperatures were generally poor predictors of developmental times at fluctuating temperatures with the same mean. Better methods of predicting developmental times at fluctuating temperature are needed.

Figures 3C–3F show the relative effectiveness of four other methods for predicting developmental times at fluctuating temperatures. These methods used three types of equations fitted to developmental times at constant temperature (C), to developmental times at fluctuating temperatures (F), and to weighted developmental times at fluctuating temperatures (W). The least-square estimates of the parameters of these regression equations are given in Table 4 for 17 insect species. Use of temperature–development equations for constant temperatures (C) and integration over the fluctuating temperature cycle (method 1, Fig. 3C) resulted in smaller percent deviations of predicted from observed developmental times at fluctuating temperatures than in Fig. 3A or 3B. However, the slope of the best-fit regression of percent deviation on temperature was significantly different than zero. A slope of zero would indicate that method 1 had eliminated the tendency for developmental time data collected at constant temperatures to overestimate (at low temperatures) and underestimate (at high temperatures) the observed developmental times at fluctuating temperatures. Integration with the fluctuating temperature equation (F) (method 2, Fig. 3D) further reduced both the percent deviation and the slope of percent deviation on temperature regression. Use of the constant temperature equations (C) and developmental weighting factor during integration (method 3, Fig. 3E) reduced percent deviation more than method 1, but less than method 2. The improvement with weighting implies that for fluctuating temperatures, the time spent at high temperatures contributes disproportionately more in determining developmental times than time spent at low temperatures. Us-

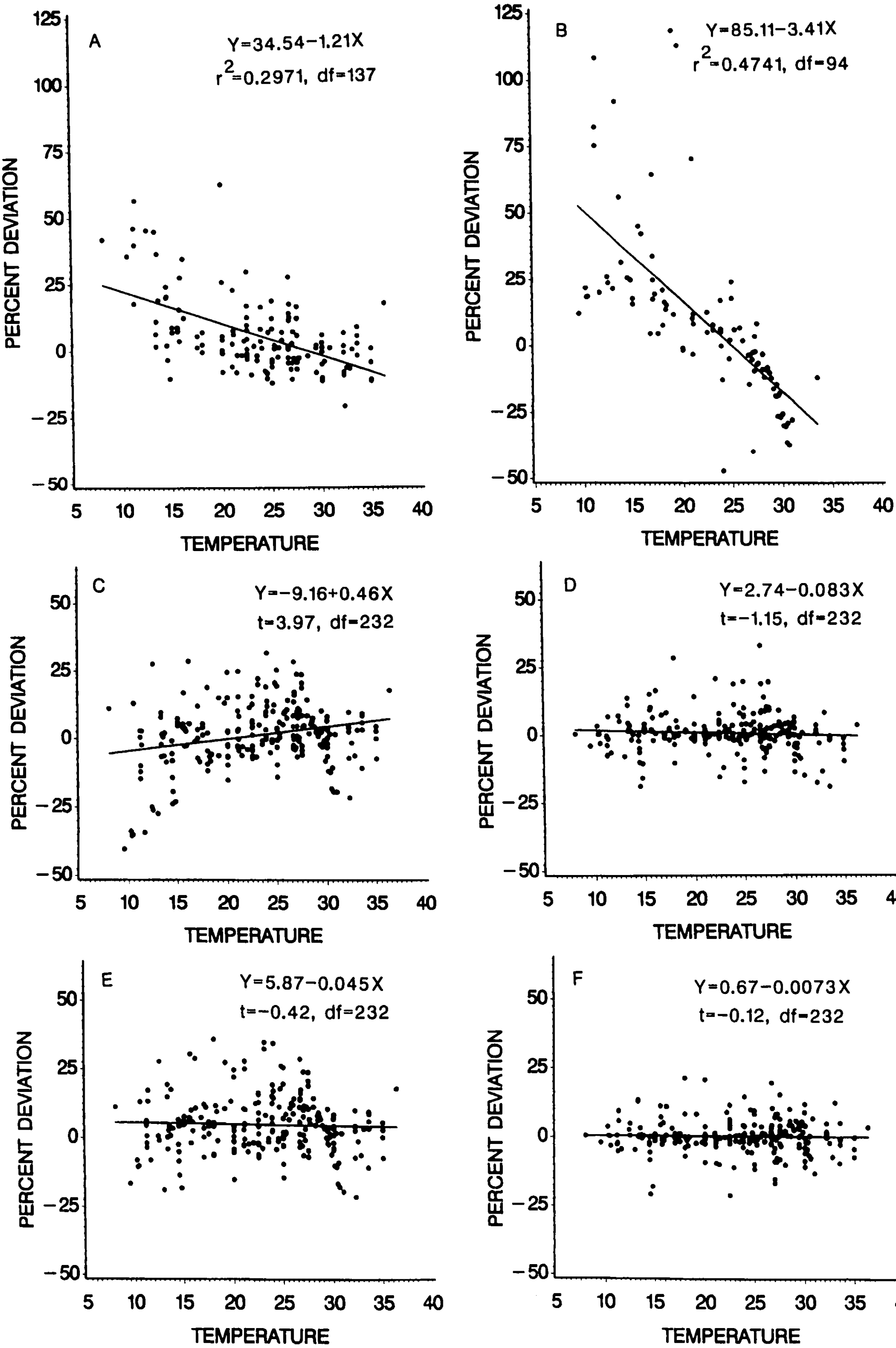

Fig. 3. Percent deviation of developmental times at constant temperatures from those at fluctuating temperatures with the same mean (A–B) or percent deviation of predicted from observed developmental times at fluctuating temperatures (C–F) as a function of temperature. See text for description of the four methods used in C–F for predicting developmental times at fluctuating temperatures. Amplitudes of fluctuations of <7°C (A) and ≥7°C (B) were combined in C–F. The *t* tests are for whether slopes are significantly different from zero in C–F.

Table 4. Parameters for equations describing relationship between temperature (°C) and development times[a] for 17 species of insects at constant temperatures (C), fluctuating temperatures[b] (F), and fluctuating temperatures with weighting factor (W)

Species	Stage	Type	RHO25	HA	HH	TH	WEIGHT	n	r^2
T. castaneum	Total	C	0.0386	46,972	48,780	300.0	—	6	0.9983
		F	0.0354	48,676	50,142	300.3	—	6	0.9842
		W	0.0492	77,225	82,331	298.7	0.90	6	0.9985
T. confusum	Egg	C	0.2472	44,656	45,721	298.3	—	32	0.9882
		F	0.4495	78,564	77,977	296.7	—	13	0.9448
		W	0.1749	42,410	55,218	302.0	1.00	13	0.9143
T. confusum	Pupa	C	0.1138	29,932	42,824	305.1	—	23	0.9684
		F	0.1600	35,999	35,000	300.0	—	10	0.9341
		W	0.1603	28,573	23,913	300.2	1.05	10	0.9417
A. quadrimaculatus	Hatch–adult	C	0.2021	36,591	45,570	298.2	—	7	0.9965
		F	0.4930	37,329	31.982	290.8	—	13	0.8554
		W	0.1975	20,409	14,505	297.9	0.85	13	0.8698
C. capitata	Egg	C	0.3612	62,297	54,212	288.7	—	18	0.9976
		F	0.1749	56,929	53,672	291.4	—	15	0.9775
		W	0.0849	47,248	56,782	295.0	0.90	15	0.9777
D. cucurbitae	Egg	C	0.4303	54,749	54,264	290.3	—	22	0.9914
		F	0.3417	50,310	46,679	289.7	—	17	0.9797
		W	0.1657	42,347	46,170	293.3	0.90	17	0.9823
D. dorsalis	Egg	C	0.0853	41,642	47,249	295.7	—	18	0.9963
		F	0.0515	34,903	50,852	299.4	—	16	0.9918
		W	0.0540	35,336	53,528	299.3	0.95	16	0.9928
D. melanogaster	Total	C	0.1478	25,826	61,557	301.2	—	7	0.9995
		F	0.4491	44,446	49,855	294.1	—	7	0.9708
		W	0.3483	36,725	42,263	294.8	0.90	7	0.9772
L. cuprina	Pupa	C	0.1760	25,194	36,966	302.0	—	8	0.9999
		F	0.1124	28,617	69,692	306.4	—	36	0.9946
		W	0.2828	35,565	60,376	299.7	0.75	36	0.9984
A. pisum	Total	C	0.8979	30,700	28,979	289.0	—	6	0.9996
		F	0.7107	28,195	28,769	290.7	—	10	0.9685
		W	0.2361	17,011	40,052	301.2	1.00	10	0.9966
C. tenellus	Egg	C	0.1494	32,099	37,337	301.0	—	12	0.9993
		F	0.0963	16,636	51,172	312.3	—	17	0.9900
		W	0.1545	16,443	13,857	305.7	0.95	17	0.9489
C. tenellus	Nymph	C	0.0738	38,991	44,283	299.6	—	11	0.9977
		F	0.0543	28,394	39,617	304.4	—	10	0.9900
		W	0.0532	24,976	37,447	305.7	1.00	10	0.9915
T. maculata	Total	C	0.7401	36,519	34,464	290.7	—	25	0.9982
		F	0.6635	35,942	44,485	294.0	—	9	0.9989
		W	0.7078	36,591	44,151	293.6	1.00	9	0.9988
T. pretiosum	Total	C	0.1172	21,907	55,876	305.5	—	10	0.9976
		F	0.0988	19,148	82,022	307.7	—	5	0.9998
		W	0.1035	19,284	80,200	307.3	0.90	5	0.9998
A. kuhniella	Total	C	0.0224	14,463	81,032	305.3	—	7	0.9996
		F	0.1046	34,657	32,290	290.6	—	8	0.9970
		W	0.0368	21,726	26,432	300.0	0.85	8	0.9990
H. zea	Egg	C	0.0124	13,550	67,447	309.8	—	6	0.9909
		F	0.0124	11,441	70,623	311.3	—	14	0.9809
		W	0.0124	10,300	86,080	311.7	0.85	14	0.9772
P. gossypiella	Total	C	0.0604	35,640	37,682	297.3	—	5	0.9996
		F	0.1987	53,994	42,776	290.6	—	5	0.9940
		W	0.0270	23,572	97,147	307.0	0.90	5	0.9998
P. idaeusalis	Larva–pupa	C	0.0975	32,403	49,982	297.6	—	6	0.9994
		F	0.0707	33,523	53,610	300.2	—	12	0.9276
		W	0.0692	31,446	55,902	301.1	0.90	12	0.9510
P. unipuncta	Egg	C	0.3039	23,771	57,951	303.1	—	6	0.9999
		F	0.4592	27,039	25,212	298.3	—	5	0.9936
		W	0.6975	30,482	25,417	293.4	1.00	5	0.9930
P. unipuncta	Larva	C	0.1189	29,772	42,000	297.3	—	6	0.9989
		F	0.1616	24,393	20,637	291.1	—	5	0.9989
		W	0.1000	21,058	21,762	297.8	1.00	5	0.9988

[a] Developmental times of *C. capitata*, *D. cucurbitae*, *D. dorsalis*, and *H. zea* eggs were in hours; otherwise developmental times were in days.

[b] Fluctuating temperature cycles were sinusoidal for *T. castaneum*, *C. capitata*, *D. cucurbitae*, *D. dorsalis*, *L. cuprina*, *T. maculata*, *T. pretiosum*, *H. zea*, and *P. idaeusalis*; and square wave for other species.

Table 5. Comparison of four methods of predicting developmental times of 17 species of insects at fluctuating temperatures (°C)

Species	Stage	n	Average percent deviation of predicted from observed developmental time				
			C vs F[a]	Method 1	Method 2	Method 3	Method 4
T. castaneum	Total	6	7.3	4.7	5.2	4.8	1.7
T. confusum	Egg	13	17.6	15.2	10.7	15.2	10.6
T. confusum	Pupa	10	9.4	5.0	5.3	5.0	5.9
A. quadrimaculatus	Hatch-adult	13	6.9	11.4	4.8	14.8	4.5
C. capitata	Egg	15	27.0	9.5	7.1	12.8	5.0
D. cucurbitae	Egg	17	18.3	10.1	11.5	9.5	7.8
D. dorsalis	Egg	16	27.3	5.2	5.7	5.5	5.9
D. melanogaster	Total	7	3.8	3.7	2.3	3.1	2.2
L. cuprina	Pupa	36	17.7	12.6	3.7	7.7	3.0
A. pisum	Total	10	7.4	4.9	2.7	4.9	0.9
C. tenellus	Egg	17	15.2	6.2	1.7	8.5	4.0
C. tenellus	Nymph	10	17.5	10.9	2.0	10.9	1.9
T. maculata	Total	9	24.2	16.5	2.0	16.5	1.7
T. pretiosum	Total	5	12.9	2.6	0.3	1.6	0.4
A. kuhniella	Total	8	1.8	4.0	0.8	2.7	0.4
H. zea	Egg	14	5.5	3.4	2.3	4.8	2.4
P. gossypiella	Total	5	3.1	7.2	4.7	6.6	0.7
P. idaeusalis	Larva-pupa	12	14.7	13.7	9.9	14.9	9.4
P. unipuncta	Egg	5	22.1	3.4	1.3	3.4	1.5
P. unipuncta	Larva	5	14.1	5.2	0.5	5.2	0.6
Average			13.7	7.8	4.2	7.9	3.5

[a] Average percent deviation between developmental times at constant temperatures and developmental times at fluctuating temperatures with the same mean.

ing weighted fluctuating temperature equations (F) and developmental weighting factor during integration (method 4, Fig. 3F) reduced the percent deviation more than other methods. However, method 4 did not reduce percent deviation much more than method 2, which is much simpler. The weighting used in method 4 was beneficial mainly for *T. castaneum, D. cucurbitae, C. capitata, A. pisum*, and *P. gossypiella*, and actually resulted in less accurate predictions of developmental times at fluctuating temperatures for *C. tenellus* eggs than method 2 (Table 5). Values of the variable WEIGHT in Table 4 that provided the best fit varied from 0.75 for *L. cuprina* pupae to 1.05 for *T. confusum* pupae. However, the values of WEIGHT ranged from only 0.85–1.00 for the other species.

Table 5 compares the average percent deviation for the four methods by species. Absolute deviations are averaged for each species; we ignored whether predicted developmental times were more or less than observed. The largest reduction in percent deviation was for *C. capitata* and the smallest was for *A. quadrimaculatus*. Five species had average percent deviations of <1%. Compared with percent deviations between developmental times at constant temperatures and those at fluctuating temperatures with same mean, methods 1 to 4 resulted in 43.1, 69.3, 42.3, and 74.5% average improvements in predicted developmental times at fluctuating temperatures, respectively.

Figure 4 shows observed and predicted developmental times as a function of temperature for *D. cucurbitae* eggs with 2.8, 5.5, and 8.3°C amplitude fluctuations. Clearly, increasing the amplitude of the fluctuation decreased developmental time of this species below 16°C and increased developmental time above this mean temperature.

Discussion

Developmental times of 17 species differed between constant and fluctuating temperatures, over a broad range of mean temperatures and amplitudes of fluctuating temperatures. Developmental time data collected at constant temperatures in the laboratory thus can only be expected to provide a rough estimate of developmental times in the field at fluctuating temperatures. Developmental times at constant temperatures tended to be shorter at temperatures above 25–30°C and longer at temperatures below this temperature range than those at fluctuating temperatures with same mean. Differences between developmental times at constant temperatures and those at fluctuating temperatures also tended to increase with the amplitude of fluctuating temperatures.

Differences between developmental times at constant temperatures and those at fluctuating temperatures may provide insight into the regulation of insect development by temperature. Integration of developmental times over the 24-h fluctuating temperature cycle adjusts for nonlinearity of temperature–development equations and results in >40% average improvement in predictions of developmental times at fluctuating temperatures. This improvement in predictions with integration may indicate that some insect development occurs at temperatures lower than those at which development can be completed at constant temperatures. There may not be a distinct low temperature de-

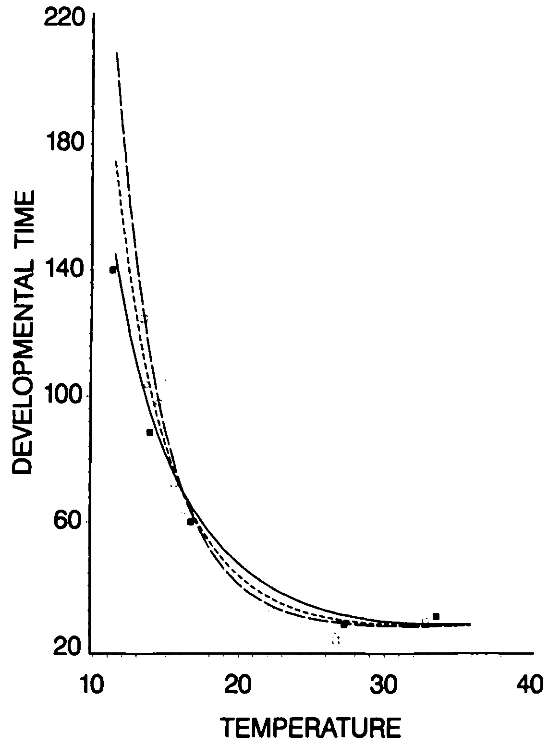

Fig. 4. Predicted (——) and observed developmental times in hours as a function of temperature for *D. cucurbitae* eggs with 2.8 (□— — —□), 5.5 (○- - -○), and 8.3 (■——■) °C amplitude of fluctuation. Data from Messenger & Flitters (1959).

velopmental threshold with fluctuating temperatures, but developmental rates may become asymptotically smaller as temperature decreases. Because developmental time data collected at fluctuating temperatures allows us to fit temperature–development equations over a broader range of temperatures above and below those favorable for survival with constant temperatures, predictions of developmental times at fluctuating temperatures can be improved by ≈70%. Further improvement in predictions with weighting indicates that high temperatures are more important than low temperatures in determining developmental times.

Species differences between developmental times at constant temperatures and those at fluctuating temperatures are partially a function of the ranges of temperatures and amplitudes of fluctuations used in different studies. For species such as *A. quadrimaculatus, D. melanogaster*, and *P. gossypiella*, the ranges of fluctuating temperatures were only 1.2, 1.0, and 0°C wider than those for constant temperatures (Table 2) and observed average percent deviations between developmental times at constant and those at fluctuating temperatures were only 6.9, 3.8, and 3.1, respectively (Table 5). In contrast, the observed percent deviations for *C. capitata, D. cucurbitae, D. dorsalis, L. cuprina, T. maculata*, and *P. idaeusalis* were >14% (Table 5)

```
01 FILENAME FTEMP 'FTEMP.DAT';
02 DATA FTEMP; INFILE FTEMP;
03 INPUT TIME TEMP;
04 TP1=TEMP; TP2=LAG1(TEMP);
05 RHO25=0.03224;
06 HA=43035.43747;
07 HH=52680.78027;
08 TH=302.01935;
09 TMN=(TP1+TP2)/2;
10 XM=1/(TMN+273.15);
11 ARGA=((1 /298.15)-XM)*HA/1.987;
12 ARGH=((1/TH)-XM)*HH/1.987;
13 EXPONA=EXP(ARGA);
14 EXPONH=EXP(ARGH);
15 NUMER=1+EXPONH;
16 DENOM=RHO25*EXPONA/(298.15*Xm);
17 IF STOP LE 1 THEN DO;
18 DEVRATE+(DENOM/NUMER)/24;
19 STOP=DEVRATE;
20 DEVTIME=TIME/24;
21 IF STOP GE 1 THEN OUTPUT; END;
22 PROC MEANS NOPRINT; VAR DEVTIME;
23 OUTPUT OUT=HTEMP MIN=DEVTIME;
24 PROC PRINT NOOBS; VAR DEVTIME;
25 QUIT;
```

Fig. 5. Statistical Analysis Systems program for predicting developmental times at fluctuating temperatures using hourly temperature readings and nonlinear temperature–development equations. Definition of variables as in Fig. 1. The line numbers are provided only for the purpose of explaining the program and should be omitted when entering the program.

as a result of a range of fluctuating temperatures >10°C wider than that for constant temperatures (Table 2). Temperature fluctuations of wide amplitude allowed temperatures as low as −2.6°C and as high as 42°C to be included in these studies.

This paper provides an alternative to the degree-day method for calculating developmental times at fluctuating temperatures, which does not require an estimation of a lower developmental threshold. The program in Fig. 2 allows temperature–development equations to include a third dimension, amplitude of the fluctuations. To most accurately predict developmental time at fluctuating temperatures, both the means and amplitudes of fluctuating temperatures must be considered. Hourly field temperatures might be used instead of sinusoidal or square wave temperature cycle (Fig. 5). The input variables in line 3 were the cumulative time since development began (TIME) and temperature readings taken each hour (TEMP). The developmental rate (DEVRATE) and developmental time (DEVTIME) are calculated in lines 18 and 20 using temperature–development equation (lines 5–16) and the mean temperature (TMN) during each one hour interval. When development is complete and developmental rate (DEVRATE) reaches one, developmental time in days (DEVTIME) is printed out.

The methods presented can predict developmental times at fluctuating temperatures better than the degree-day accumulation method. The improvement of predictions increases as mean temperatures deviate more from the 25–30°C range and as the amplitude of fluctuations increases. Use of temperature–development equations based upon constant temperature data often requires extrapolation beyond fitted data for integration over the fluctuating temperature cycle. Extrapolation is unnecessary when developmental times at fluctuating temperatures are used to fit temperature–development equations, because a wider range of temperatures can be considered, including some that are unsuitable for insect survival at constant temperatures. The methods presented allow both the mean and amplitude of fluctuating temperatures to be considered in predicting developmental times.

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