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TEMPERATURE-DEPENDENT DEVELOPMENT IN CAPITAL-BREEDING LEPIDOPTERA

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ABSTRACT. Temperature-dependent development is described by three variables termed thermal characteristics: the developmental zero temperature, below which no development is assumed to occur; the high cutoff temperature, above which development slows; and the developmental index, a measure of physiological time required for a given phase to develop. Physiological time in this study refers to number of degree-days, units that combine temperature and time. The phase of interest here is the entire larval stage. Degree-days track developmental progress more precisely than calendar days and better alert the observer for optimally timing planned interventions. Thermal characteristics are usually derived from simple Type I regressions fitted to the linear portion of plots of rate of development on rearing temperature, where rate is the reciprocal of duration. Existing thermal characteristics for 131 published datasets are revised here using an improved Type II regression proposed by Ikemoto & Takai (2000). These datasets represent species in 11 families and originated between 1927 and 2007 on six continents. Each dataset consists of ≥4 associated rates and temperatures. Revised developmental zero temperatures ranged from 3.9 to 16.0. They varied directly with mean annual temperatures at localities of dataset origin, forming a continuum of low to high values between cool and warm climates. Among other relations, the mathematical product of voltinism × the natural logarithm (ln) of developmental index, which encompasses multivoltinism, varied directly with developmental zeros. In 91% of datasets, number of degree-days for the larval phase calculated using official mean daily air temperatures agreed within ±2 calendar days with those using constant laboratory temperatures. Official temperatures were summarized from records at 18 mid-temperate North American weather stations. Thermal characteristics are found to be adapted to climatic regimes, and local weather-station temperatures are usually suitable for degree-day summations.

Additional key words: Degree-day, day-degree, temperature summation, developmental zero, developmental index.

Differing air temperature patterns among growth seasons create differing thermal environments for most insects and other ectotherms. Development may be accelerated if weather is warmer than average, or slowed if cooler. This often makes calendar dates unreliable for forecasting temperature-dependent events such as egg hatching, pupation, or eclosion. A physiological rather than calendrical time scale may offer a more precise and more useful basis for prediction. Degree-days (or day-degrees) combine temperature with calendar days to provide such a time scale. Summing degree-days measures physiological time and tracks temperature-dependent development. It alerts the observer when pest management treatments or other time-sensitive actions are required. It is useful also in other contexts, such as risk analysis, in which thermal characteristics may indicate how successful a pest might prove where it does not yet occur (Gould et al. 2005). The method provides no formal technique for making predictions in advance, but improvisation enables short-range forecasting once a summation has begun.

The present report focuses on the larval stage of development, when capital breeding lepidopterans, including most lepidopteran pests, accumulate the bulk of their reproductive resources (Boggs 1992; Miller 1996; Tammaru & Haukioja 1996). It is typically the longest developmental stage (Honék & Kocourek 1990) and therefore the stage most representative of temperature-dependent development. 'Development' refers to progress through set phases of life history, while 'growth' refers to increase in biomass.

Practical application of temperature-dependent development consists of summing degree-days in the field to track and predict developmental mileposts in time or life history. Typical mileposts are egg hatching, adult eclosion, or completion of larval development as in this study. A beginning milepost also might be an arbitrary calendar date. Where it is not possible to introduce a temperature sensor into the larval habitat, official temperatures recorded at a nearby weather station may be substituted. Actually, weather station temperatures can be used in most situations, as in this study.

Three thermal characteristics describe temperature-dependent development: L, the developmental zero temperature, often termed lower developmental threshold, below which no development is assumed to occur; H, the high cutoff temperature above which development slows; and K, the developmental index or physiological time in accumulated degree-days required to complete a particular phase of development. H, usually >30º C, proved least important in this study because such temperatures did not occur for significant periods at mid-temperate North American weather stations used in this study. 'Lower developmental threshold' is somewhat misleading, as discussed further on.

Although sometimes referred to in the literature as constants and coefficients, thermal characteristics are not fixed for a species, but often differ from population to population and are subject to local adaptation and evolution, as shown here. Ikemoto & Takai (2000) pointed out that published thermal characteristics for many species, including capital-breeding lepidopterans, may be suspect because of problems with conventional linear derivation procedure. These problems are detailed further on. Before thermal characteristics were deployed in this study, a major effort was made to revise them for as many capital-breeding lepidopterans as feasible using a derivation proposed by Ikemoto & Takai (2000), here termed the improved linear model procedure.

Surprisingly, degree-day summation from field temperatures, although basic to tracking field development, has been inadequately investigated. Published thermal characteristics for only 22% of the 108 species here were accompanied by field-testing or other evaluation. Moreover, most of the reported testing was based on existing, unrevised thermal characteristics. Field-testing is essential because of the potential for summation errors posed by certain effects to be described.

The three aims of this report are (1) to revise existing thermal characteristics as already noted; (2) to examine how revised thermal characteristics relate to climate, geography, voltinism, and to one another; and (3) to ascertain how well phase durations based on fluctuating field temperatures agree with those based on constant laboratory temperatures. The report also touches on how rate of degree-day accumulation might affect fecundity, a fitness factor influenced by temperature (Miller 2005).

Notable overviews of temperature-dependent development are given by Uvarov (1931), Allee et al. (1949), Andrewartha & Birch (1954), Wilson & Barnett (1983), Wagner et al. (1984), Ratte (1984), Delahaut (2003), Régnière & Logan (2003), and Herms (2007). Taylor (1981) specifically treats physiological time. Baskerville & Emin (1969), Pruess (1983), Higley et al. (1986), and Worner (1992) deal with issues of methodology, and Wang (1960) and Baker (1980) offer methodological critiques. Additional reports are cited later in relevant contexts.

MATERIALS AND METHODS

Degree-day terminology and computation. Symbols and definitions used are shown in Table 1. All temperatures in this report refer to °C. By definition, one DD accumulates when T for all 24 h of one calendar day is one degree higher than L. During any calendar day, number of DDs accumulated is T - L, assuming T > L. Thus, if T for a calendar day averages 20°, and L is 12°, then 20 minus 12, or 8 DDs, accumulate that day. For n calendar days, number of DDs accumulate as

$$\sum_{i=1}^{n} (T_i - L)$$

The progression of natural temperatures through daily lows and highs resembles a sine wave, and a sine function (Allen 1976) is built into the summation algorithm used here, as described later. Hourly temperatures can be used, but the 24-h calendar day used here is most common. In the absence of an accurately estimated developmental zero temperature, an arbitrary approximation or 'base temperature' is used.

When DDs have accumulated in field summation to an ending milepost, that number is designated W, the field version of the laboratory developmental index, K (Table 1). Ideally, median-to-median or mean-to-mean individuals in the population should be used when developmental intervals defined by phenological mileposts are attained. Because plant development is also temperature dependent, phenological events such as bud-break or blooming in particular plants can serve as DD indicators if they correspond to mileposts in insect development (Herms 2007).

Thermal characteristics are components of phenological models, which range from the conventional linear type with two parameters to more complex nonlinear, multiparameter types. Linear and nonlinear refer to the straight or curved shape of the line that relates developmental rate to temperature. This study used only linear models—conventional or improved—fitted to datasets with ≥4 successive graphed points that formed a reasonably straight line. Most published models for capital-breeding lepidopterans are linear and of the conventional simple Model I regression type. The conventional model, which is the source of 'unrevised' thermal characteristics, is discussed more fully further on.

Phenological models are based on experimental data obtained when D is recorded for an insect at different Ts, usually in the laboratory, but in the field if the subject insect is not amenable to laboratory rearing. Laboratory Ts are usually constant, and were so in nearly all datasets here, but the methodology can accommodate laboratory Ts programmed to fluctuate diurnally . In the event that a field rather than a laboratory study is used to create a model, mean temperatures during the phase of interest in different years or locations, or in manipulated habitats, serve as Ts (Legg et al. 1998b). One dataset here for *Pthorimaea operculella* (Saunders) (Gelechiidae) is of this type (Langford & Cory 1932). The rest used constant laboratory Ts.

In laboratory or field, other environmental factors may influence thermal characteristics, as shown later, and should be monitored or controlled.

TABLE 1. Symbols and definitions used in this study.

DD, degree-day, a measure of physiological time; the mathematical product of units of calendar time x degrees of rearing temperature; further defined in text.

T, temperature in degrees Celsius.

D, duration of larval development—egg hatching to pupation in this study—in median number of calendar days whenever possible as recommended by Legg et al. (2003), otherwise in mean number of calendar days.

R, rate of larval development, 1/D, the fraction of total larval development occurring in one calendar day.

L, 'unrevised' zero developmental temperature; temperature below which, based on the conventional model, no development is assumed to occur; further defined in the text.

L', revised L based on Reduced Major Axis (RMA) Type II regression of the improved linear model; further defined in text.

K, 'unrevised' developmental index, the total number of DDs accumulated during the larval phase usually at constant laboratory temperatures based on the conventional model.

K', revised developmental index, the total number of DDs accumulated usually at constant laboratory temperatures based on the improved linear model.

DA, mean number of DDs accumulating in the field per calendar day; further defined in text.

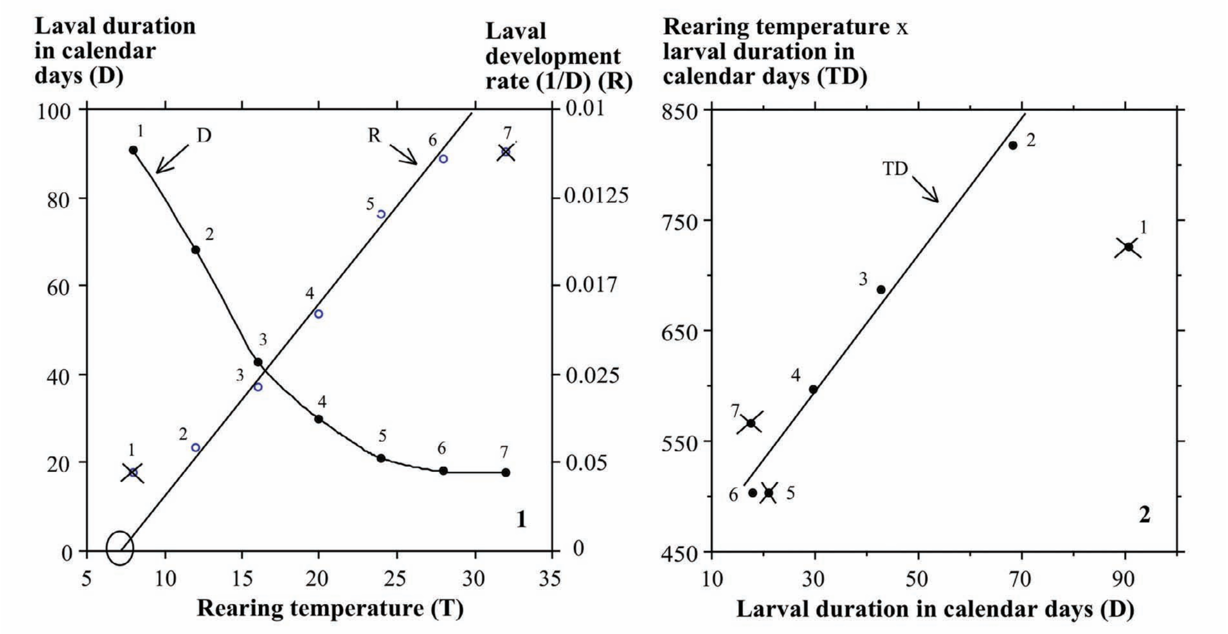
W, field developmental index, the total number of DDs accumulated based on official weather-station temperatures; mathematical product of DA x D; field equivalent of K'; further defined in text.

Revision of thermal characteristics. An extensive search yielded 223 published datasets that met the following criteria for admission to the study: ≥4 associated D and T values for larval cohorts reared throughout development at the same Ts, same photoperiods, and on the same food. If results were reported by gender, female data were used here; otherwise the combined sexes were used. Humidities were generally uncontrolled. Datasets for which nonlinear models originally had been fitted were admitted if they otherwise met the above criteria. In several datasets multiple observations of D at one T were averaged to obtain a single value to avoid pseudoreplication. The assembled datasets were subjected to additional requirements such as more stringent testing for linearity, as described later. Ultimately, L' and K' were calculated for 131 of the original 223 datasets using the improved linear model of Ikemoto & Takai (2000) (Table 2). Species nomenclature, although updated in a few cases, generally follows that used in dataset sources.

Conventional model. This model begins with the hyperbola, or reverse-J shaped curve, formed when D is plotted on T. It is illustrated here for *Mamestra configurata* Walker (Noctuidae) (Fig. 1: curve D). Next, the reciprocal of D, 1/D, is plotted on T (Fig. 1: line R), an operation that usually transforms at least part of any hyperbola into a straight line (Sokal & Rohlf 1981; Ikemoto & Takai 2000). Finally, simple Model I regression—$y = a + bx$—is fitted to the straight-line portion of the R–T plot (Fig. 1). The temperature where the reverse-extrapolated regression line intersects the T axis is taken as L (Fig. 1: circle on horizontal axis). L can be estimated visually, or more exactly from model parameters as $-a/b$. It should be noted for future discussion that L is technically a theoretical value; in practice it cannot be estimated experimentally. The reciprocal $1/b$ is taken as K. For *Mamestra configurata*, the conventional model gives L as 6.8° and K as 376 (Table 2: No. 36). Unrevised thermal characteristics were recomputed using the conventional model and included in Table 2 for reference. They sometimes diverged from those in original sources because of different rounding, differing interpretations of linearity, or other reasons. Methods of estimating L and K are discussed by Arnold (1959), Pruess (1983), Legg et al. (1998b), and others.

Requisite linearity is based on inspection of the graphed R–T data. Data points are often too scanty for useful statistical evaluation of linearity. Data interpreted as linear in conventional model procedure may not be so interpreted in improved linear model procedure (Figs. 1, 2). As discussed in the next section, the range of effective developmental temperatures usually is defined as those from L to H, and not based on temperatures selected to define it. Curiously, the temperature of fastest development—illustrated here by point No. 6 in Fig. 1—is sometimes wrongly termed 'optimum temperature' (Martin & Huey 2008). Points that depart from linearity are deleted before regression computation.

Problems with the conventional model alluded to earlier are that (1) linear portions of plotted data can be difficult to delimit; (2) variances are not constant along the regression line so that lower and upper y-values are disproportionately weighted; and (3) x is untenably



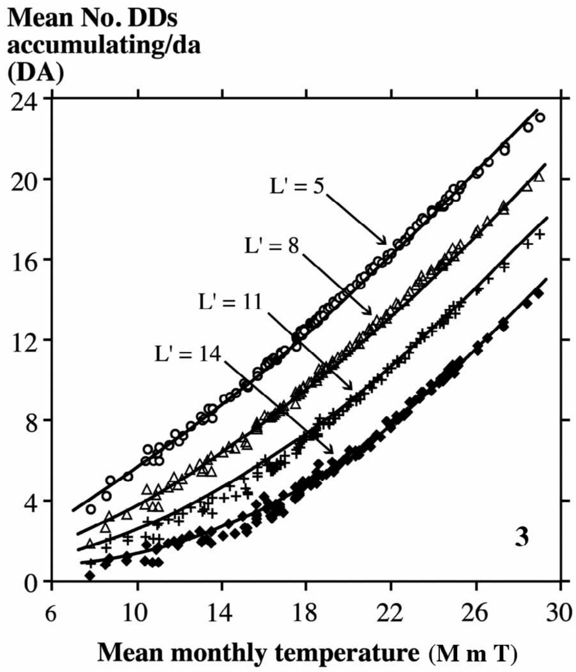
FIGS. 1–2. **1.** Hyperbolic relation of larval developmental duration, D, to rearing temperature, T, in *Mamestra configurata* Walker (Noctuidae), the line fitted by connecting data points, and its conversion to a conventional phenological model. The model relates larval developmental rate, R, to T, as fitted by Model I regression, R = 0.000265 T - 0.018; r2 = 0.99. Data points numbered in order of increasing temperature. Points 1 and 7 (shown crossed out) were omitted from regression because they departed from linearity. Circled intersection of regression line and bottom horizontal axis defines zero developmental temperature, L'. Data of Bailey (1976). **2.** Improved linear phenological model for *M. configurata* relating the mathematical product of rearing temperature, T, x larval developmental duration, D (TD) to larval duration, D. Line fitted by Model II regression, TD = 405.1 + 6.19 D; r2 = 0.99. Data points numbered in order of increasing temperature, which is reversed from the conventional model. Points 1, 5, and 7 (shown crossed out) were omitted from regression because they departed from linearity. Data of Bailey (1976).

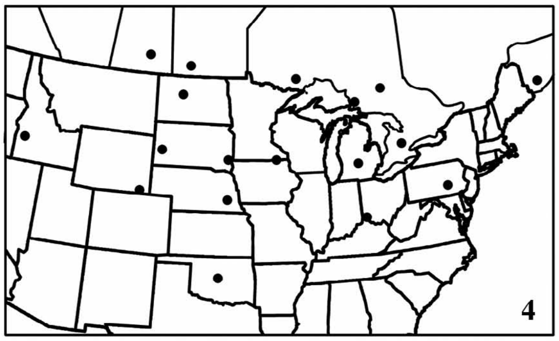
treated as error-free, which may depress the slope parameter b. The latter two problems result from usual assumptions of Model I regression (Sokal & Rohlf 1981). Improved linear model procedure addresses these problems, as discussed below.

Improved linear model. The form of this model is the same as that of the conventional model, y = a + bx, but assumptions are those of Model II reduced major axis (RMA) regression in which both y and x are treated as subject to error instead of y alone (Sokal & Rohlf 1981; Ikemoto & Takai 2000). The same experimental values of D and T are used to create the model, but y becomes the mathematical product T × D instead of R (1/D), and x becomes D instead of T (Fig. 2). The order of plotted data points relative to T is reversed from that of the conventional model (Figs. 1, 2). Linearity is again ascertained subjectively from the graphed (T × D)–D data, but because of model linearizing, departures stand out and a more stringent test of linearity results. Points excluded due to nonlinearity were mostly in the tails of distributions. The 'confirmed effective temperature range' as defined here and displayed in Table 2 does not begin with L' and end with H. It is instead defined by the Ts of the highest and lowest values of T × D on the straight line, 818.4 and 504.0 (Fig. 2), which yield a range of 12–28°. Although not ideal, this definition seems more realistic because little development occurs in the several degrees between L' and the beginning of the straight line.

Although linear in form, Model II RMA regression was computed by nonlinear methods (Fleury 1991). First, a Model I regression of T × D on D was fitted, and its parameters a and b then used as start values for iterative computation of final parameter values by means of the nonlinear SYSTAT option (SYSTAT 1992). The final a becomes K', and the final b becomes L'. For *Mamestra configurata*, L' is 6.19° (rounded to 6.2) and K' is 404 (Table 2: No.36). Not surprisingly, these values differ from their counterparts of 6.8° and 376 obtained with the conventional model. In this report, some variables, notably K', are sometimes transformed to natural logarithms (ln) before analysis to improve linearity. Thus far, it seems that only Liu et al. (2002) have used the improved linear model for a capital-breeding lepidopteran.

Summation with official temperatures. Field developmental index, W, was obtained as the mathematical product DA × D, where DA is mean





FIGS. 3–4. **3.** Expected number of DDs per calendar day, DA, at mean monthly field temperatures, MmT, for four developmental zero temperatures, L' 5-14, at the 18 weather stations used in this study. Regressions for different L's follow: DA L' 5 = 0.315 T + 0.0.0297 T^2 - 0.000444 T^3- 0.12. For L' 8, 11, and 14, corresponding coefficients are, respectively, - 0.164, 0.0475, - 0.000659T, 1.17; 3.20, - 0.646, 0.0623, - 0.000795; and - 0.771, 0.0559, - 0.000568, 3.87. All r^2 values >0.99. Further explanation in text. **4.** Map locations of the 18 North American weather stations used in this study. Station names and details are given in Appendix 1.

number of DDs accumulating/day at a given mean monthly field temperature, and D is the median developmental duration at constant T values in the laboratory (Table 1). Thus W is equivalent to K' except that the Ts underlying W are weather-station daily minima and maxima. Number of calendar days represented by W and K' were compared, and how closely the number based on W agreed with that based on K' (Table 2) indicates the usefulness of W.

To readily estimate W for the field-based part of the study, Table 3 was prepared to provide DAs necessary for the DA × D computation. This table gives DAs for mean field Ts of 8–31° in 0.5° increments, and for L' of 5.0, 8.0, 11.0, and 14.0°. Only datasets with values of T and L' in the tabulated ranges were used to prepare Table 3, a restriction that excluded 37 datasets with uncommonly large or small values of L' or T (Table 2: Nos. 3, 14-17, 19, 22, 24-29, 43-45, 47-49, 54-56, 79, 80, 82-86, 93, 99, 100, 105-107, 109, 111, and 113). Also excluded were datasets for stored-product capital breeders (Table 2: Nos. 118–124), as W was not estimated for them because they typically develop under artificial storage rather than natural conditions. Table 3 provided expected DAs not only for this study but also for anticipated future studies. Its use often required linear interpolation to obtain a desired DA because input values of T and L' were often intermediate between tabulated values.

Table 3 was generated in four steps as follows: (1) Accumulated DDs for each of the four selected months (May–August) of each included year were computed from temperature records of the 18 weather stations using a spreadsheet devised by R. D. Moon, Department of Entomology, University of Minnesota. The selected months encompass the period of most larval development. Spreadsheet inputs were daily temperature maxima (daytime) and minima (nighttime) as well as each of the four L' values. The spreadsheet computed DDs between a specified L' and the sine curve of temperatures for that day (Allen 1976). (2) Resulting number of DDs accumulating above each L' for each month were divided by number of days in the month to obtain mean number of DDs accumulating per day per month (DA). (3) Mean DAs for each month of each year for each L' at each weather station were plotted on corresponding mean monthly field T values, to which third-order polynomial regressions were fitted (Fig. 3). (4) Overall mean DAs were estimated with the regression equations in Fig. 3 for each 0.5° T-step and L', and then assembled as Table 3.

Table 2. Thermal characteristics and related values for datasets used in this study. Dash signifies undetermined or unknown value.

No.	Dataset	Locality	Latitude °N or °S	Mean annual temp.	L	L'	K	K'	W^a	DA^a	Voltinism	Confirmed effective T range	Cal. da. diff^a	Source
	Noctuidae													
1	*Agrotis ipsilon* Hufn.	Japan	39.8 N	10.0	5.6	5.8	388	383	370	20.0	–	20-30	0.6	Hasegawa & Chiba 1969
2	"	USA IL	40.6 N	10.8	11.0	11.6	341	323	315	10.6	3.5	18.3-26.7	0.8	Luckmann et al. 1976
3	"	USA OH	40.8 N	12.0	7.3	7.5	495	489	–	–	3.0	13-34	–	Archer et al. 1980
4	"	Egypt	25.0 N	20.0	5.6	6.0	645	627	600	16.0	2.0	15-30	1.7	Nasr & Moawad 1972
5	"	"	30.0 N	19.8	11.3	11.1	267	270	264	9.5	2.0	17.4-23.4	0.7	Fahmy et al. 1973
6	*A. segetum* D. & S.	India	53.0 N	16.8	7.4	7.1	613	624	611	12.5	2.0	10-30	1.1	Singh 1962
7	*Pseudaletia unipuncta* (Haw.)	Can. ON	45.0 N	5.8	9.5	9.3	292	298	312	9.1	2.5	13-25	-0.1	Guppy 1969
8	*Leucania loreyi* Dup. (solit.)	Japan	34.4 N	16.1	9.3	9.4	366	362	285	10.4	3.0	15-30	7.4	Hirai 1975
9	*L. loreyi* (Crwd.)	"	34.4 N	16.1	8.0	8.7	432	410	391	13.4	3.0	15-30	1.4	"
10	*L. separata* Wlk.	"	43.0 N	8.5	6.7	7.8	397	367	347	14.2	3.0	15-30	1.4	"
11	*Trichoplusia ni* (Hbn.)	USA AZ	32.2 N	20.2	8.7	9.0	260	254	240	15.5	3.0	15-30	0.9	Jackson et al. 1969
12	*Simyra henrici* (Grt.) (7-instar)	USA IL	40.6 N	11.3	9.9	9.8	481	484	477	12.0	1.0	18.3-29.4	0.6	Decker & Maddox 1971
13	" (8-instar)	"	40.6 N	11.3	9.5	9.8	545	530	515	12.0	1.0	18.3-29.4	1.2	"
14	*Helicoverpa zea* (Bod.) (cotton)	USA AZ, GA	31.8 N	20.2	7.4	8.5	438	416	–	–	4.5	22.5-32	–	Butler 1976
15	" (corn)	"	31.8 N	20.2	14.0	14.0	245	245	–	–	4.5	22.5-32	–	"
16	" (art. diet)	"	31.8 N	20.2	12.7	12.9	206	203	–	–	4.5	17.5-32	–	"
17	"	USA WV	39.7 N	11.4	4.2	5.3	235	219	–	–	3.0	10-35	–	Peairs 1927
18	*H. armigera* (Hbn.)	Japan	32.4 N	17.0	11.9	11.7	213	218	217	11.7	4.0	16.4-30.5	0.1	Jallow & Matsumura 2001
19	"	India	29.2 N	25.1	12.8	12.3	238	248	–	–	7.5	20-35	–	Sharma & Chaudhary 1988
20	"	Australia	27.6 S	19.8	11.5	11.1	234	247	212	8.9	–	13.1-27.1	3.9	Twine 1978

Table 2. Continued.

							Noctuidae							
21	*Anticarsia gemmatalis* Hbn.	Brazil	9.4 S	21.4	14.2	13.4	178	180	175	10.3	3.0	18-30	0.5	Magrini et al. 1996
22	*Mythimna convecta* (Wlk.)	Australia	37.5 S	14.0	8.1	7.6	390	404	–	–	3.5	15-33	–	Smith 1984
23	*Heliothis virescens* (F.)	USA AZ	32.1 N	20.2	12.8	12.8	199	199	201	11.8	4.5	17.5-30	-0.1	Butler & Hamilton 1976a
24	"	USA AZ	32.1 N	20.2	13.0	13.7	224	213	–	–	5.0	20-33	–	Fye & McAda 1972
25	*H. virescens* (10:14 phot.)	USA AZ	33.0 N	22.5	13.5	12.7	178	197	–	–	3.5	15.6-32.2	–	Henneberry et al. 1993
26	“ (12:12 phot.)	"	33.0 N	22.5	12.8	13.0	178	175	–	–	3.5	15.6-32.2	–	"
27	“ (12:12 phot.)	"	33.0 N	22.5	12.6	13.2	170	161	–	–	3.5	15.6-32.2	–	"
28	"	USA TX	30.8 N	20.3	12.8	12.5	205	211	–	–	–	17.5-34	–	Butler et al. 1979
29	"	USA AZ	33.0 N	22.5	11.7	11.2	212	226	–	–	5.0	15-34	–	"
30	"	USA NC	36.3 N	14.6	11.9	11.5	194	204	211	10.7	–	15-30	-0.6	"
31	" (cotton)	USA AZ	33.0 N	22.5	8.5	8.5	433	433	422	16.0	5.0	20-30	0.7	"
32	*H. subflexa*	USA MS	33.4 N	17.5	12.9	12.4	214	232	232	9.2	–	16.7-30.3	0.0	"
33	" (grnd.cherry)	"	33.4 N	17.5	9.8	9.6	376	380	375	13.7	–	20.6-30.3	0.4	"
34	*Noctua pronuba* L.	UK	52.9 N	16.8	6.6	6.6	607	684	661	12.0	1.0	10-25	1.9	Singh 1962
35	*Mamestra brassicae* L.	Romania	47.0 N	7.2	8.8	8.9	344	341	330	13.2	–	15-30	0.8	Stan 1998
36	*M. configurata* Wlk.	Can. MB	49.6 N	2.6	6.8	6.2	376	404	419	11.5	1.0	12-28	-1.3	Bailey 1976
37	*Plathypena scabra* (F.)	USA IA	42.0 N	13.0	5.7	5.8	401	397	383	17.5	2.0	15.6-29.5	0.8	Hammond et al. 1979
38	*Peridroma saucia* (Hbn.)	USA OH	40.8 N	9.8	6.2	7.2	395	355	385	10.8	2.0	12.8-26.7	-2.7	Simonet et al. 1981
39	*Autographa gamma* (L.)	UK	53.2 N	8.2	7.9	7.9	265	265	264	9.4	2.0	13-25	0.1	Hill & Gatehouse 1992
40	*Eudocima salaminia* (Cram.)	Australia	27.5 S	19.9	11.9	12.1	280	272	274	8.7	–	15-27	-0.3	Sands et al. 1991
41	*Dargida procincta* (Grt.)	USA OR	44.6 N	11.6	6.6	6.8	421	414	401	13.8	1.0	15-27	1.0	Kamm 1991
42	*Spodoptera cosmioides* (Wlk.)	Brazil	31.8 S	17.5	11.3	11.2	253	256	254	13.3	–	14-30	0.1	Bavaresco et al. 2002

Table 2. Continued. Thermal characteristics and related values for datasets used in this study. Dash signifies undetermined or unknown value.

No.	Dataset	Locality	Latitude °N or °S	Mean annual temp.	L	L’	K	K’	W^a	DA^a	Voltinism	Confirmed effective T range	Cal. da. $diff^a$	Source
							Noctuidae							
43	*S. exigua* (Hbn.)	USA AZ	32.2 N	22.5	12.3	12.2	182	171	–	–	–	20-33	–	Fye & McAda 1972
44	" (art. diet)	USA AL	31.4 N	18.3	13.1	13.1	128	128	–	–	–	18-36	–	Ali & Gaylor 1992
45	" (cotton)	"	31.4 N	18.3	13.5	13.1	159	128	–	–	–	18-36	–	"
46	"	USA AZ	32.2 N	20.2	8.6	9.9	251	220	210	11.5	5.0	15-30	0.9	Butler 1966
47	*Spodoptera frugiperda* (J. E. Smith) (art. diet)	USA MS	33.4 N	16.4	12.4	12.4	193	193	–	–	4.5	21-33	–	Ali et al. 1990
48	" (cotton)	"	33.4 N	16.4	13.0	13.0	270	270	–	–	4.5	21-33	–	"
49	*Spodoptera litura* (F.)	India	17.5 N	22.8	10.0	12.3	305	253	–	–	12.0	15-35	–	Ranga Rao et al. 1989
50	"	Japan	35.7 N	15.6	12.0	12.1	258	256	242	11.1	4.0	16-31	1.2	Miyashita 1971
51	*Sesamia nonagrioides* Léf.	Spain	42.0 N	12.8	12.0	12.1	414	393	415	–	3.0	15-27.5	-1.9	Lopez et al. 2001
52	*S. calamistis* Hampson (art. diet)	Benin	6.8 N	25.5	12.0	11.3	391	420	434	10.9	6.0	15-30	-1.2	Shanower et al. 1993a
53	*Copitarsia decolora* (Gn.) (asparagus)	Peru	14.1 S	20.0	5.2	5.1	466	474	467	11.9	–	9.7-24.9	0.6	Gould et al. 2005
54	*Orthosia hibisci* Gn.	Can. BC	49.6 N	6.0	4.5	4.4	263	257	–	–	1.0	7.5-20	–	Judd et al. 1994
55	*Papaipema nebris* (Gn.)	USA IL	40.5 N	10.4	4.0	4.0	1391	1395	–	–	1.0	12.8-23.9	–	Levine 1983
56	*Panolis flammea* D. & S.	Germany	49.0 N	7.8	4.0	3.9	434	436	–	–	1.0	10-22		Zwölfer 1931
							Tortricidae							
57	*Adoxophyes honmai* Yasuda	Japan	35.8 N	16.0	8.9	8.6	257	262	245	13.9	4.5	15-28	1.2	Nabeta et al. 2005
58	*Epiphyas postvittana* (Wlk.) (*Rumex*)	Australia	37.7 S	19.8	7.1	7.8	334	310	294	10.2	3.0	11.5-25	1.6	Danthanarayana 1975
59	" (*Plantago*)	"	37.7 S	19.8	8.0	8.2	310	304	295	9.9	3.0	11.5-25	0.9	"
60	" (*Malus*)	"	37.7 S	19.8	7.1	7.8	351	327	304	10.2	3.0	11.5-25	1.7	"
61	" (1st)	"	35.5 S	22.0	9.9	9.6	404	417	482	11.4	3.0	15.7-25	-5.7	Dumbleton 1939
62	" (2nd)	"	35.5 S	22.0	7.8	7.2	510	541	549	12.0	3.0	11.7-25	-0.6	"
63	"	"	37.7 S	16.6	7.7	7.7	319	325	320	9.1	3.0	10.3-25.2	0.5	Dantharayana et al. 1995

Table 2. Continued.

							Tortricidae							
64	*Epichoristodes acerbella* (Wlk.)	S. Africa	25.7 S	18.7	7.0	7.0	413	416	423	12.4	2.5	9.5-25	-0.5	Bolton 1979
65	"	Italy	43.9 N	15.0	10.2	10.2	341	341	324	1.4	4.0	16-28	1.5	Quaglia 1983 (1985)
66	*Homona magnanima* Diak.	Japan	37.0 N	15.6	9.4	9.8	276	274	258	9.9	4.0	15-28	1.6	Mao & Kunimi 1990
67	*Ancylis comptana* (Froel.)	USA IA	41.7 N	9.9	9.8	10.0	255	251	237	11.7	3.0	14-30	1.2	Gabriel & Obrycki 1990
68	*Crocidosema plebejana* Z.	Australia	27.0 S	22.0	11.2	11.1	208	212	192	9.7	8.0	14-31	2.0	Hamilton & Zalucki 1991
69	*Argyrotaenia sphaleropa* (Meyr.)	Brazil	31.8 S	17.5	10.8	11.6	245	236	196	10.2	4.0	14-30	4.0	Manfredi-C. et al. 2001
70	*A. velutinana* (Wlk.) (1st)	USA NC	35.2 N	15.2	6.3	6.4	471	469	459	10.8	4.0	10-25	0.9	Hawthorne et al. 1988
71	" (2nd)	"	35.2 N	15.2	7.0	6.7	410	425	427	10.6	4.0	10-25	-0.2	"
72	*Paralobesia viteana* (Clem.)	USA PA	42.0 N	9.5	6.8	6.6	240	242	236	15.0	2.5	15-30	0.4	Tobin et al. 2001
73	*Platynota idaeusalis* (Wlk.)	USA NC	35.3 N	12.9	10.5	9.7	324	365	373	8.3	4.0	13-27	-0.9	Rock 1985
74	"	USA VA	38.5 N	13.3	7.1	7.9	437	403	423	2.7	2.0	12.8-26.7	-1.6	David et al. 1989
75	*P. flavedana* Clem.	"	38.5 N	13.3	8.7	8.9	370	360	391	11.8	2.0	12.8-26.7	-2.6	"
76	*Zeiraphera canadensis* Mut. & Free.	Can. NB	47.6 N	7.3	6.4	6.6	265	260	262	12.5	1.0	12.3-27.7	-0.2	Régnière & Turgeon 1989
77	*Choristoneura pinus* Free.	Can. ON	–	–	9.9	9.7	366	380	398	9.0	1.0	12.5-25	-2.0	Lysik & Nealis 1988
78	*C. fumiferana* (Clem.)	"	48.4 N	9.0	7.0	6.4	501	534	547	10.9	1.0	10-25	-1.2	Régnière 1987
79	*Rhyacionia frustrana* (Comst.)	USA AR	34.3 N	16.8	10.8	9.8	309	355	–	–	3.0	14-34	–	Haugen & Stephen 1984
80	*Cydia pomonella* (L.)	USA CA	38.7 N	16.0	11.6	12.0	239	224	–	–	3.0	15.6-32.2	–	Pitcairn et al. 1991
81	*Merophyas divulsana* (Wlk.)	Australia	27.4 S	19.9	8.1	7.9	278	283	285	11.1	7.0	11.3-27.5	-0.2	Allsopp et al. 1983
							Gelechiidae							
82	*Pectinophora gossypiella* (Saund.) (sooty)	USA AZ	33.5 N	22.5	15.4	15.5	167	165	–	–	4.5	22.5-30	–	Bartlett et al. 1980
83	" (wild-F)	"	33.5 N	22.5	12.7	12.4	217	222	–	–	4.5	17-32	–	"
84	" (sooty-F)	"	33.5 N	22.5	12.3	11.9	220	227	–	–	4.5	17-32	–	"

Table 2. Continued. Thermal characteristics and related values for datasets used in this study. Dash signifies undetermined or unknown value.

No.	Dataset	Locality	Latitude °N or °S	Mean annual temp.	L	L’	K	K’	W[a]	DA[a]	Voltinism	Confirmed effective T range	Cal. da. diff[a]	Source
							Gelechiidae							
85	*Pthorimaea operculella* (Z.)	Japan	33.6 N	16.3	11.1	10.9	162	164	–	–	–	15-33	–	Koizumi 1955
86	"	USA MD	38.0 N	14.2	12.0	12.0	184	182	–	–	5.0	17.5-31.9	–	Langford & Cory 1932
87	"	Peru	12.1 S	11.0	13.6	9.2	174	252	254	14.8	–	16.1-30	0.1	Sporleder et al. 2004
88	*Pectinophora gossypiella* (Saund.) (WCRL)	USA AZ	32.2 N	20.2	13.2	13.4	240	234	236	8.9	4.5	17.5-30	-0.2	Butler & Hamilton 1976b
89	" (wild)	"	32.2 N	20.2	13.6	13.5	235	236	224	10.0	4.5	17.5-30	1.2	"
90	" (orange)	"	32.2 N	20.2	13.5	13.4	202	202	193	10.0	4.5	17.5-30	0.9	"
91	" (APHIS)	"	32.2 N	20.2	11.4	11.5	253	251	–	–	4.5	20-32	–	"
92	" (WCRL-78)	"	33.5 N	22.5	13.3	14.0	232	214	201	9.5	4.5	16.7-30	1.4	Bartlett et al. 1980
93	" (4-instar)	"	33.5 N	22.5	12.3	12.3	226	227	–	–	4.5	20-32.5	–	Huchison et al. 1986
94	" (5-instar)	"	33.5 N	22.5	12.2	12.3	274	272	262	11.1	4.5	20-27.5	0.9	"
95	*Scrobipalpuloides absoluta* (Meyr.)	Uruguay	35.0 S	13.0	6.3	6.6	265	262	246	13.0	–	12-30	1.2	Bentancourt et al. 1996
96	*Keiferia lycopersicella* (Wlsm.)	USA CA	33.7 N	18.3	10.8	11.4	211	191	207	7.2	7.5	14-26	-2.3	Lin & Trumble 1985
							Crambidae							
97	*Diatraea saccharalis* (F.) (1st)	USA MS	33.3 N	17.2	11.5	11.9	348	338	323	14.7	4.5	22-30	1.0	King et al. 1975
98	“ (2nd)	"	33.3 N	17.2	9.6	10.0	390	381	362	17.5	4.5	22-31	1.1	"
99	"	Cuba	22.0 N	25.0	15.7	14.9	324	361	–	–	6.6	19-28	–	Jasic 1967
100	*Diatraea grandiosella* Dyar	USA MS	38.0 N	14.4	8.9	9.9	575	539	–	–	2.0	18.3-32.2	–	Whitworth & Poston 1979
101	*Udea ferrugalis* (Hbn.) (1st)	Korea	37.6 N	11.8	11.3	11.5	162	159	154	9.8	–	15-27	0.5	Lee et al. 2002
102	“ (2nd)	"	37.6 N	11.8	12.2	12.0	140	144	150	8.0	–	15-25	-0.7	"
103	*Maruca vitrata* (F.)	China	31.6 N	–	10.9	11.1	184	180	173	11.1	2.0	15-30	0.6	Chi et al. 2006
104	*Ostrinia nubilalis* (Hbn.)	USA ND	46.9 N	10.8	12.3	13.6	334	293	284	11.2	1.0	17-30	0.8	Calvin et al. 1991
105	"	USA MO	36.4 N	15.5	13.0	13.7	310	293	–	–	3.0	17-32	–	"
106	"	USA DE	38.7 N	12.7	13.2	14.3	326	295	–	–	1.0	17-32	–	"
107	*Ostrinia nubilalis* (Hbn.)"	USA IL	40.1 N	10.8	11.2	11.3	263	262	–	–	2.0	15.7-32.2	–	Matteson & Decker 1965
108	*Cnaphaloerocis medinalis* Guenée	Japan	33.6 N	16.3	12.2	12.0	204	208	203	9.1	5.0	15-27.5	0.6	Wada & Kobayashi 1980
109	*Chilo auricilius* Dudg.	India	26.8 N	24.0	15.1	16.0	501	458	–	–	5.0	20-30	–	Mitra & Verma 1981
110	*C. sacchariphagus* (Bojer)	Réunion	21.0 S	23.7	12.7	12.8	582	577	575	9.5	4.5	17-30	0.2	Goebel 2006
111	*Crambus trisectus* (Wlk.)	USA IL	40.1 N	10.8	10.5	11.0	539	522	–	–	2.0	21.1-32.2	–	Banerjee 1969

Table 2. Continued.

	Crambidae													
112	*Diaphania nitidalis* (Stoll)	USA NC	27.2 N	25.0	10.5	10.8	214	208	197	11.3	2.5	15.5-29.4	1.0	Elsey 1980
113	*D. indica* (Saund.)	India	11.4 N	27.0	13.1	14.0	240	229	–	–	–	25-40	–	Peter & David 1992
	Plutellidae													
114	*Plutella xylostella* (L.)	China	30.2 N	16.2	8.4	8.0	134	139	143	11.6	–	12-30	-0.3	Liu et al. 2002
115	"	Japan	35.0 N	16.7	9.6	10.0	146	141	142	12.1	–	17.5-27.5	0.0	Yamada & Kawasaki 1983
116	“ (cauliflower)	Iran	35.8 N	17.1	6.2	6.7	152	146	154	12.9	–	10-28	-0.6	Golizadeh et al. 2007
117	“ (cabbage)	"	35.8 N	17.1	8.2	6.9	138	159	170	12.7	–	10-28	-0.9	
	Pyralidae[b]													
118	*Ephestia kuehniella* Zell. (70% RH)	UK	–	–	6.8	7.0	1136	1115	–	–	–	12-25	–	Jacob & Cox 1977
119	*E. figulilella* Gregson	Cyprus	–	–	12.2	11.7	533	560	–	–	–	17.5-30	–	Cox 1974
120	*Cadra cautella* Wlk. (60% RH)	India	–	–	13.0	11.7	437	512	–	–	–	15-30	–	Tuli et al. 1966
121	“ (75% RH)	"	–	–	11.1	11.2	500	500	–	–	–	15-35	–	"
122	“ (90% RH)	"	–	–	10.3	11.6	435	390	–	–	–	15-35	–	"
123	“ (70% RH)	Argentina & Nigeria	–	–	12.8	12.8	358	356	–	–	–	17.5-30	–	Burges & Haskins 1964
124	*Plodia interpunctella* (Hbn.) (50% RH)	Nigeria	–	–	12.1	12.4	298	290	–	–	–	17.5-30	–	Prevett 1971
	Arctiidae													
125	*Hyphantria cunea* Drury (P2L)	Japan	35.7 N	16.0	9.8	9.1	474	503	480	13.5	2.0	17-26.5	1.7	Itô & Miyashita 1968
126	“ (P1L)	"	35.7 N	16.0	9.4	10.0	505	473	473	11.0	2.0	14-26	1.3	"
127	“ (1CL)	"	35.7 N	16.0	9.1	8.9	515	521	514	15.9	2.0	19-30	0.5	"
	Galacticidae													
128	*Homadaula anisocentra* Meyr.	USA IA	42.0 N	9.9	11.8	10.9	208	233	245	10.4	2.0	14-30	-1.2	Bastian & Hart 1991
	Cossidae													
129	*Zeuzera coffeae* Nietner	Taiwan	24.5 N	23.6	12.1	12.0	1401	1411	1345	13.6	2.0	20-30	4.8	Chang 1987
	Carposinidae													
130	*Carposina sasakii* Mats.	Korea	37.3 N	12.3	9.4	9.1	272	280	279	13.0	1.5	16-28	0.0	Kim et al. 2001
	Lasiocampidae													
131	*Streblota panda* Hbn.	Spain	37.3 N	19.2	12.5	11.9	521	563	607	10.0	4.0	16-28	-4.4	Calvo & Molina 2005

[a] Values for T and L' given only within ranges included in Table 3.

[b] All Pyralidae here infest stored products and develop in artificial environments; only their thermal characteristics, localities of origin, and revised effective Ts are given.

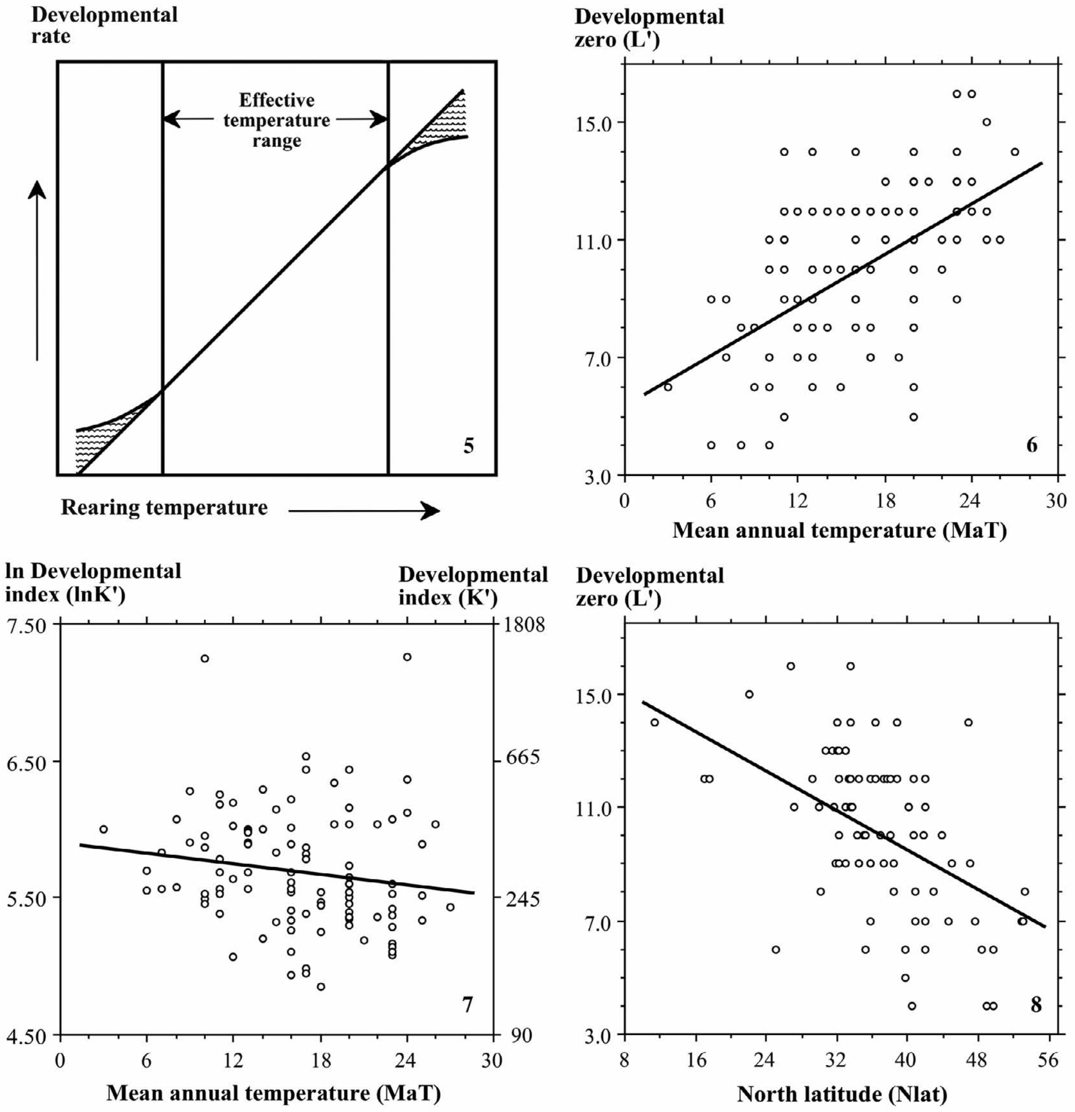
TABLE 3. Mean DD accumulations per day (DA) at weather-station mean monthly temperatures from 8-31° C (T) and L' from 5-14° C based on equations in Fig. 3.

T	L'=5	L'=8	L'=11	L'=14
8	4.08	2.56	1.61	0.99
8.5	4.44	2.80	1.72	1.01
9	4.80	3.06	1.85	1.04
9.5	5.18	3.34	2.00	1.10
10	5.56	3.62	2.17	1.18
10.5	5.95	3.92	2.36	1.28
11	6.35	4.24	2.57	1.39
11.5	6.76	4.57	2.80	1.53
12	7.18	4.91	3.04	1.68
12.5	7.60	5.26	3.30	1.85
13	8.02	5.62	3.58	2.04
13.5	8.46	5.99	3.87	2.25
14	8.90	6.38	4.18	2.47
14.5	9.34	6.77	4.50	2.71
15	9.79	7.18	4.84	2.96
15.5	10.25	7.59	5.19	3.23
16	10.71	8.01	5.55	3.51
16.5	11.17	8.44	5.92	3.81
17	11.64	8.88	6.31	4.12
17.5	12.11	9.32	6.71	4.44
18	12.59	9.77	7.11	4.78
18.5	13.06	10.22	7.53	5.13
19	13.54	10.69	7.95	5.50
19.5	14.03	11.15	8.39	5.87
20	14.51	11.62	8.83	6.26
20.5	15.00	12.10	9.28	6.65
21	15.48	12.58	9.74	7.06
21.5	15.97	13.06	10.20	7.48
22	16.46	13.54	10.66	7.90
22.5	16.95	14.03	11.14	8.34
23	17.43	14.51	11.61	8.78
23.5	17.92	15.00	12.09	9.24
24	18.41	15.49	12.58	9.70
24.5	18.89	15.98	13.06	10.17
25	19.38	16.47	13.55	10.64
25.5	19.86	16.95	14.04	11.12
26	20.34	17.44	14.53	11.61
26.5	20.82	17.92	15.02	12.11
27	21.29	18.41	15.51	12.61
27.5	21.76	18.88	16.00	13.11
28	22.23	19.36	16.49	13.62
28.5	22.70	19.83	16.97	14.13
29	23.16	20.30	17.45	14.65
29.5	23.61	20.76	17.93	15.17
30	24.06	21.22	18.41	15.69
30.5	24.51	21.67	18.88	16.22
31	24.95	22.11	19.34	16.75

As the calendar day is usually the ultimate currency in DD applications, how closely W approximated K' was compared in terms of calendar days (Table 2), which were computed as (K'-W)/DA.

Mamestra configurator can again serve to illustrate how W was estimated and how Table 3 assisted. In laboratory rearing of this species, the four surviving values of T and D yielded an L' of 6.19º (rounded to 6.2) (Fig. 2, Table 2: No. 36) and T and D medians of 18.0º and 36.4, respectively. Turning to Table 3, T of 18.0º and L' of 6.19º indicates a DA intermediate between 12.59 for L' = 5 and 9.77 for L' = 8, which after interpolation is 11.5. The mathematical product of 11.5 × 36.4 (DA × D) yields W of 418.6 (rounded to 419) (Table 2: No. 36). Then K' of 404 less W of 419 equals -15 DDs, which, when divided by 11.5 DDs per calendar day (DA), gives a difference of -1.3 calendar days between W and K' (Table 2: No. 36).

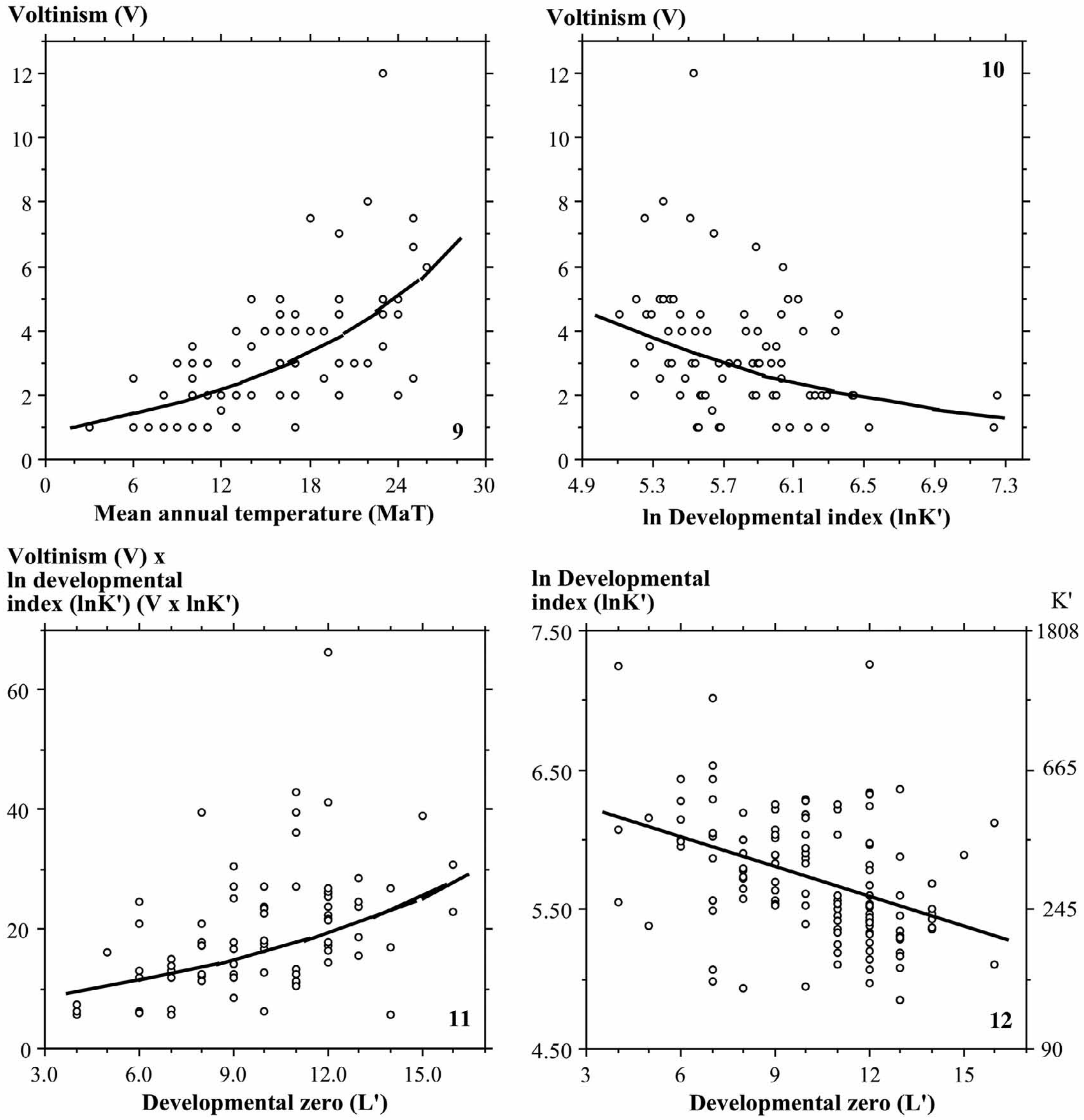
Field temperatures used in this study originated from 1920–2000, and the 18 official weather stations providing them were believed representative of temperatures where more than 25 North American datasets originated (Fig. 4, Appendix 1). U. S. temperature records, except those for Minnesota, were obtained at http://cdo.ncdc.noaa.gov/CDO/cdo; temperatures for the one Minnesota station were obtained at http://climate.umn.edu/MnlocMS/MNlocNEW.asp. Official Canadian temperature records were obtained at http://climate.weatheroffice.ec.go.ca/climateData/canada_e.html.



FIGS.. 5–8. **5.** Diagram illustrating the Kaufmann or rate summation effect. The effect occurs when field temperatures used in summation fall beyond the limits of the straight line (lower and upper shaded areas). Further explanation in text.**6.** Empirical relation of developmental zero, L', to mean annual temperature, MaT, at or near localities of dataset origin; n reduced to 101 by unavailability of some values of MaT, and by dataset removals to avoid pseudoreplication. L' = 5.37 + 0.287 MaT, r^2 = 0.29, P <0.001. **7**. Empirical relation of ln developmental index, lnK', to mean annual temperature, MaT, at or near localities of dataset origin for 101 n; n reduced as in Fig. 6. lnK' = -0.013 MaT + 5.9, r^2 = 0.01, P = 0.12. Arithmetic equivalents of lnK' are on right-hand vertical axis. **8.** Empirical relation of developmental zero, L', to latitude at or near origins of northern hemisphere datasets, Nlat; n reduced to 85 by unavailability of Nlat for some datasets, and by dataset removals to avoid pseudoreplication. L' = 16.5 - 0.173 Nlat, r^2 = 0.26, P < 0.001.

Mean annual temperatures, latitudes, and voltinism were compiled from dataset source publications, maps, and on-line resources. These variables as well as others appear in or are derivable from Table 2. Temperatures originally reported in °F were converted to ºC before use. Statistics were generated with SYSTAT software (SYSTAT 1992), and SE refers to standard error.

Kaufmann and related effects. A fundamental problem with all linear phenological models is that the full range of any R–T relation is actually curvilinear at its lower and upper ends (Ruel & Ayres 1999; Worner 1992; Liu et al. 1995). At the lower end, the curve is accelerating or concave-upward, and at the upper end, decelerating or concave-downward (Fig. 5). Nonlinear



FIGS. 9–12. **9.** Empirical relation of voltinism, V, to mean annual temperature, MaT, at or near localities of dataset origin; n reduced to 77 because of unavailability of V and MaT for some datasets. $V = 0.950 \times 10^{0.0304\ \mathrm{MaT}}$, $r^2 = 0.43$, $P < 0.001$. **10.** Empirical relation of voltinism, V, to ln developmental index, lnK', for 81 n; n reduced as in Fig. 9. $V = 60.51 \times 10^{-0.231\ \ln K'}$, $r^2 = 0.14$, $P < 0.01$. **11.** Empirical relation of mathematical product of voltinism, V, times ln developmental index, lnK' [V x lnK'] to developmental zero (L') for 81 n; n reduced as in Fig. 9. $V \times \ln K' = 6.054 \times 10^{0.0430\ L'}$, $r^2 = 0.23$, $P < 0.001$. **12.** Empirical relation of ln developmental index, lnK', to developmental zero, L', for 131 n. $\ln K' = 6.43 - 0.0697\ L'$, $r^2 = 0.18$, $P < 0.001$. Arithmetic equivalents of lnK' are on right-hand vertical axis.

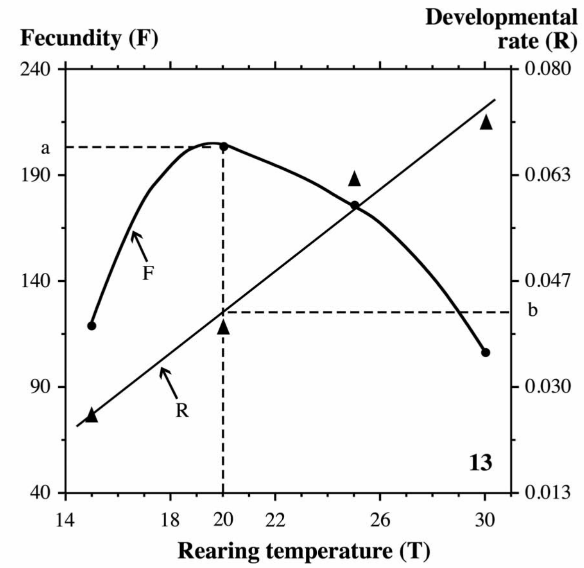


FIG. 13. Fecundity, F, as related to rearing temperature, T, and rate of larval development, R, in *Adoxophyes honmai* Yasuda (Tortricidae). Curve F fitted by connecting data points. Line R fitted by the improved linear model; R = 0.00435 T - 0.0462. Data of Nabeta et al. (2005).

models can be fitted to the full range of data, but linear model simplicity is thereby lost, and more parameters must be estimated—their number often approaching the number of observations in small datasets. Temperatures that fluctuate beyond the effective temperature range (Fig. 5: shaded areas) create summing errors. These errors constitute the Kaufmann or rate-summation effect (Kaufmann 1932). The straight line underestimates developmental rate in the lower shaded area, and overestimates it in the upper shaded area. Total summation error will depend on how often unusually low and high temperatures occur. The possibility of such occurrences underscores the importance of generating adequate numbers of T–D points for modeling to ensure that removal of points that later prove to depart from linearity does not reduce model accuracy.

The Kaufmann effect is encompassed by Jensen's Inequality (Ruel & Ayres 1999), a broader phenomenon involving more than the tails of the rate response distribution. The inequality refers to the difference between actual and predicted DDs when the rate response to temperature is nonlinear. In such cases, field temperature variance acts independently of average field temperature. As discussed further on, these potential effects appear to have had minimal impact in this study.

RESULTS AND DISCUSSION

Revision of thermal characteristics. Among the 223 datasets originally meeting study criteria, 16 (7%) were convincingly curvilinear and therefore dropped. Most of the dropped datasets had been fitted with nonlinear models. One or more of these were published by Bari & Lange (1980), Butler et al. (1975), Butturini & De Berardinis (1992), Chen & Su (1982), Daoud et al. (1999), Gould et al. (2005), Johansen (1997), Jones (2005), Legaspi & Legaspi (2007), Madge (l962), Miner (1947), Snyder (1954), and Tiso et al. (1991-92).

More significantly, 207 (93%) of the 223 datasets had ≥4 linear points. However, application of the improved linear model during thermal characteristic revision resulted in reductions to <4 linear points in more than 70 of the 207 datasets, causing them also to be dropped (Appendix 2). Such wholesale exclusion of datasets again underscores the importance of generating sufficient numbers of T–R points for modeling—at least six, preferably eight or more (Legg et al. 2002)—in case points must be removed because of nonlinearity.

The 131 surviving datasets (Table 2) originated from 1927–2007 on six continents, and represent species in 11 families. Across all families, L' ranged 3.9 ± SE 0.58–16.0 ± SE 0.62. The statistical distribution of revised thermal characteristics shifted only slightly: L and L' medians were 10.8 and 10.9, respectively, L' exceeding L in 62 (47%) of datasets, and medians of K and K', each 280, K' exceeding K in 55 (42%) (Table 2). Lack of greater overall differences is of little consequence, however, as the focus of thermal characteristic revision was the individual dataset and its purpose the improvement of dataset quality and reliability.

L' tended to reflect local climates, values changing by nearly 1° for each 3° change in mean annual temperature at the site of data collection, forming a continuum of low to high values from cool to warm conditions (Fig. 6). Low L' values enable earlier development in short, cool growth seasons. K' appeared uninfluenced by mean annual temperature (Fig. 7), but it assumed more importance when combined with other variables, as shown further on.

Noctuidae was the best-represented family among surviving datasets. Although many noctuids are capable of feeding as adults, and a few may approach butterfly income breeding in amount of adult feeding, all were considered capital breeders here because not enough is known at present to classify them more accurately. Mean values of L' and K' for Noctuidae (56 n) were 9.9 and 336 (ln = 5.817), and for the next three best represented families were Tortricidae (25 n), 8.6 and 341 (ln = 5.832), Crambidae (17 n) 12.4 and 320 (ln = 5.768), and Gelechiidae (15 n) 12.0 and 220 (ln = 5.394).

Trudgill & Perry (1994) suggested that high L values serve to delay development until lethal spring frosts have mostly passed. Theoretical and empirical studies of unrevised thermal characteristics have further suggested that tropical ectotherms would have higher L and lower K values than temperate ones (Honék 1996b; Trudgill & Perry 1994; Trudgill 1995). The revised thermal characteristics strongly support these suggestions.

Not surprisingly, L' declined with increasing north latitude (Fig. 8) as it did with decreasing mean annual temperature, the former also noted for unrevised values of L by Honék (1999). The trend in L' relative to increasing south latitude was positive but not statistically significant. The south latitude sample was small (14 n), but a different trend is perhaps to be expected because of the larger ratio of ocean to landmass in the southern hemisphere. Response of one species to differing geography is well illustrated by *Agrotis ipsilon* (Hufnagel) (Noctuidae) with L's ranging 5.8–11.6 among three continents (Table 2: Nos. 1–5), although for reasons thus far unclear, relations between L' and climatic variables in this example do not mirror statistical outcomes across families.

Voltinism across all families ranged from 1–12 (Table 2). It declined like L' with declining mean annual temperature (Fig. 9), but increased with decreasing K' (Fig. 10). Joint relations among voltinism, V, ln K', and L' are readily understandable at high values of L' where multiple generations develop in one growth season (Fig. 11). It is assumed in Fig. 11 that L' for a species at a given locality does not change appreciably between generations during the same growth season.

As emphasized by Honék (1996a) for unrevised thermal characteristics L and K, revised thermal characteristics L' and K' were themselves inversely correlated among species (Fig. 12). For a 1° change in L' near its median, K' changed by ~31 DDs.

Body size is not addressed in the present study, but it is noteworthy in passing that Honék (1999) showed that body mass and unrevised K are directly correlated. Honék concluded that, other things being equal, larger bodied species require longer developmental durations than smaller ones and thus have larger Ks.

Examples of environmental factors other than temperature influencing thermal characteristics include humidity where at 90–60% R. H. K' at the same Ts ranged 390–512 (Table 2: Nos. 120–122); photoperiod where K' among photophases of 10–14 h of daylight ranged 161–197 (Table 2: Nos. 25–27); and food quality where L' and K' were, respectively, 8.5° and 416 on cotton, and 14.0° and 245 on corn (Table 2: Nos. 14 and 15).

In summary, thermal-characteristic revision does not appear to have overturned any broad conclusions based earlier on unrevised values, but instead strengthens such conclusions with higher quality surviving datasets. For instance, the inverse correlation of L' and mean annual temperature (Fig. 6) confirms that thermal characteristics of populations are adaptive and subject to evolution.

Summation with official temperatures. Agreement of calendar-day differences between W and K' here for a period as long as the entire larval phase exceeded expectations. Some 91%—all but 9—agreed within ±2 calendar days (Table 2). Agreement was doubtless enhanced by the exclusion of datasets that were weak or had extreme values. Most divergences of >2 calendar days were from coastal or near coastal oceanic and lacustrine environments in Japan, Australia, Taiwan, (Table 2: Nos. 8, 20, 38, 61, 69, 75, 96,129), the U. S. and Canada (Table 2: Nos. 38, 75, 96), Brazil, and Spain (Table 2: Nos. 69, 131). Association of divergences with these environments may be coincidental, however, as other datasets from similar environments did not diverge excessively (Table 2: Nos. 2, 9-10, 18, 50, 57, 62, 66, 108, 115, 125-127).

Methods of estimating W gave values that agreed reasonably well with K' even in warm-climate species. Most W estimates involved temperatures in the confirmed effective range of ~15–28º; only 32 datasets (26%) had upper values >31º (stored product lepidopterans excluded) (Table 2). During the May–August period of official temperatures used to estimate DA and W, field temperatures averaged ~20º. In 64 datasets that included a T of 20°, resulting D values ranged 11.9–173.6, with a median of 29.2 days, or ~1 month. Mean monthly temperatures ≥29º were never observed in the North American weather-station records used (Fig. 3). For instance, the 30-yr July 'normal' (long-term average) temperature at Sioux Falls, SD, was 23.5 ± SD 1.7º, with 99 percent confidence limits of 19.1–27.9º. This makes a warmer average July temperature unlikely to occur there oftener than once a century. Of course, very warm temperatures may occur for less than monthly durations, and even regularly in the Torrid Zone (<24° latitude on either side of the equator). Six surviving datasets originated in the Torrid Zone, and in all four for which W was calculated (Table 2: Nos. 21, 52, 53, 87), agreement of W with K' proved to be well within ±2 calendar days. As emphasized by Ruel & Ayres (1999), however, hourly or other less than half-day field temperatures would provide more accurate results. The degree of agreement between W and K' suggests that Jensen's Inequality had little adverse impact on DAs in Table 3 and thus on W.

Lack of attention to egg and pupal development probably detracts little from the uses of this study, as previous surveys found that unrevised thermal characteristics were similar for egg, larval, and pupal stages of Lepidoptera (Honék 1996a, b).

Interestingly, Podolsky (1984) has written at length about a forecasting method that bypasses thermal characteristics. This method first assembles phase durations at different habitat temperatures. As the temperatures in this first step are uncontrolled, many more observations may be required than with a thermal-characteristic approach. Next, mean temperatures at the location of interest are assembled by successive 10-day or other intervals. Finally, the two assemblies are combined into a nomogram allowing phase durations to be predicted starting on any of a range of dates. Perhaps because of the large amount of data required and uncertainty whether results are transferable between localities, Podolsky's method has not been widely adopted.

Finally, agreement of W with K' seems sufficient to warrant exploration of weather-station temperatures for new developmental applications. One topic for study is the effect of temperature on growth-related population fitness factors such as fecundity. Capital-breeding Lepidoptera reared at different temperatures differ in maternal body size and fecundity (Honék 1993; Miller 2005) with, surprisingly, cooler rather than warmer temperatures having the greater positive impact (Atkinson 1994; Miller 2005) (Fig. 13). Martin & Huey (2008) explained why cool, seemingly suboptimal temperatures are actually optimal. What may have been overlooked in past work on capital-breeding Lepidoptera is that rate of development also may affect fecundity. For instance, fecundity in *Adoxophyes honmai* Yasuda (Tortricidae) peaked at a rather slow developmental rate of ~0.042 (Fig. 13: b) and midrange T of 20º (Fig. 13: a). Because developmental rate, R, is the reciprocal 1/D, peak fecundity occurred at a larval duration of 24 calendar days, which is protracted compared with the shortest D of 14 days at a T of 30º. This suggests that DD summation, in so far as it indicates developmental rate, might predict fecundity. In future work, fecundity and other fitness factors relative to temperature-dependent developmental rates and associated population indices such as capacity for increase should be explored.

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LITERATURE CITED

ADATI, T., S. NAKAMURA, M. TAMO & K. KAWAZU. 2004. Effect of temperature on development and survival of the legume pod borer, *Maruca vitrata* (Fabricius) (Lepidoptera: Pyralidae) reared on a semi-synthetic diet. Appl. Entomol. Zool. 39: 139-145.

ALI, A. & M. J. GAYLOR. 1992. Effects of temperature and larval diet on development of the beet armyworm (Lepidoptera: Noctuidae). Environ. Entomol. 21: 780-786.

ALI, A., B. G. LUTTRELL & J. C. SCHNEIDER. 1990. Effects of temperature and larval diet on development of the fall armyworm (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Amer. 83: 725-733.

ALLEE, W. C., O. PARK, A. E. EMERSON, T. PARK & K. P. SCHMIDT. 1949. Principles of animal ecology. Saunders, Philadelphia. 837 pp.

ALLEN, J. C. 1976. A modified sine wave method for calculating degree days. Environ. Entomol. 5: 388-396.

ALLSOPP, P. G., B. A. COWIE & B. A. FANZMANN. 1983. Development of immature stages of the lucerne leafroller *Merophyas divulsana* (Walker) (Lepidoptera: Tortricidae) under constant temperatures and on several larval diets. J. Austral. Entomol. Soc. 22: 287-291.

ANDREWARTHA, H. G. & L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. of Chicago. 782 pp.

ARNOLD, C. Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Amer. Soc. Horticult. Sci. 74: 430-445.

ARCHER, T. L., G. L. MUSICK & R. L. MURRAY. 1980. Influence of temperature and moisture on black cutworm (Lepidoptera: Noctuidae) development and reproduction. Can. Entomol. 112: 665-673.

ÅSMAN, K. 2001. Effect of temperature on development and activity periods of the leek moth *Acrolepiopsis assectella* Zell. (Lep., Acroplepiidae). J. Appl. Entomol. 125: 361-364.

ATKINSON, D. 1994. Temperature and organism size—a biological law for ectotherms? Adv. Ecol. Res. 25: 1-58.

ATKINSON, P. R. 1980. On the biology, distribution and natural host-plants of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). J. Entomol. Soc. So. Africa 43: 171-194.

BAILEY, C. G. 1976. Temperature effects on non-diapause development in *Mamestra configurata* (Lepidoptera: Noctuidae). Can. Entomol. 108: 1339-1344.

BAKER, C. R. B. 1980. Some problems in using meteorological data to forecast the timing of insect life cycles. Bull. OEPP (Org. Eur. Medit. Prot. Pl.) 10: 83-91.

BANERJEE, A. C. 1969. Development of *Crambus trisectus* at controlled constant temperatures in the laboratory. J. Econ. Entomol. 62: 703-705.

BARI, M. A. & W. H. LANGE. 1980. Influence of temperature on the development, fecundity, and longevity of the artichoke plume moth. Environ. Entomol. 9: 673-676.

BARKER, J. F. & J. W. ENZ. 1993. Development of laboratory reared banded sunflower moth, *Cochylis hospes* Walsingham (Lepidoptera: Cochylidae), in relation to temperature. J. Kansas Entomol. Soc. 66: 420-426.

BARTLETT, A. C., G. D. BUTLER & A. G. HAMILTON. 1980. Developmental rate of the sooty strain of *Pectinophora gossypiella.* Ann. Entomol. Soc. Am. 73: 164-166.

BASKERVILLE, G. L. & P. EMIN. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514-517.

BASTIAN, R. A. & E. R. HART. 1991. Temperature effects on developmental parameters of the mimosa webworm (Lepidoptera: Plutellidae). Environ. Entomol. 20: 1141-1148.

BAVARESCO, A., M. S. GARCIA, A. D. GRÜTZMACHER, J. FORESTI & R. RINGENBERG. 2002. Biologia e exigências térmicas de *Spodoptera cosmioides* (Walk.) (Lepidoptera: Noctuidae). Neotrop. Entomol. 31: 49-54.

BECKWITH, R. C. 1982. Effects of constant laboratory temperatures on the Douglas-fir tussock moth (Lepidoptera: Lymantriidae). Environ. Entomol. 11:1159-1163.

BENTANCOURT, C. M., I. B. SCATONI & J. J. RODRÍGUEZ. 1996. Influencia de la temperatura sobre la reproducción y el desarollo de *Scrobipalpuloides absoluta* (Meyrick) (Lepidoptera, Gelechiidae). Rev. Brasil. Biol. 56: 661-670.

BERKETT, L. P., P. D. MOWERY & W. M. BODE. 1976. Rate of development of *Platynota idaeusalis* at constant temperatures. Ann. Entomol. Soc. Amer. 69: 1091-1094.

BOGGS, C. L. 1992. Resource allocation: exploring connections between foraging and life history. Funct. Ecol. 6: 508-518.

BOLTON, M. C. 1979. Some effects of temperature, humidity and larval diet on the life cycle of the South African carnation worm, *Epichoristodes acerbella* (Walker) (Lepidoptera: Tortricidae). J. Entomol. So. Afr. 42: 129-135.

BUES, R. & S. POITOUT. 1980. Étude du développement larvaire et nymphal de *Phlogophora meticulosa* L. (Lep. Noctuidae) sous différentes interactions contrôlées de températures et de durées d'éclairement. Acta Oecol. Oecol. Appl. 1: 127-138.

BURGES, H. D. & K. P. F. HASKINS. 1964. Life cycle of the tropical warehouse moth, *Cadra cautella* (Wlk.), at controlled temperatures and humidities. Bull. Entomol. Res. 55: 775-789.

BUTLER, G. D. 1966. Development of the beet armyworm and its parasite *Chelonus texanus* in relation to temperature. J. Econ. Entomol. 59: 1324-1327.

———. 1976. Bollworm: development in relation to temperature and larval food. Environ. Entomol. 5: 520-522.

BUTLER, G. D. & A. G. HAMILTON. 1976a. Development time of *Heliothis virescens* in relation to constant temperature. Environ. Entomol. 5: 759-760.

———. 1976b. Temperature-dependent development rates for four strains of *Pectinophora gossypiella*. Ann. Entomol. Soc. Amer. 69: 450-452.

BUTLER, G. D., A. G. HAMILTON & A. C. BARTLETT. 1975. Development of the dark strain of cabbage looper in relation to temperature. Environ. Entomol. 4: 619-620.

BUTLER, G. D., A. G. HAMILTON & F. I. PROSHOLD. 1979. Developmental times of *Heliothis virescens* and *H. subflexa* in relation to constant temperature. Ann. Entomol. Soc. Am. 72: 263-266.

BUTTURINI, A., R. TISO & E. DE BERARDINIS. 1992. Influenza della temperatura sullo sviluppo di *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). Bull. Ist. Entomol. G. Grandi Univ. Bologna 47: 123-134.

CALVIN, D. D., R. A. HIGGINS, M. C. KNAPP, F. J. POSTON, S. M. WELCH, W. B. SHOWERS, J. F. WITKOWSKI, C. E. MASON, H. C. CHIANG & A. J. KEASTER. 1991. Similarities in developmental rates of geographically separate European corn borer (Lepidoptera: Pyralidae) populations. Environ. Entomol. 20: 441-449.

CALVO, D. & J. M. MOLINA. 2005. Developmental rates of the lappet moth *Striblote panda* Hübner [1820] (Lepidoptera: Lasiocampidae) at constant temperatures. Span. J. Agr. Res. 3: 319-325.

CHANG, C.-P. 1987. The effect of temperature on the development of *Zeuzera coffeae* Nietner in grape-vine (Cossidae: Lepidoptera). Plant Prot. Bull. (Taiwan) 29: 157-164.

CHEN, C.-N. & W.-Y. SU. 1982. Influence of temperature on development and leaf consumption of three caterpillars on cauliflower. Plant Prot. Bull. (Taiwan) 24: 131-141.

CHI, Y., Y. SAKAMAI, T. KATSUO & K. KANETOSI. 2006. [Effects of temperature on the development of legume pod borer, *Maruca vitrata* (Fabricius) (Lepidoptera, Crambidae)]. Kagoshima Daigaku Noyakubu Gakujmutsu hōkoku. [Bull. Fac. Agric. Kagoshima Univ.] 56: 19-23. [Japanese, English abstract]

COX, P. D. 1974. The influence of temperature and humidity on the life-cycles of *Ephestia figulilella* Gregson and *Ephestia calidella* (Guenée) (Lepidoptera: Phycitidae). J. Stored Prod. Res. 10: 43-55.

DANTHANARAYANA. W. 1975. The bionomics, distribution and host range of the light brown apple moth, *Epiphyas postvittana* (Walk.) (Tortricidae). Austral. J. Zool. 23: 419-437.

DANTHANARAYANA, W., H. GU & S. ASHLEY. 1995. Population growth potential of *Epiphyas postvittana,* the lightbrown apple moth (Lepidoptera: Tortricidae), in relation to diet, temperature and climate. Austral. J. Zool. 43: 381-394.

DAOUD, M. A., G. B. EL-SAADANY, F. M. A. MARIY & M. Y. IBRAHIM. 1999. The thermal threshold units for *Phthorimaea operculella* (Zeller). Ann. Agric. Sci. Ain-Shams Univ. 44: 379-303.

DAVID, P. J., R. L. HORSBURGH & G. I. HOLTZMAN. 1989. Development of *Platynota flavedana* and *P. idaeusalis* (Lepidoptera: Tortricidae) at constant temperatures in the laboratory. Environ. Entomol. 18: 15-18.

DE BERARDINIS, E., A. BUTTURINI & R. TISO. 1991-92. Influenza della temperatura sullo sviluppo di *Pandemis cerasana* (Hb.) (Lepidoptera: Tortricidae). Bull. Ist. Entomol. G. Grandi Univ. Bologna 46: 211-222.

DECKER, G. C. & J. V. MADDOX. 1971. Effect of temperature on rate of development and survival of *Simyra henrici*. J. Econ. Entomol. 64: 94-98.

DELAHAUT, K. 2003. Insects, pp. 405-419. *In:* M. D. Schwartz (ed.). Phenology: an integrative environmental science. Kluwer, Boston. 564 pp.

DESHMUKH, P. D., Y. S. RATHORE & A. K. BHATTACHARYA. 1982. Effect of temperature on the growth and development of *Diacrisia obliqua* (Walker) on five host plants. Indian J. Entomol 44: 21-33.

DOERR, M. D., J. F. BRUNNER & V. P. JONES. 2002. Temperature-dependent development of *Lacanobia subjuncta* (Lepidoptera: Noctuidae). Environ. Entomol. 31: 995-999.

DUMBLETON, L. J. 1939. Contribution to the physical ecology of *Tortrix postvittana*, Walk. (Lep.). Bull. Entomol. Res. 30: 309-319.

ELSEY, K. D. 1980. Pickleworm: effect of temperature on development, fecundity, and survival. Environ. Entomol. 9: 101-103.

El-Shaarawy, M. F., A. A. Gomaa & A. T. El-Garhy. 1975. Biological studies on the Eri silk worm, *Attacus ricini* Boisd. (Lepid., Saturniidae). Z. Angew. Entomol. 78: 82-86.

Fahmy, H. S. M., M. H. Zaazou, A. A. M. Kamel & A. H. El-Hemaesy. 1973. Effect of temperature and humidity on the immature stages of the greasy cutworm, *Agrotis ipsilon* (Hufn.). Bull. Soc. Entomol. Egypte 57: 153-164.

Fleury, P. 1991. Model II regression. Sysnet 8(2): 2-3.

Foerster, L. A. 1996. Efeito da temperatura no desenvolvimento das fases imaturas de *Pseudaletia sequax* Franclemont (Lepidoptera: Noctuidae). An. Soc. Entomol. Brasil 25: 27-32.

Fye, R. E. & W. C. McAda. 1972. Laboratory studies on the development, longevity,and fecundity of six lepidopterous pests of cotton in Arizona. U. S. Dept. Agric. Tech. Bull. 1454, 73 pp.

Gabriel, A. D. & J. J. Obrycki. 1990. Thermal requirements for preimaginal development of the strawberry leafroller (Lepidoptera: Tortricidae). Environ. Entomol. 19: 339-344.

Gal, A. 1978. Der Einfluss der Temperatur auf die Fruchtbarkeit, Entwicklungs- und Überlebensrate von *Paramyelois transitella* (Lep., Pyralidae). Mitt. Deutsch. Ges. Allg. Angew Entomol. 1: 265-269.

Galán, M. & J. Rodriguez. 1992. Estimation of thermic constants for modeling biological cycle of *Diatraea saccharalis* (F.) (Lepidoptera: Pyralidae). Proc. Intern. Soc. Sugarcane Technol. 21: 638-647.

Ghulam-Ullah, C. 1955. The development and fecundity of the oriental fruit moth, *Grapholitha* (Cydia) *molesta* (Busck) under controlled temperatures and humidities. Bull. Entomol. Res. 46: 869-898.

Goebel, R. 2006. The effect of temperature on development and reproduction of the sugarcane stalk borer, *Chilo sacchariphagus* (Bojer 1856) (Lepidoptera: Crambidae). African Entomol. 14: 103-111.

Golizadeh, A., K. Kamali, Y. Fathipour & H. Abbasipour. 2007. Temperature-dependent development of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) on two brassicaceous host plants. Insect Sci. 14: 309-316.

Gomaa, A. A. 1973. Biological studies on the eri silkworm *Attacus ricini* Boisd. (Lepidoptera-Saturniidae). Z. Angew. Entomol. 74: 120-126.

Gould, J., R. Venette & D. Winograd. 2005. Effect of temperature on development and population parameters of *Copitarsia decolora* (Lepidoptera: Noctuidae). Environ. Entomol. 34: 548-556.

Guppy, J. C. 1969. Some effects of temperature on the immature stages of the armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), under controlled conditions. Can. Entomol. 101: 1320-1327.

Hamilton, J. G. & M. P. Zalucki. 1991. Effect of temperature on development rate, survival and fecundity of cotton tipworm, *Crocidosema plebejana* Zeller (Lepidoptera: Tortricidae). Austral. J. Zool. 39: 191-200.

Hammond, R. B., F. L. Poston & L. P. Pedigo. 1979. Growth of the green cloverworm and a thermal-unit system for development. Environ. Entomol. 8: 639-642

Hardy, J. E. 1938. *Plutella maculipennis*, Curt., its natural and biological control in England. Bull. Entomol. Res. 29: 343-372.

Hasegawa, T. & T. Chiba. 1969. Relations of temperature to the development of the egg and larval stage of *Agrotis ipsilon* and *Agrotis fucosa* (Preliminary report). Nihon oyo dobutsu konchugakkai. [Jap. J. Appl. Entomol. Zool.] 13: 124-128.

Haugen, D. A. & F. M. Stephen. 1984. Development rates of Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), life stages in relation to temperature. Environ. Entomol. 13: 56-60.

Hawthorne, D. J., G. C. Rock & R. E. Stinner. 1988. Redbanded leafroller (Lepidoptera: Tortricidae): thermal requirements for development and simulation of within-season phenology in North Carolina. Environ. Entomol. 17: 40-46.

Henneberry, T. J., G. D. Butler & D. L. Coudriet. 1993. Tobacco budworm (Lepidoptera: Noctuidae): effects of temperature and photoperiod on larval and pupal development, larval mortality and induction of pupal diapause. Southwest. Entomol. 18: 269-279.

Herfs, W. 1963. Laboratoriums-Untersuchungen zur Biologie des Nelkenwicklers (*Tortrix pronubana* Hb.) 2. Z. Pflanzenkr. (Pflanzenpath.) Pflanzenschutz 70: 73-81.

Herms, D. 2007. http//www.ipm.msu.edu/landscapeipm/addland-chart.htm.

Higley, L. G., L. P. Pedigo & K. R. Ostlie. 1986. DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ. Entomol. 15: 999-1016.

Hill, J. K. & A. G. Gatehouse. 1992. Effects of temperature and photoperiod on development and pre-reproductive period of the silver Y moth *Autographa gamma* (Lepidoptera: Noctuidae). Bull. Entomol. Res. 82: 335-341.

Hirai, K. 1975. The influence of rearing temperature and density on the development of two *Leucania* species, *L. loreyi* Dup. and *L. separata* Walker (Lepidoptera; Noctuidae). Appl. Entomol. Zool. 10: 234-237.

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66: 483-492.

———. 1996a. The relationship between thermal constants for insect development: a verification. Acta Soc. Zool. Bohem. 60: 115-152.

———. 1996b. Geographical variation in thermal requirements for insect development. Eur. J. Entomol. 93: 303-312.

———. 1999. Constraints on thermal requirements for insect development. Entomol. Sci. 2: 615-621.

Honěk, A. & F. Kocourek. 1990. Temperature and development time in insects: a general relationship between thermal constants. Zool. Jahrb. Syst. 117: 401-439.

Howell, J. F. & L. G. Neven. 2000. Physiological development time and zero development temperature of the codling moth (Lepidoptera: Tortricidae). Environ. Entomol. 29: 766-772.

Huang, C. C. & W. K. Peng. 2002. Effect of temperatures on the development of legume pod borer, *Maruca vitrata* (Lepidoptera: Pyralidae) on *Sesbania cannabina*. Plant Prot. Bull. (Taiwan) 44: 245-248.

Hutchison. W. D., G. D. Butler & J. M. Martin. 1986. Age-specific developmental times for pink bollworm (Lepidoptera: Gelechiidae): three age classes of eggs, five larval instars, and pupae. Ann. Entomol Soc. Am. 79: 482-487.

Ikemoto, T. & K. Takai. 2000. A new linearized formula for the law of total effective temperature and the evaluation of line-fitting methods with both variables subject to error. Environ. Entomol. 29: 671-682.

Itô, Y. & K. Miyashita. 1968. Biology of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) in Japan 6. Effect of temperature on development of immature stages. Appl. Entomol. Zool. 3: 163-175.

Jackson, C. G., G. D. Butler & D. E. Bryan. 1969. Time required for development of *Voria ruralis* and its host, the cabbage looper, at different temperatures. J. Econ. Entomol. 62: 69-70.

Jacob, T. A. & P. D. Cox. 1977. The influence of temperature and humidity on the life-cycle of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). J. Stored Prod. Res. 13: 107-118.

Jallow, M. F. A. & M. Matsumura. 2001. Influence of temperature on the rate of development of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Appl. Entomol. Zool. 36: 427-430.

Janisch, E. 1933. Untersuchungen über die Oekologie und Epidemiologie der Nonne 1. Die Abhängigkeit der Entwicklungsdauer von Temperatur und Luftfeuchtigkeit. Arb. Biol. Reichsanst. Land. Forstw. 20: 269-290.

Jasic, J. 1967. Influencia de las condiciones de temperatura en la evolución de *Diatraea saccharalis* (Fabricius). Poeyana (Ser. A) No. 35, 9 pp.

Johansen, N. S. 1997. Influence of temperature on development, fecundity and survival of the cabbage moth *Mamestra brassicae* (L.) (Lep., Noctuidae) in relation to the improvement of forecasting and control methods. J. Appl. Entomol. 12: 81-88.

Jones, V. P. 2005. A synthesis of the temperature dependent development rate for the obliquebanded leafroller, *Choristoneura rosaceana*. J. Ins. Sci. 5: 1-8.

Judd, G. J. R., J. E. Cossentine & M. G. T. Gardiner. 1994. Temperature-dependent development of the speckled green fruit-worm, *Orthosia hibisci* Guenée (Lepidoptera: Noctuidae). Can. Entomol. 126: 1263-1275.

Kamata, N. & M. Igarashi. 1995. Relationship between temperature, number of instars, larval growth, body size, and adult fecundity of *Quadricalcarifera punctatella* (Lepidoptera: Notodontidae): cost-benefit relationship. Environ. Entomol. 24: 648–656.

Kamm, J. A. 1991. Larval development of *Dargida procincta* (Grote) (Lepidoptera Noctuidae) in the Pacific Northwest. Pan-Pac. Entomol. 67: 20-23.

Kaufmann, O. 1932. Einige Bemerkungen über den Einfluss von Temperaturschwankungen auf die Entwicklungsdauer und Streuung bei Insekten und seine graphische Darstellung durch Kettenlinie und Hyperbel. Z. Morph. Ökol. Tiere 25: 353-361.

Kim, D.-S., J.-H. Lee & M.-S. Yiem. 2001. Temperature-dependent development of *Carposina sasakii* (Lepidoptera: Carposinidae) and its stage emergence models. Environ. Entomol. 30: 298-305.

King, E. G., F. D. Brewer & F. Martin. 1975. Development of *Diatraea saccharalis* (Lep. Pyralidae) at constant temperatures. Entomophaga 20: 301-306.

Kinjo, K. & N. Arakaki. 2002. Effect of temperature on development and reproductive characteristics of *Diaphania indica* (Saunders) (Lepidoptera; Pyralidae). Appl. Entomol. Zool. 37: 141-145.

Koizumi, K. 1955. Effect of constant temperature upon the development of the potato tuber moth, *Gnorimoschema operculella* (Zeller). Okayama Daigaku Nogkubu Gakujutsu Hokuku. [Scientific Reports, Faculty of Agriculture Okayama University] 7: 36-45.

Kwon, M., H.-J. Kwon & S.-H. Lee. 2005. Temperature-dependent development and seasonal occurrence of cabbage armyworm (*Mamestra brassicae* L.) at highland Chinese cabbage fields. Korean J. Appl. Entomol. 44: 225-230. [Korean and English]

Langford, G. S. & E. N. Cory. 1932. Observations on the potato tuber moth. J. Econ. Entomol. 25: 625-634.

Lee, K.-Y., K.-S. Ahn, H.-J. Kang, S.-K. Park & T.-S. Kim. 2002. Effects of temperature on reproduction and development of *Udea ferrugalis* (Lepidoptera: Pyralidae). Korean J. Appl. Entomol. 41: 205-209.

Legaspi, J. C. & B. C. Legaspi. 2007. Life table analysis for *Cactoblastis cactorum* immatures and female adults under five constant temperatures: implications for pest management. Ann. Entomol. Soc. Am. 100: 497-505.

Legg, D. E., J. M. Struttmann, S. M. Van Vleet & J. E. Lloyd. 1998a. Bias and variability in lower developmental thresholds estimated from field studies. J. Econ. Entomol. 91: 891-898.

Legg, D. E., S. M. Van Vleet, J. E. Lloyd & K. M. Zimmerman. 1998b. Calculating lower developmental thresholds of insects from field studies. Recent Res. Devel. Entomol. 2: 163-172.

Legg, D. E., S. M. Van Vleet, D. W. Ragsdale, R. W. Hansen, B. M. Chen, L. Skinner & J. E. Lloyd. 2002. Required number of location-years for estimating functional lower developmental thresholds and required thermal summations of insects: the first emergence of adult *Apthona nigriscutis* Foudras as an example. Int. J. Pest Mgt. 48: 147-154.

Levine, E. 1983. Temperature requirements for development of the stalk borer, *Papaipema nebris* (Lepidoptera: Noctuidae). Ann. Entomol. Soc Am. 76: 892-895.

Li, X., K. Wu & P. Gong. 1990. Effects of temperature on population growth and intake of food by the army worm, *Mythimna asparata* (Walker). J. Environ. Sci. (China) 2: 39-44.

Lin, S. Y. H. & J. T. Trumble. 1985. Influence of temperature and tomato maturity on development and survival of *Keiferia lycopersicella* (Lepidoptera: Gelechiidae). Environ. Entomol. 14: 855-858.

Liu, S.-S., G.-M. Zhang & J. Zhu. 1995. Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. Ann. Entomol. Soc. Amer. 88: 107-ll9.

Liu, S.-S., F.-Z. Chen & M. P. Zalucki. 2002. Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. Environ. Entomol. 31: 221-231.

Lopez, C., A. S. L. Asin & M. Eizaguirre. 2001. Phenological model for *Sesamia nonagrioides* (Lepidoptera: Noctuidae). Environ. Entomol. 30: 23-30.

Luckmann, W. H., J. T. Shaw, D. W. Sherrod & W. G. Ruesink. 1976. Development rate of the black cutworm. J. Econ. Entomol. 69: 386-388.

Lysyk, T. J. & V. G. Nealis. 1988. Temperature requirements for development of the jack pine budworm (Lepidoptera: Tortricidae) and two of its parasitoids (Hymenoptera). J. Econ. Entomol. 81: 1045-1051.

Madge, D. S. 1962. The biology of the cutworm *Tryphaena pronuba* L. (Lepidoptera Noctuidae). Entomol. Exp. Appl. 5: 261-269.

Magrini, E. A., S. S. Neto, J. R. P. Parra, P. S. M. Botellho & M. L. Haddad. 1996. Biologia e exigências térmicas de *Anticarsia gemmatalis* Hübner (Lepidoptera:) em laboratório. An. Soc. Entomol. Brasil 25: 513-519.

Maksimovic, M. 1963. Experimental research on the influence of temperature upon the development and the population dynamics of the gypsy moth (*Liparis dispar* L.). [Translated from Serbo-Croatian] U. S. Dept. Agric. and Nat. Sci. Found., Washington, D. C., NOLIT Publ. House, Belgrade, Serbia.

Manfredi-Coimbra, S., M. S. Garcia & M. Botton. 2001. Exigências térmicas e estimativa do número de gerações de *Argyrotaenia sphaleropa* (Meyrick) (Lepidoptera: Tortricidae). Neotrop. Entomol. 30: 553-557.

Mao, H. & Y. Kunimi. 1990. Effects of temperature and photoperiod on development of the oriental tea tortrix, *Homona magnanima* Diakonoff (Lepidoptera: Tortricidae). Japan. J. Appl. Entomol. Zool. [Nihon oyo dobutsu konchugakkai] 34: 127-130.

Martin, T. L. and R. B. Huey. 2008. Why "suboptimal" is optimal: Jensen's Inequality and ectotherm thermal preferences. Am. Nat. 171E102-E118.

Matteson, J. W. & G. C. Decker. 1965. Development of the European corn borer at controlled constant and variable temperatures. J. Econ. Entomol. 58: 344-349.

Mawby, L. P., P. D. Mowery & W. M. Bode. 1976. Rate of development of *Platynota idaeusalis* at constant temperatures. Ann. Entomol. Soc. Am. 69: 1091-1094.

Miller, W. E. 1996. Population behavior and adult feeding capability in Lepidoptera. Environ. Entomol. 25: 213-226.

———. 2005. Extrinsic effects on fecundity-maternal weight relations in capital-breeding Lepidoptera. J. Lepid. Soc. 59: 143-160.

Milonas, F. G. & M. Savopoulou-Soultani. 2000. Development, survivorship, and reproduction of *Adoxophtyes orana* (Lepidoptera: Tortricidae) at constant temperatures. Ann. Entomol. Soc. Am. 93: 96-102.

Miner, F. D. 1947. Life history of the diamondback moth. J. Econ. Entomol. 40: 581-583.

Mitra, K. & A. Verma. 1981. Effect of temperature and relative humidity on the development of sugarcane stalk borer *Chilo auricilius* Dudg. Indian J. Ecol. 8: 217-222.

Miyashita, K. 1971. Effects of constant and alternating temperatures on the development of *Spodoptera litura* F. (Lepidoptera: Noctuidae). Appl. Enbtomol. Zool. 6: 105-111.

Nabeta, F. H, M. Nakai & Y. Kunimi. 2005. Effects of temperature and photoperiod on the development and reproduction of *Adoxophyes honmai* (Lepidoptera: Tortricidae). Appl. Entomol. Zool. 40: 231-238.

Nasr, E.-S. A. & G. M. Moawad. 1972. Some biological aspects concerning the black cutworm, *Agrotis ipsilon* (Hufn.). Bull. Soc. Entomol. Egypte 46: 139-144.

Oliviera, M. L., M. V. Vieira & P. V. Garcia. 2004. Effect of temperature on the biology of *Noctua atlantica* (Lepidoptera: Noctuidae), a species endemic to the Azores. Eur. J. Entomol. 101: 423-426.

Parrella, P. & L. T. Kok. 1977. The development and reproduction of *Bedellia somnulentella* on hedge bindweed and sweet potato. Ann. Entomol. Soc. Am. 70: 925-928.

Peairs, L. M. 1927. Some phases of the relation of temperature to the development of insects. W. Va. Agric. Expt. Stn. Bull. 208, 62 pp.

PETER, C. & B. V. DAVID. 1992. Studies on the thermal requirement for development of *Diaphania indica* (Saunders) (Lepidoptera: Pyralidae). J. Ins. Sci. 5: 172-174.

PITCAIRN, M. J., C. PICKEL, L. A. FALCON & F. G. ZALOM. 1991. Development and survivorship of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) at ten constant temperatures. Pan-Pac. Entomol. 67: 189-194.

PODOLSKY, A. S. 1984. New phenology: elements of mathematical forecasting in ecology. Wiley, New York. 504 pp.

PREVETT, P. F. 1968. Some laboratory observations on the life-cycle of *Cadra calidella* (Guen.) (Lepidoptera: Phytcitidae). J. Stored Prod. Res. 4: 233-238.

———. 1971. Some laboratory observations on the development of two African strains of *Plodia interpunctella* (Hübn.) (Lepidoptera: Phycitidae), with particular reference to the incidence of diapause. J. Stored Prod. Res 7: 253-260.

PRUESS, K. P. 1983. Day-degree methods for pest management. Environ. Entomol. 12: 613-619.

QUAGLIA, F. 1983 (1985). Influenza della temperatura costante sullo sviluppo pre-maginale di *Epichoristodes acerbella* (Walker) (Lepidoptera: Tortricidae). Frustula Entomol. 6: 255-280.

RAHMAN, M. T. & M. KHALEQUZZAMAN. 2004. Temperature requirements for the development and survival of rice stemborers in laboratory conditions. Entomol. Sinica. 11: 47-60.

RANGA RAO, G. V., J. A. WIGHTMAN & D. V. RANGA RAO. 1989. Threshold temperatures and thermal requirements for the development of *Spodoptera litura* (Lepidoptera: Noctuidae). Environ. Entomol. 18: 548-551.

RATTE, H. T. 1984. Temperature and insect development, pp 33-66. *In:* Hoffman, K. H. (ed.). Environmental physiology and biochemistry of insects. Springer, Berlin.

RÉGNIÈRE, J. 1987. Temperature-dependent development of eggs and larvae of *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. Can. Entomol. 119: 717-728.

RÉGNIÈRE, J. & J. A. LOGAN. 2003. Animal life cycle models. Pp. 237-254, *In*: M. D. Schwartz (ed.). Phenology: an integrative environmental science. Kluwer, Boston. 564 pp.

RÉGNIÈRE, J. & J. J. TURGEON. 1989. Temperature-dependent development of *Zeiraphera canadensis* and simulation of its phenology. Entomol. Exp. Appl. 50: 185-193.

RICHMOND, J. A. & J. E. BACHELER. 1989. A comparison of two temperature-dependent development models for immature stages of the Nantucket pine tip moth (Lepidoptera: Tortricidae). J. Entomol. Sci. 24: 117-123.

ROBERTS, S. L. & D. L. MAHR. 1986. Development of cranberry girdler, *Chrysoteuchia topiaria* (Lepidoptera: Pyralidae) in relation to temperature. Great Lakes Entomol. 19: 85-90.

ROCK, G. C. 1985. Thermal and thermoperiodic effects on larval and pupal development and survival in tufted apple bud moth (Lepidoptera: Tortricidae). Environ. Entomol. 14: 637-640.

ROLTSCH, W. J., M. A. MAYSE & K. CLAUSEN. l990. Temperature-dependent development under constant and fluctuating temperatures: comparison of linear versus nonlinear methods for modeling development of western grapeleaf skeletonizer (Lepidoptera: Zygaenidae). Environ. Entomol. 19: 1689-1697.

RUEL, J. J. & M. P. AYRES. 1999. Jensen's inequality predicts effects of environmental variation. Trends Ecol. Evol. 14: 361-366.

SANDS, D. P. A., M. SCHOTZ & A. S. BOURNE. 1991. Effects of temperature on development and seasonality of *Eudocima salaminia* (Lepidoptera: Noctuidae) in eastern Australia. Bull. Entomol. Res. 81: 291-296.

SHANOWER, T. G., F. SCHULTHESS & N. BOSQUE-PEREZ. 1993a. Development and fecundity of *Sesamia calamistis* (Lepidoptera: Noctuidae) and *Eldana saccharina* (Lepidoptera; Pyralidae). Bull. Entomol. Res. 83: 237-243.

SHANOWER, T. G., A. P. GUTIERREZ & J. A. WIGHTMAN. 1993b. Effect of temperature on development rates, fecundity and longevity on the groundnut leaf miner, *Aproaerema modicella* (Lepidoptera: Gelechiidae), in India. Bull. Entomol. Res. 83: 413-419.

SHARMA, S. K. & J. P. CHAUDHARY. 1988. Effects of different levels of constant temperature and humidity on the development and survival of *Heliothis armigera* (Hübner). Indian J. Entomol. 50: 76-81.

SHIELDS, E. S. 1983. Development rate of variegated cutworm (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 76: 171-172.

SIDIBÉ, B. & G. LAUGÉ. 1977. Incidence de thermopériodes et de temperatures constantes sur quelques critéres biologiques de *Spodoptera littoralis* Boisduval (Lepidoptera Noctuidae). Ann. Soc. Entomol. France (N. S.) 13: 369-379.

SIMONET, D. E., S. L. CLEMENT, W. L. RUBINK & R. W. RINGS. 1981. Temperature requirements for development and oviposition of *Peridroma saucia* (Lepidoptera: Noctuidae). Can. Entomol. 113: 891-897.

SINCHAISRI, N. & K. SÖGAWA. 1969. The influence of temperature on the development of armyworm, *Leucania separata* Walker (Lepidoptera: Noctuidae). Appl. Entomol. Zool. 4: 102-103.

SINGH, M. P. 1962. Environmental factors influencing the development of the cutworms 1. Temperature reactions. Proc. Zool. Soc. (Calcutta) 15: 27-37.

SMITH, A. M. 1984. Larval instar determination and temperature-development studies of immature stages of the common armyworm, *Mythimna convecta* (Walker) (Lepidoptera: Noctuidae). J. Austral. Entomol. Soc. 23: 91-97.

SNYDER, K. D. 1954. The effect of temperature and food on the development of the variegated cutworm *Peridroma margaritosa* Haw. (Order Lepidoptera, Family Noctuidae). Ann. Entomol. Soc. Am. 47: 603-613.

SOKAL, R. R. & F. J. ROHLF. 1981. Biometry, ed 2. Freeman, New York. 859 pp.

SPORLEDER, M., J. KROSCHEL, M. R. GUTIERREZ QUISPE & A. LAGNOUI. 2004. A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; Gelechiidae). Environ. Entomol. 33: 477-486.

STAN, G. 1998. Influence of temperature on growth, development and food consumption by larvae of *Mamestra brassicae* L. (Lepidoptera: Noctuidae) under laboratory conditions. Stud. Univ. Babes-Bolyai. Biol. 43: 51-63.

SYSTAT. 1992. Statistics, version 5.2. SYSTAT Inc. Evanston, Illinois.

TAMMARU, T. & E. HAUKIOJA. 1996. Capital breeders and income breeders among Lepidoptera—consequences to population dynamics. Oikos 77: 561-564.

TAKEDA, M. & G. M. CHIPPENDALE. 1982. Phenological adaptations of a colonizing insect: the southwestern corn borer, *Diatraea grandiosella*. Oecologia (Berl.) 53: 386-393.

TAVERAS, R., L. HILJE & M. CARBALLO. 2004. Development of *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) in reponse to constant temperatures. Neotrop. Entomol. 33: 1-6.

TAYLOR, F. 1981. Ecology and evolution of physiological time in insects. Amer. Nat. 117: 1-23.

TISO, R., E. DE BERARDINIS, A. BUTTURINI & G. BRIOLINI. 1991-92. Influenza della temperatura sullo sviluppo di *Argyrotaenia pulchellana* (Hw.) (Lepidoptera: Tortricidae). Boll. Ist. Entomol. G. Grandi Univ. Bologna 46: 161-172.

TOBIN, P. C., S. NAGARKATTI & M. C. SAUNDERS. 2001. Modeling development in grape berry moth (Lepidoptera: Tortricidae). Environ. Entomol. 30: 692-699.

TRUDGILL, D. L. 1995. Why do tropical poikilothermic organisms tend to have higher threshold temperatures for development than temperate ones? Funct. Ecol. 9: 136-137.

TRUDGILL, D. L. & J. N. PERRY. 1994. Thermal time and ecological strategies—a unifying hypothesis. Ann. Appl. Biol. 125: 521-532.

TULI, S., P. B. MOOKHERJEE & G. C. SHARMA. 1966. Effect of temperature and humidity on the fecundity and development of *Cadra cautella* Wlk. in wheat. Indian J. Entomol. 28: 305-317.

TWINE, P. H. 1978. Effect of temperature on the development of larvae and pupae of the corn earworm, *Heliothis armiger*a (Hübner) (Lepidoptera: Noctuidae). Queensland J. Agric. Anim. Sci. 35: 23-28.

UVAROV, B. P. 1931. Insects and climate. Trans. Entomol. Soc. London 79: 1-247.

WADA, T. & M. KOBAYASHI. 1980. Effects of temperature on development of the rice leaf roller, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). Appl. Entomol. Zool. 15: 207-214.

WAGNER, T. L., H.-I WU, P. J. H. SHARPE, R. M. SCHOOLFIELD & R. N. COULSON. 1984. Modeling insect development rates: a literature review and application of a biophysical model. Ann. Entomol. Soc. Am. 77: 208-225.

WANG, J. Y. 1960. A critique of the heat unit approach to plant response studies. Ecology 41: 785-790.

WEINBERG, H. L. & W. H. LANGE. 1980. Development rate and lower temperature threshold of the tomato pinworm. Environ. Entomol. 9: 245-246.

WHITWORTH, R. J. & F. L. POSTON. 1979. A thermal-unit accumulation system for the southwestern corn borer. Ann. Entomol. Soc. Am. 72: 253-255.

WILSON, L. T. & W. W. BARNETT. 1983. Degree-days: an aid in crop and pest management. Calif. Agric. 37(1-2): 4-7.

WORNER, S. P. 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. Environ. Entomol. 21: 689-699.

YAMADA, H. & K. KAWASAKI. 1983. The effect of temperature and humidity on the development, fecundity and multiplication of the diamondback moth, *Plutella xylostella* (L.). Nihon oyo dobutsu konchugakkai. [Jap. J. Appl. Entomol. Zool.] 27: 17-21.

YAMADA, H. & T. KOSHIHARA. 1976. Development of the Hawaiian beet webworm, *Hymenia recurvalis* (Fabricius) (Lepidoptera: Pyralidae). Japan. J. Appl. Entomol. Zool. [Nihon oyo dobutsu konchugakkai] 20: 213-214. [Japanese]

ZWÖLFER, W. 1931. Studien zur Ökologie und Epideiologie der Insekten 1. Die Kieferneule, *Panolis flammea* Schiff. Z. Angew. Entomol. 17: 475-562.

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Appendix 1. Weather stations and data used in this study

Station	Months and years
	Canada
Fredericton, NB	May-Aug. 1940, 1950
Montreal River, ON	May-Aug. 1933, 1965
Timmins, ON	May-Aug. 1930, 1953
Guelph Arboretum, ON	May-Aug. 1985, 1990
Sioux Lookout, ON	May-Aug. 1920, 1932
Brandon CDA, MB	May-Aug. 1927, 2000
Regina CDA, SK	May-Aug. 1970
	United States
Harrisburg, PA	May-Aug. 1935, 1940
Cincinnati, OH	May-Aug. 1990, 2000
Lansing, MI	May-Aug. 1960, 1965
Le Roy, MN	May-Aug. 1950, 1960
Lincoln AFB, NE	May-Aug. 1950, 1955
Sioux Falls, SD	July-Aug. 1995
Oklahoma City, OK	June-Aug. 1950, 1960,1970
Minot, ND	July 1936
Rapid City, SD	July-Aug. 1955, July 1980
Cheyenne, WY	May-Aug. 1990, 2000
Boise, ID	May-Aug. 1955

Appendix 2. Sources containing one or more datasets dropped from the study because fewer than four linear points survived thermal characteristic revision with improved linear model procedure.

Adati et al. (2004), Åsman (2001), Atkinson (1980), Barker & Enz (1993), Beckwith (1982), Berkett et al. (1976), Bues & Poitout (1980), Calvin et al. (1991), Chen & Su (1982), Cox (1974), Danthanarayana (1975), Danthanarayana et al. (1995), De Berardinis et al. (1991-92), Deshmukh et al. (1982), Doerr et al. (2002), El-Shaarawy et al. (1975), Foerster (1996), Fye & McAda (1972), Gal (1978), Galán & Rodriguez (1992), Ghulam-Ullah (1955), Goebel (2006), Gomaa (1973), Hardy (1938), Hasegawa & Chiba (1969), Herfs (1963), Hirai (1975), Howell & Neven (2000), Huang & Peng (2002), Jacob & Cox (1977), Janisch (1933), Jones (2005), Kamata & Igarashi (1995), Kinjo & Arakaki (2002), Koizumi (1955), Kwon et al. (2005), Li et al. (1990), Maksimovic (1963), Mawby et al. (1976), Milonas & Savopoulou-Soultani (2000), Miyashita (1971), Oliviera et al. (2004), Parrella & Kok (1977), Prevett (1968), Rahman & Khalequzzaman (2004), Richmond & Bacheler (1989), Roberts & Mahr (1986), Roltsch et al. (1990), Shanower et al. (1993b), Shields (1983), Sidibé & Laugé (1977), Sinchaisri & Sögawa (1969), Singh (1962), Takeda & Chippendale (1982), Taveras et al. (2004), Weinberg & Lange (1980), and Yamada & Koshihara (1976).