Temperature-Dependent Development of Mexican Bean Beetle (Coleoptera: Coccinellidae) Under Constant and Variable Temperatures

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ABSTRACT Development of immature stages of the Mexican bean beetle, *Epilachna varivestis* Mulsant, on dry beans, *Phaseolus vulgaris* L. (cv. 'Maine Yellow eye'), was assessed at six constant temperatures from 15 to 30°C. Relationships between temperature and developmental rate were described by linear degree-day and nonlinear biophysical models. Minimum threshold values in the degree-day model for the egg, larval, and pupal stages were 8.6, 7.6, and 9.3°C, respectively. Development of the egg, first, second, third, and fourth instars, and pupae required 98.2, 61.7, 50.5, 60.6, 105.9, and 90.3 degree-days, respectively. First-instar developmental data were fit to a two-parameter biophysical model; egg, second-, third-, and fourth-instar and pupal developmental data were fit to a four-parameter biophysical model with high temperature inhibition. Two laboratory experiments with thermoperiodic regimes and observations from field cage studies showed that the degree-day model resulted in more accurate predictions than the biophysical model.

KEY WORDS *Epilachna varivestis*, temperature effects, model

THE MEXICAN BEAN BEETLE, *Epilachna varivestis* Mulsant, is an introduced economic pest of field beans, *Phaseolus* spp., and soybean, *Glycine max* (L.) Merril, throughout the United States. In less than a century, it has extended its distribution from Central America to Canada (Auclair 1959). Predicting the occurrence of developmental stages is a crucial factor in Integrated Pest Management (IPM) decision making because economic damage is often heaviest during certain stages. Temperature is paramount among the factors that influence the developmental rate of Mexican bean beetle though host species and cultivar also have an effect (Kogan 1972).

Developmental times of the Mexican bean beetle have been reported on soybean in Georgia (Bernhardt & Shepard 1978) and Virginia (McAvoy & Smith 1979) and on field beans in Mexico (Cardenas et al. 1980). All these studies were conducted at two or three temperatures, which are too few data points to describe the whole profile of relationship between temperature and the Mexican bean beetle developmental rate. Hammond (1984) evaluated the effect of a range of constant temperatures on Mexican bean beetle developmental times on both soybean and green bean in Ohio, but he did not quantify the relationship between temperature and developmental rate. Waddill et al. (1976) developed a simulation model of Mexican bean beetle population using "physiological day," a 24-h period at 27°C and a threshold of 15°C. Though Bernhardt & Shepard (1978) utilized this model in their validation study, their data indicated that a lower threshold (9.3°C) may be more accurate for predicting Mexican bean beetle development.

There are many forms of model available to describe mean developmental times or rates of development as a function of temperature. The degree-day model and the nonlinear models of Stinner et al. (1974), Logan et al. (1976), and Sharpe & DeMichele (1977) are used most frequently. The basic assumption of the degree-day model is that a linear relationship exists between developmental rate and temperature. The nonlinearity between developmental rate and temperature exhibited by some insect species is often regarded as a limitation in application of the degree-day model (Wang 1960, Wagner et al. 1984, Logan et al. 1985). Much experimental evidence indicates that daily temperature cycles can influence predictions of insect development, especially when some temperatures in the cycling regimes exceed upper or lower thresholds (Beck 1983). However, slower developmental rates and higher mortality observed in experi-

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ments with exposures to constant, extreme temperature may not reflect the response under natural conditions of fluctuating temperatures (Logan et al. 1985). In our study, we determined the temperature-dependent development of each of the immature stages of the Mexican bean beetle under constant temperatures and evaluated the fit of these developmental rate data to a linear degree-day model and a nonlinear biophysical model (Sharpe & DeMichele 1977) using Mexican bean beetle developmental data from laboratory and field cage experiments under thermoperiodic temperature regimes.

Materials and Methods

A Mexican bean beetle colony was established from adults collected in a commercial green bean field in Belgrade, ME, in July 1988. Larvae were reared in a greenhouse on potted dry beans (*P. vulgaris* cv. 'Maine Yellow eye') in 0.9 by 0.6 by 1.2 m cages. Pupae were collected and held in ventilated plastic boxes in a growth chamber at 21 ± 1°C, about 90% RH, and a photoperiod of 16:8 (L:D) h. Adults were also kept in ventilated, plastic boxes lined with moist paper towel and fed excised bean leaves three times a week. All experimental plants were grown in a greenhouse with potting mix and inoculated with *Rhizobium* at planting. Individuals from the third to sixth generations of the laboratory colony were used.

Constant-Temperature Experiments and Model Development. Egg masses used in the development studies were collected every 24 h, carefully cut away from the leaf, and placed in covered, plastic petri dishes (10 cm diameter) lined with moistened filter paper. Egg masses were divided into two or more submasses that were assigned to different, constant temperature chambers. Egg development was monitored at the following constant temperatures: 15 (n = 16), 18 (n = 17), 21 (n = 42), 24 (n = 41), 27 (n = 19), and 30°C (±1°C) (n = 20). All chambers were set at about 90% RH and a photoperiod of 16:8 (L:D) h. The egg masses were assumed to have undergone an average of 6 h of development in the oviposition chamber before removal and exposure to the test temperatures, so adjustments in the estimate of developmental rate were made accordingly (Logan et al. 1985). Egg masses were checked every 12 h, and an egg mass was considered "hatched" when ≥50% of the eggs in the egg mass had hatched.

The same constant temperatures listed above were used to assess larval and pupal development. Newly hatched first instars (≤12 h old) were placed individually in petri dishes (10 cm diameter) lined with moist filter paper and containing fresh, excised bean leaves. Foliage was replaced with fresh foliage every other day; to reproduce plant quality under Maine field conditions, leaves were taken only from plants between flowering and pod-filling stages. Developmental status was recorded every 12 h until adults emerged.

Two replicate studies of larval and pupal developmental rate were conducted at all temperatures except 15°C, at which only one replicate study was conducted. The initial number of first instars was 15–20 per temperature per replicate. Adjustments in estimates of first-instar development were made to account for time spent at 21°C before being transfered to the test temperatures. In all cases, the midpoint of the two observations was used to calculate the length of each life stage. Data from the two replicates were pooled for the following analyses.

Developmental minimum thresholds for each of the immature Mexican bean beetle stages were calculated using the x-intercept method of Arnold (1959) (GLM, SAS Institute 1985). Ninety-five percent confidence intervals of the estimates were computed (Sokal & Rohlf 1981) to compare thresholds among instars. Degree-days required for each of the immature stages were computed from the mean degree-days needed at each temperature. Because temperatures of 30°C or higher are infrequent during June, July, and August in Maine, developmental data at 30°C were not included in the calculations of thresholds and degree-days required.

The same data were fit to the biophysical, poikilotherm model developed by Sharpe & DeMichele (1977) and modified by Schoolfield et al. (1981):

$$r(T) = \frac{\mathrm{RHO25}\,\frac{T}{298.15}\exp\left[\frac{HA}{R}\left(\frac{1}{298.15}-\frac{1}{T}\right)\right]}{1+\exp\left[\frac{HL}{R}\left(\frac{1}{TL}-\frac{1}{T}\right)\right]+\exp\left[\frac{HH}{R}\left(\frac{1}{TH}-\frac{1}{T}\right)\right]}$$

where $r(T)$ is the developmental rate at temperature T(°K); RHO25 is the developmental rate at 25°C with no enzyme inhibition; HA is the enthalpy of activation of the reaction catalyzed by a rate-controlling enzyme; TL is the temperature (°K) at which the rate-controlling enzyme is half inactive because of low-temperature inhibition; HL is the change in enthalpy associated with low-temperature inhibition of the enzyme; TH is the temperature (°K) at which the rate-controlling enzyme is half inactive because of high-temperature inhibition; HH is the change in enthalpy associated with high-temperature inhibition of the enzyme; and R is the universal gas constant (1.987 cal °C^{-1} mol^{-1}). Schoolfield et al. (1981) discussed the physiochemical interpretations of all parameters. Estimation of parameters was done by using a SAS program (Wagner et al. 1984) with slight modification in fitting the pupal

developmental rate data by increasing TLIMIT from 15 to 20.

Model Validation. *Variable-Temperature Experiments.* Studies were conducted to evaluate the accuracy of the degree-day and biophysical models for Mexican bean beetle reared at variable temperatures. The egg masses and larvae were exposed to one of the following thermoperiodic regimes (8:16, C/T [C, cryophase; T, thermophase]): 11/21, 13/23, 15/25, and 17°C/27°C (±1°C). The developmental times of 56, 52, 71, 61, and 59 egg masses and 54, 22, 22, and 40 first instars were monitored at the above thermoperiodic regimes, respectively. The procedures and experimental conditions were the same as in the constant-temperature experiments except that the observation interval was increased to 24 h.

In a second set of experiments, three thermoperiodic regimes with the same average temperature (25.7°C) were evaluated. The thermoperiodic regimes were 19/29, 23/31, and 24.2°C/33.0°C (±1°C) for 8:18, 16:8, and 20:4 (C/T), respectively. Fifty-nine, 55, and 57 egg masses and 30, 40, and 60 first instars were observed at each of the above thermoperiodic regimes, respectively. Photoperiod and relative humidity were as described above.

Field Experiments. Field studies were conducted in the summers of 1989 and 1990 at the University of Maine Sustainable Agriculture Research Farm, Stillwater, ME. Dry beans (*P. vulgaris* cv. 'Maine Yellow eye') were grown with both conventional and low-input production practices (Fan 1991). The former system included plowing, use of the herbicides glyphosate, chloramben, and ethalfluralin at rates of 4.7 liter/ha, 3.4 kg/ha, and 2.3 liter/ha, respectively, and application of fertilizer (10:20:10) at a rate of 447 kg/ha at planting in 1989 and at the primary leaf stage in 1990. The low-input system included no-till planting, rye mulch cover, and no fertilizers or herbicides. Experimental plots were arranged in a randomized complete-block design with five replications in 1989 and a completely randomized design with three replications in 1990. The experiments were conducted during the flowering to pod-filling stages of growth.

In 1989, one plant in each plot was covered with a 0.3 by 0.3 by 0.6 m cage and infested with 6–10 newly hatched first instars. In 1990, four plants in each plot were caged individually and infested with 5, 10, 15, or 20 newly hatched first instars. Development was monitored daily and stages of development were recorded for all cages when about 50% of the individuals in a cage were entering the next stage. Weighted mean instar (=stadium) (Haynes 1976) was calculated to estimate the mean population age for each observation and plot in 1990. A repeated measures design ANOVA (SAS Institute 1985) was used to test for differences between the two cropping systems and density effects. Daily maximum and minimum temperatures were recorded at a nearby weather station (≈50 m away). Degree-days were calculated with the sine wave approximation method (Baskerville & Emin 1969, Allen 1976), coded with a FORTRAN 77 program. Development times from first instar to pupa predicted by the biophysical models were computed with a FORTRAN 77 program. Daily temperature fluctuations were simulated with a sine function. Temperatures every 2.4 h were calculated and used as inputs to drive the biophysical model.

Results

Constant-Temperature Experiments and Model Development. Larval mortality ranged from 15.6 to 27.3% with no significant correlation with temperature ($r = 0.09$; $n = 5$; $P > 0.86$). Pupal mortality was <5.0% except at 30°C, where 28.6% mortality was observed.

At higher, constant temperatures within the range of 15 to 27°C, times required to complete development for all immature stages decreased. However, at 30°C, no egg development occurred, and developmental rates of other stages (except first instars) increased only slightly or not at all (Fig. 1). The results suggest that there is an upper developmental rate maximum near 30°C for Mexican bean beetle reared at constant temperatures.

High r^2 values (ranging from 0.969 to 0.997) indicate a good fit of the data to the linear degree-day model within the temperature range of 15 to 27°C (Table 1; Fig. 1). Estimates of minimum thresholds for egg and pupal development were 8.6 and 9.3°C, respectively. There were no significant differences ($\alpha = 0.05$) among instars in minimum thresholds, as 95% CIs overlapped broadly. Therefore, the minimum threshold estimated for the total larval stage was used for determining the number of degree-days required to complete development for each instar.

In fitting the biophysical model, developmental data at 30°C were incorporated. Using the SAS program (Wagner et al. 1984), first-instar developmental data were fitted to a two-parameter model, while the egg, second-, third-, fourth-instar, and pupal developmental data were fitted to a four-parameter model with high temperature inhibition (Fig. 1). Parameter estimates and r^2 values were as follows: egg, $HA = 22252.0$, RHO25 = 0.2583, $HH = 62383.8$, $TH = 301.0$, and $r^2 = 0.999$; first instar, $HA = 11097.9$, RHO25 = 0.2798, and $r^2 = 0.992$; second instar, $HA = 14151.9$, RHO25 = 0.3659, $HH = 73735.9$, $TH = 305.3$, and $r^2 = 0.999$; third instar, $HA = 17006.3$, RHO25 = 0.3541, $HH = 49069.6$, $TH = 303.7$, and $r^2 = 0.998$; fourth instar, $HA = 19933.2$, RHO25 = 0.2361, $HH = 43082.0$, $TH = 301.9$, and $r^2 = 1.000$; pupae, $HA = 15903.2$,

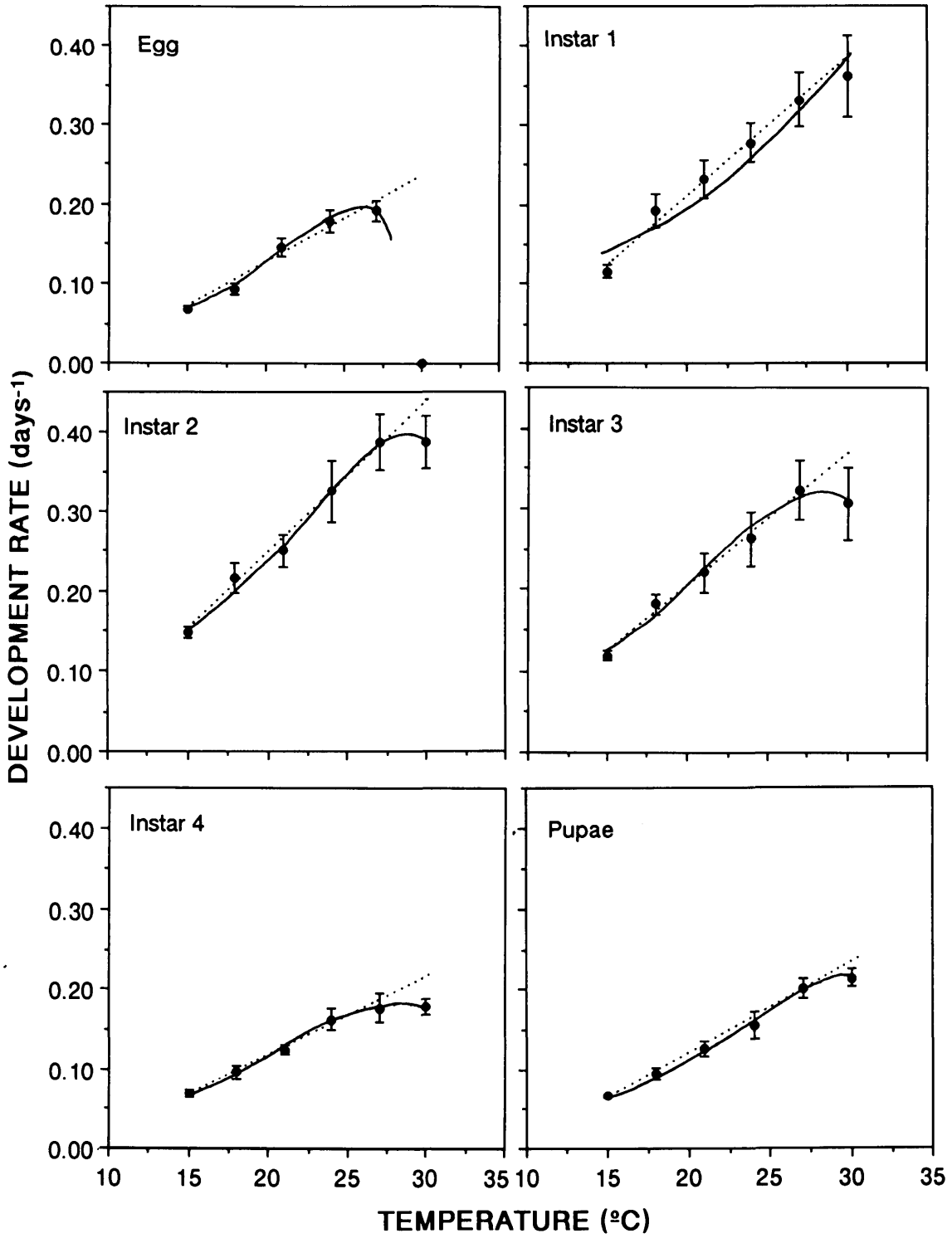

Fig. 1. Developmental rates of Mexican bean beetle immatures: observed rates (closed circles with standard deviations) and rates predicted with the linear degree-day (dotted lines) (fitted to data for 15–27°C) and the nonlinear biophysical (solid lines) (fitted to data for 15–30°C) models.

Table 1. Regression equations describing the relationship between temperature (x) and percentage development per day (y), predicted minimum threshold temperatures (t_i), and degree-days (DD) required for the stages and instars of the Mexican bean beetle

Stage	Equations	CV	r^2	t_i (95% CI) (°C)	DD ($\bar{x}$ ± SEM), d°C
Egg	$y = -0.0942 + 0.0110x$	7.97	0.969	8.6 (3.3–10.8)	98.2 ± 6.1
Larvae:					
1st instar	$y = -0.1305 + 0.0172x$	4.81	0.986	7.6 (4.6– 9.3)	61.7 ± 3.8
2nd instar	$y = -0.1442 + 0.0195x$	3.98	0.990	7.4 (5.0– 8.9)	50.5 ± 2.0
3rd instar	$y = -0.1217 + 0.0163x$	3.73	0.992	7.4 (5.2– 8.9)	60.6 ± 2.2
4th instar	$y = -0.0733 + 0.0095x$	4.58	0.988	7.7 (4.9– 9.4)	105.9 ± 3.2
Total	$y = -0.0276 + 0.0036x$	2.23	0.997	7.6 (6.3– 8.5)	278.0 ± 7.2
Pupae	$y = -0.1030 + 0.0111x$	4.58	0.991	9.3 (7.0–10.9)	90.3 ± 3.7

RHO25 = 0.1808, HH = 80930.8, TH = 305.6, and r^2 = 0.995. For each stage or instar, the higher r^2 value for the biophysical model indicates a slightly better fit to the data than achieved by the degree-day model (Table 1).

Model Validation. *Variable-Temperature Experiments.* Developmental times for each instar and immature stage predicted with the biophysical and degree-day models were compared with observed developmental times (Fig. 2). At low temperature, thermoperiodic regimes of 11/21 and 13/23°C (8:16, C/T), predictions by the degree-day model, were generally more accurate than the biophysical model (Figs. 2A, B). Errors for predicted egg developmental times were 0.6 (5.9%) and 0 (0%) d, respectively, for the degree-day model and 0.8 (7.8%) and 1.2 (13.5%) d, respectively, for the biophysical model. Errors for predicted larval + pupal developmental times were 3.2 (7.8%) and 1.3 (4.0%) d, respectively, for the degree-day model and 4.4 (10.7%) and 1.7 (5.2%) d, respectively, for the biophysical model. At temperature regimes 15/25 and 17/27°C, errors for predicted egg developmental times were 0.5 (7.1%) and 0.4 (6.6%) d, respectively, for the degree-day model and 0.3 (4.3%) and 0.3 (4.5%) d, respectively, for the biophysical model. Errors for predicted larval + pupal developmental times were less than 0.4 (1.5%) d for both models (Figs. 2C, D).

Developmental times predicted with the degree-day model were frequently more accurate than those predicted with the biophysical model under high-temperature, thermoperiodic regimes (Fig. 3). Differences between observed and predicted egg developmental times were 0.3 (5.5%), 0.1 (1.8%), and 0.2 (3.6%) d for the degree-day model and 1.0 (18.2%), 0.6 (10.5%), and 0.3 (5.4%) d for the biophysical model at temperature regimes of 19/29, 23/31, and 24.2/33°C (8:16, 16:8, 20:4; C/T), respectively. For the larval + pupal developmental times, the errors were less than 0.6 (2.8%) d for the degree-day model and more than 1.2 (5.7%) d for the biophysical model at all three temperature regimes.

Field Experiments. There were no observed differences in the rates of larval development in the conventional and low-input bean cropping systems: 1989 (F = 0.24; df = 1, 8; P = 0.64) and 1990 (F = 0.03; df = 1, 4; P = 0.87). Larval density also had no impact on the rate of larval development: F = 1.22; df = 1, 22; P = 0.28, F = 0.10; df = 1, 22; P = 0.75, F = 0.5; df = 1, 22; P = 0.48, and F = 0.012; df = 1, 22; P = 0.91 for the first to fourth instars, respectively. In 1989, both models accurately (within 95% confidence intervals) predicted average stadium of Mexican bean beetle larvae under field conditions (Fig. 4). In 1990, the biophysical model accurately predicted average stadium (within 95% confidence intervals of the observed values) during the first stadium but significantly underestimated average stadium during the second, third, and fourth stadia. The degree-day model accurately (within 95% confidence intervals) predicted average stadium during the first, second, and third stadia but significantly underestimated average stadium during the fourth stadium.

Discussion

The degree-day model is the most widely used approach in describing insect developmental rates and in predicting insect developmental times as a function of temperature. The degree-day model requires minimal data for formulation, is easy to calculate and apply, and more important, often yields the desired accuracy. It has been successfully used in many IPM and research programs (Duncan et al. 1972, Arnold 1974, Gutierrez et al. 1975, Tummala et al. 1975, Obrycki & Tauber 1981, Higley et al. 1986, Rolstch et al. 1990). However, inability to include the effects of a nonlinear trend in developmental rates at high constant temperature has been considered a major limitation of the degree-day model (Wang 1960, Wagner et al. 1984, Logan et al. 1985). The nonlinear biophysical model of Sharpe & DeMichele (1977) is regarded by some as the most suitable model of nonlinear effects of temperature on insect developmental rates under constant temperature conditions (Wagner et al. 1984). Our study has shown that the biophysical model can slightly more accurately describe the relationship between temperature and developmental rates of Mexican bean

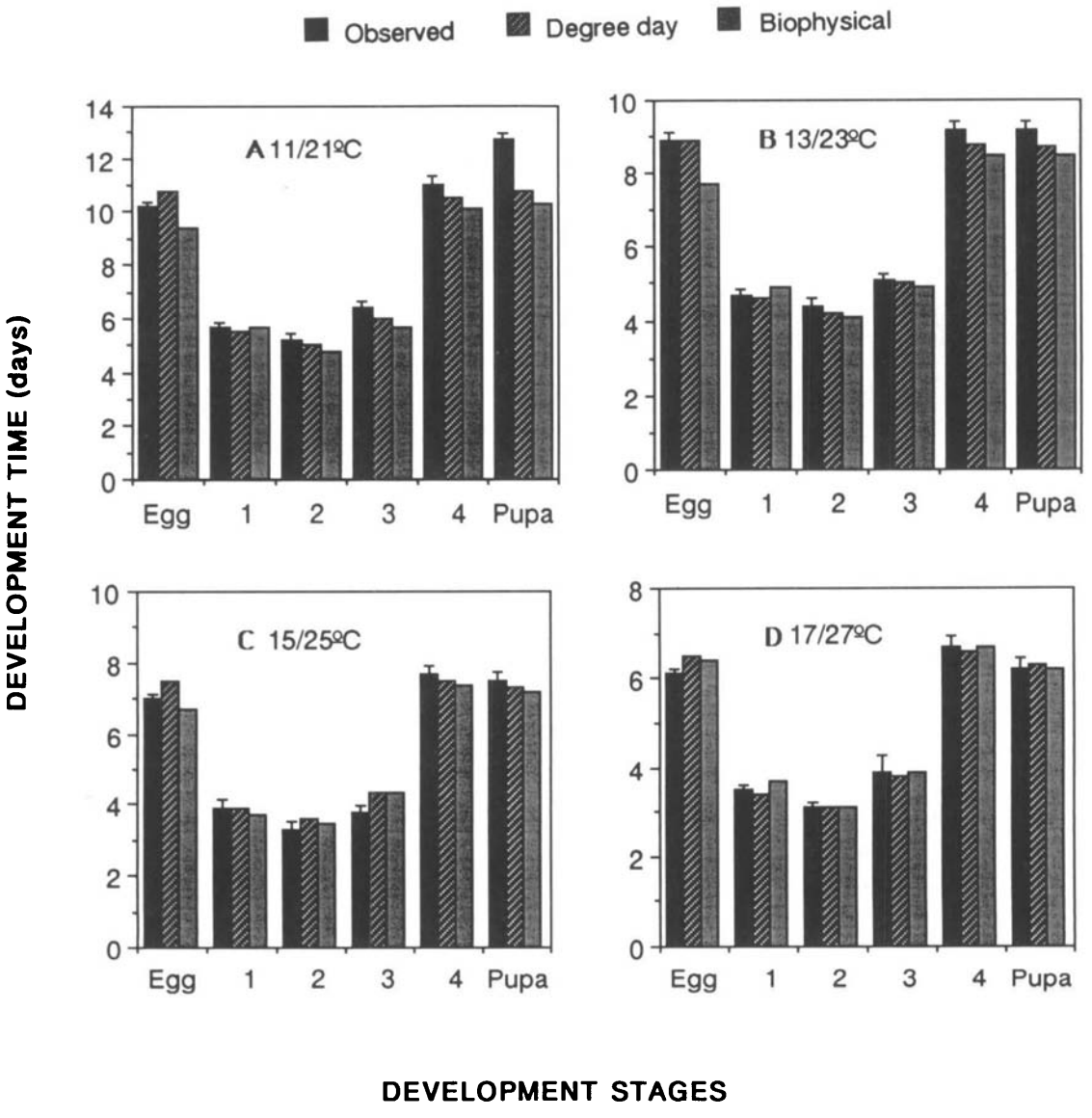

Fig. 2. Observed and predicted developmental times of Mexican bean beetle immatures under thermoperiodic regimes of 11/21 (A), 13/23 (B), 15/25 (C), and 17/27°C (D) (8:18, C/T). Vertical bars represent 95% confidence intervals.

beetle under a wide range of constant temperatures than can the degree-day model. However, with daily-fluctuating temperatures typical of those experienced during the growing season in Maine, Mexican bean beetle development was better predicted with the linear degree-day model. The superiority of the degree-day model over the biophysical model when applied to conditions of variable temperature has been found for the following species: fall armyworm, *Spodoptera frugiperda* (J. E. Smith); western grapeleaf skeletonizer, *Harrisina brillians* Barnes & McDunnough (Rolstch et al. 1990); and aphids, *Acyrthosiphon pisum* (Harris) and *A. kondoi* Shinji (Hochberg et al. 1986).

The biophysical model (Sharpe & DeMichele 1977) assumes rapid high-temperature enzyme inactivation and reaction times (Logan et al. 1985). Logan et al. (1985) found that for the eggs of Colorado potato beetle, *Leptinotarsa decemlineata* (Say), at 32°C there is a time lag of more than 3 h before inhibition of development occurs. Our laboratory study supports the conclusion that 8 h exposure at 31°C and 4 h exposure at 33°C generally does not result in high-temperature inhibition of developmental rates for Mexican bean beetle immatures (Fig. 3). High-temperature inhibition of development predicted with the biophysical model may not be experienced with short-term exposures under

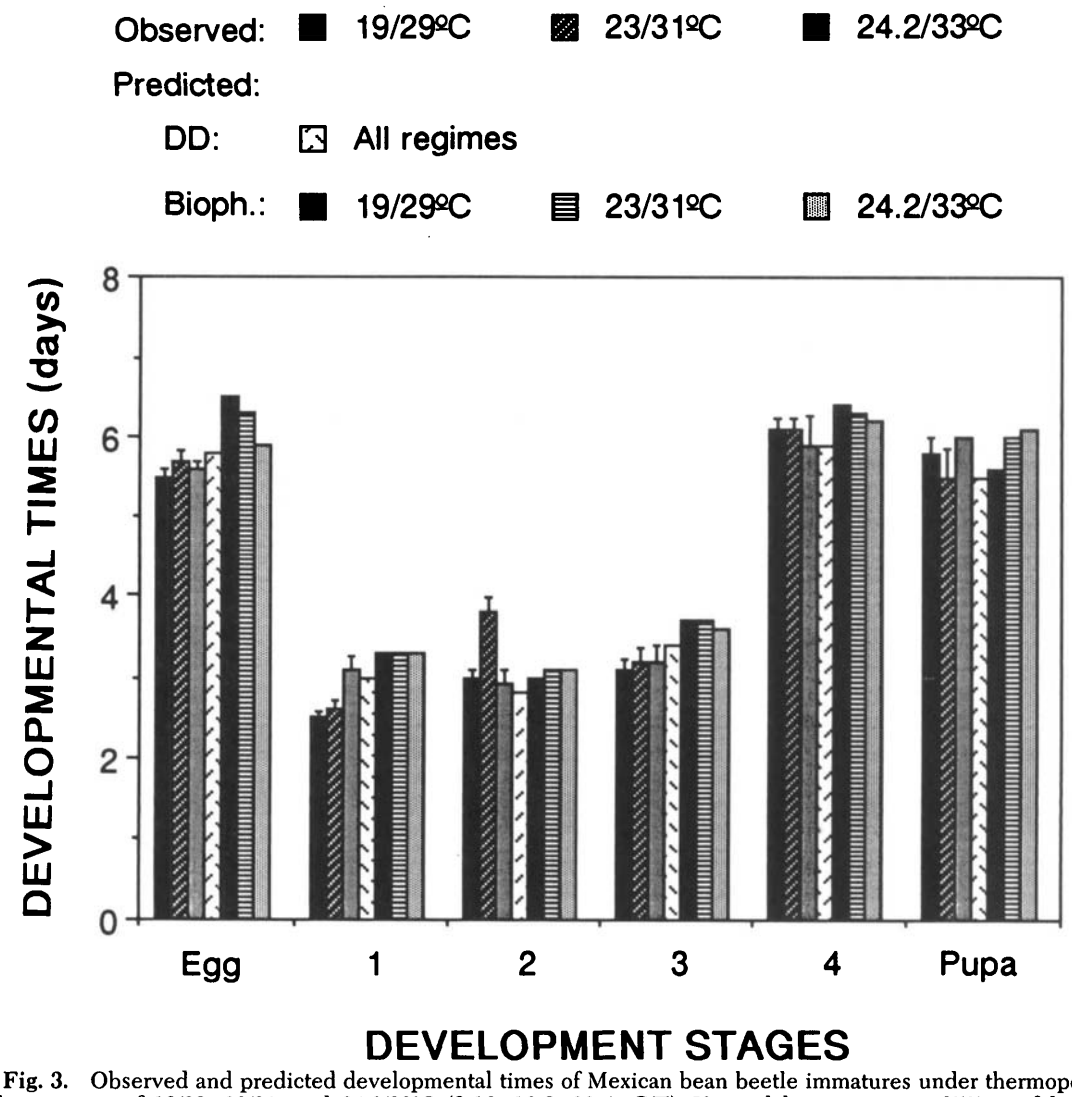

Fig. 3. Observed and predicted developmental times of Mexican bean beetle immatures under thermoperiodic regimes of 19/29, 23/31, and 24.2/33°C (8:16, 16:8, 20:4; C/T). Vertical bars represent 95% confidence intervals. There was no variation in developmental times of pupae under the 24.2/33°C thermoperiodic regime (DD, degree-day model; Bioph., biophysical model).

field conditions. In field cage studies, Mexican bean beetle larval development was accurately predicted with the biophysical model in 1989 but underestimated in 1990. During the study in 1989, there were 5 d with daily maximum temperatures over 31°C; however, three of these days occurred during the period of time the larvae were first instars, which are not predicted to experience high-temperature inhibition in the temperature range tested (Fig. 1). In 1990, there were 9 d during the period of time larvae were second and third instars with daily maximum temperatures over 31°C. Under these conditions, the biophysical model would predict longer developmental times than were actually experienced because of its assumption of high-temperature inhibition of development though, given laboratory results, such was unlikely to have occurred.

Our results for developmental rates of the Mexican bean beetle in Maine are comparable to those previously reported for the Mexican bean beetle on *P. vulgaris* in Ohio (Hammond 1984). The developmental minimum thresholds and degree-day requirements were not significantly different between the two populations. Our results did not agree with the developmental minimum threshold of 15°C for larvae on *P. vulgaris* used by Waddill et al. (1976). Data from a validation study of the model of Waddill et al. (1976) by Bernhardt & Shepard (1978) indicated a minimum threshold of 9.3°C. Cardenas et al. (1980) reported that the minimum thresholds for a Mexican population on *P. vulgaris* were 11.2, 10.2,

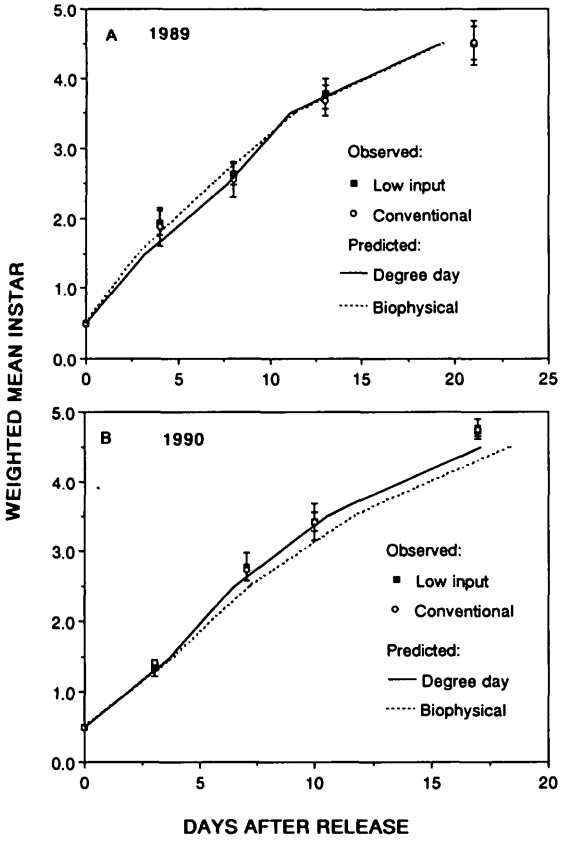

Fig. 4. Observed and predicted population age (weighted mean instar = stadium) (Haynes 1976) of Mexican bean beetle immatures under field conditions of 1989 (A) and 1990 (B). Vertical bars represent 95% confidence intervals.

and 12.5°C for the egg, larval, and pupal stages, respectively. However, the studies by Bernhardt & Shepard (1978) and Cardenas et al. (1980) were both conducted at only three temperatures, which might result in imprecise estimates based on a single degree of freedom.

Host plant species has also been found to influence the rate of Mexican bean beetle development but not the minimum thresholds. Earlier studies showed longer developmental times for Mexican bean beetle on *G. max* than on *P. vulgaris:* 31.1%, Hammond (1984) at 15.6, 18.3, 21.1, 23.9, 26.7, and 29.4°C; 25.9%, Bernhardt & Shepard (1978) in cumulative physiological days; and 42.4%, Bernhardt & Shepard (1979) at 27°C. Assays of Kogan (1972) at 27°C indicated a 10.1 to 35.7% slower development of Mexican bean beetle larvae on a series of varieties of *P. vulgaris* ranging from normal to resistant. The data of Hammond (1984) also indicated that the minimum thresholds of Mexican bean beetle on *G. max* did not differ significantly ($P > 0.05$) from those for Mexican bean beetle on *P. vulgaris*.

Other environmental factors reported to affect the Mexican bean beetle developmental rate on *G. max* are host suitability induced because of feeding damage and severe water deficit, but these may not be important in normal field conditions. Lin & Kogan (1990) showed that host resistance induced delays Mexican bean beetle developmental times by 9.1% for the first three instars. However, the difference in calendar days was only 0.8 d. Moderate water deficit does not affect Mexican bean beetle developmental rate though Mexican bean beetle larvae reared on *G. max* subjected to the severe water deficit develop significantly slower than siblings reared on foliage from well-watered plants (McQuate & Connor 1990).

The results reported here suggest that a simple degree-day model suffices for predicting Mexican bean beetle phenology on *P. vulgaris* in northern temperate regions; but, because of host-plant suitability, determination of parameter values specific for predicting Mexican bean beetle phenology on *G. max* would be necessary.

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