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Preimaginal Development and Reproductive Responses to Temperature in Two Populations of the Colorado Potato Beetle (Coleoptera: Chrysomelidae)

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ABSTRACT The pattern of geographical differences in two populations of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), suggests that preimaginal developmental responses and imaginal reproductive responses to temperature are under different selective pressures. Immatures from the warm, coastal (Long Island) area developed slightly slower, had slightly higher thermal thresholds for development, and suffered more mortality at low temperature than immatures from cooler, Upstate New York. However, more females from the Long Island population oviposited fertile eggs at lower temperatures than females from the upstate population. The data suggest that early planting dates and/or bivoltinism in the warm coastal area cause significant selection pressure for fast reproductive development under low temperatures. However, these factors do not seem to cause similar selection in the Long Island population for fast preimaginal development under low temperature. Immatures from a single egg mass show considerable variation in developmental rates in the field, especially on Long Island. Such large variation was not evident under constant temperatures, nor did laboratory-derived thermal responses to temperature provide accurate predictions of development in the field at either the coastal or the inland site. Thus, models for predicting development in the Colorado potato beetle should be modified to include environmental factors in addition to temperature; genetically and environmentally mediated variation in development should also be explored.

KEY WORDS *Insecta*, *Leptinotarsa decemlineata*, phenology, geographical variation

THE LIFE HISTORIES of insects comprise sets of interacting developmental and reproductive traits that allow the organisms to adapt to the special conditions of their habitat and locality. The success of colonizing species therefore depends, at least in part, on their abilities to modify their life histories to the requirements of the new areas. As a result, to predict colonization by introduced species or range expansion by native species, biologists must understand the variation in developmental and reproductive responses to primary environmental factors. This knowledge also subserves the construction of accurate predictive phenological models.

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), illustrates these points. A native North American species, it has expanded rapidly in host association and geographical range. Largely because of its importance as an agricultural pest in North America and Europe, aspects of its life history have received intensive investigation. These studies, which focused on the physiological (largely photoperiodic) basis for seasonal reproduction and

the relationship between the insect and its host plants, suggest that the Colorado potato beetle has considerable genotypic and phenotypic flexibility in its life history (e.g., de Kort et al. 1980; de Wilde & Hsiao 1981; Hsiao 1981, 1982, 1985; Hare & Kennedy 1986; Tauber et al. 1988a,b).

Despite these studies, recent efforts to model Colorado potato beetle phenology have concentrated almost entirely on temperature (Walgenbach & Wyman 1984, Ferro et al. 1985, Logan et al. 1985). Each study dealt with a single population and used laboratory-derived data to predict development under field conditions. Verification of predictions was either lacking or was based on data from a single field season.

Our purpose is to compare the temperature-dependent developmental rates, survival, and reproduction in two geographically separated populations from climatically diverse regions in New York. We address the questions: Do Colorado potato beetle populations differ geographically in their developmental responses to temperature? Are temperature-driven phenological models sufficient to predict rates of development in the field? Are environmental factors other than temperature important determinants of development?

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Table 1. Developmental times of Colorado potato beetles at constant temperatures (16:8 photoperiod)

Stage	Temperature (°C)					
	15.6	18.3	21.1	23.9	26.7	29.4
Freeville, N.Y.						
Egg	12.0 ± 1.1	8.5 ± 0.3	7.5 ± 0.6	5.3 ± 0.1	4.3 ± 0.2	4.4 ± 0.4
Instar I	8.1 ± 0.7	5.3 ± 0.5	4.4 ± 0.4	3.1 ± 0.1	2.6 ± 0.0	2.2 ± 0.2
Instar II	5.5 ± 0.4	3.8 ± 0.4	3.2 ± 0.0	2.2 ± 0.2	1.6 ± 0.1	1.7 ± 0.1
Instar III	6.3 ± 0.8	4.4 ± 0.3	3.6 ± 0.2	2.5 ± 0.1	2.1 ± 0.1	1.8 ± 0.1
Instar IV	22.8 ± 1.7	16.8 ± 0.6	13.5 ± 0.2	11.4 ± 0.5	9.7 ± 0.5	8.5 ± 0.2
Pupa	16.4 ± 2.2	11.6 ± 0.3	9.5 ± 0.6	7.0 ± 0.3	5.5 ± 0.2	4.9 ± 0.3
Total development	70.9 ± 2.4	50.4 ± 1.3	41.6 ± 1.7	31.6 ± 0.5	25.7 ± 0.8	23.5 ± 0.3
Total no. ^a	(34)	(68)	(81)	(72)	(70)	(51)
Riverhead, Long Island, N.Y.						
Egg	11.5 ± 0.7	8.9 ± 0.5	7.6 ± 0.0	5.4 ± 0.3	4.8 ± 0.2	4.2 ± 0.1
Instar I	9.5 ± 1.4	6.1 ± 0.7	5.4 ± 1.3	3.7 ± 0.6	2.8 ± 0.3	2.7 ± 0.5
Instar II	8.0 ± 2.2	4.4 ± 0.5	4.0 ± 0.9	2.8 ± 0.5	2.3 ± 0.3	2.0 ± 0.3
Instar III	7.3 ± 0.2	4.9 ± 0.3	4.2 ± 0.4	3.1 ± 0.3	2.5 ± 0.2	2.0 ± 0.3
Instar IV	25.4 ± 0.2	18.4 ± 0.5	13.8 ± 0.2	10.1 ± 0.3	8.8 ± 0.6	7.8 ± 1.0
Pupa	16.6 ± 0.1	11.7 ± 0.4	9.6 ± 0.4	7.3 ± 0.3	6.1 ± 0.5	4.9 ± 0.3
Total development	76.9 ± 4.8	54.4 ± 1.9	44.6 ± 2.9	32.3 ± 2.1	27.3 ± 1.2	23.7 ± 1.5
Total no. ^a	(15)	(46)	(62)	(60)	(72)	(60)

Data are expressed in days, mean ± SE.

^a Minimum total no. from three repetitions of experiment. At some stages and temperatures total was slightly more.

Materials and Methods

All of our experiments used first-generation offspring of Colorado potato beetle adults from Freeville, Tompkins County, and Riverhead, Long Island, Suffolk County. Pairs of field-collected adults were maintained in 0.24-liter cages on *Solanum tuberosum* (cv. Katahdin) foliage at 22 or 24 ± 1°C and a photoperiod of 16:8 (L:D). In all our laboratory rearings, temperature fluctuated 0.5°C on either side of the designated constant temperature. Reference specimens from the Long Island and Freeville populations have been deposited in the Cornell University Insect Collection (Lot #1158).

Development and Reproduction at Constant Temperatures. Individuals from each population were reared from egg to egg under a range of temperatures from 15.6 to 29.4°C at 16:8 photoperiod (Table 1). Each experiment was performed three times for each population. Parental beetles from Freeville consisted of overwintering adults that terminated diapause in the laboratory (first two experiments) or that were field collected in the spring (third experiment). Adults from Riverhead were dug from the ground in the fall and held until diapause terminated (first experiment) or they were field collected in the spring (second experiment) or summer (third experiment).

We collected egg masses daily from individual females and placed one egg mass from each female into each of the temperatures. There were 6–7 females from Freeville and 9–15 females from Riverhead for each experiment. When hatching within an individual egg mass extended over more than one day, we included late-hatching larvae by setting up daily cohorts in approximate proportion to the total number of hatched larvae. Up to six larvae of the same stage from the same egg mass were

reared together in a single 0.24-liter cage until they reached the fourth instar. Any larvae that were out of synchrony (slow or fast developers) were removed and reared individually. After reaching the fourth instar, no more than two larvae were kept together.

All larvae had continuous access to potato foliage; the stems of the foliage were placed in water-filled vials that were plugged with cotton. First and second instars received young potato foliage; third and fourth instars received bouquets of medium-age (fully expanded) potato leaves. When larvae entered the fourth instar, we added a layer of moistened vermiculite, which served as a medium for pupation. We checked all vials and cages daily and recorded dates of egg hatch, ecdysis, larval digging, pupation, adult eclosion, and mortality.

We considered the termination of the fourth instar and the beginning of the pupal stage to be ecdysis to the pupa. The end of the pupal stage was determined by ecdysis to the adult—not emergence from the vermiculite.

After eclosion, males and females of the same age, but different parents, were paired and maintained at their respective temperatures. Cages contained bouquets of young and medium-aged potato foliage in water and moist vermiculite. We recorded the dates of the first and subsequent ovipositions for a total of at least 7 consecutive days. Eggs were collected, counted, and placed in plugged vials at 26.7°C (16:8 photoperiod) to determine their viability.

Photoperiodic Effects on Development. Individuals were reared as noted above under a range of constant photoperiods (10:14 to 16:8) at 23.9°C. This experiment was done only with the Riverhead population and was repeated three times. Parental stock was collected from the field in spring (overwintered generation) for the first and third exper-

Table 2. Thermal requirements for development of Colorado potato beetles

Stage	Freeville		Riverhead, Long Island	
	<i>t</i> (°C)	<i>K</i> (DD)	<i>t</i> (°C)	<i>K</i> (DD)
Egg	8.3 ± 2.9	86.8 ± 10.0	8.2 ± 1.6	88.9 ± 5.6
Instar I	10.8 ± 1.1	10.6 ± 2.0	10.6 ± 2.0	48.2 ± 4.3
Instar II	10.3 ± 3.2	30.2 ± 4.0	10.5 ± 1.4	37.0 ± 2.2
Instar III	10.7 ± 1.3	33.6 ± 1.8	10.7 ± 1.6	39.3 ± 2.7
Instar IV	7.1 ± 0.3	189.9 ± 2.1	9.9 ± 1.1	148.3 ± 6.8
Pupa	10.2 ± 1.3	94.2 ± 4.9	10.1 ± 1.3	98.4 ± 5.3
Total development	9.1 ± 1.2	470.2 ± 22.1	9.8 ± 1.0	463.3 ± 19.9
Preoviposition period ^a	17.2 ± 0.8	60.5 ± 3.5	14.2 ± 2.1	80.0 ± 9.3

Data are mean ± SE.

^a Fertile oviposition only; temperature range for Freeville: 21.1–29.4°C, for Riverhead: 18.3–29.4°C.

iments and in late summer for the second experiment.

Analysis of Developmental Data. To analyze the relationship between temperature and development, we computed the reciprocal of the developmental times for individual beetles and then fitted a regression line to the data using least-squares analysis. We calculated the lower thermal threshold, *t*, for each stage of each population by extrapolating the regression line through the *x*-axis (temperature). We then derived *K* (heat-degree days) from the equation, $K = 1/y(x - t)$, in which *y* = mean developmental rate and *x* = temperature (°C). The developmental times of each individual larva constituted independent observations.

All of the regression analyses and analyses of variance (ANOVA) were done using the SAS statistical package (SAS Institute 1985). Differences were considered significant when *P* = 0.05.

Development in the Field. To provide data for comparing the rates of development under constant temperature with those in the field, we reared individuals outdoors in cages during three field seasons at both localities. The studies were initiated with eggs collected when Colorado potato beetles were available in the field, and they continued for two generations. The rearing methods were as described above. Outdoor temperatures were recorded with hygrothermographs in ventilated boxes at the same height as the rearings and near the plots in which we conducted our rearings. In calculating heat accumulations, we used *t* = 8.2°C (egg) or *t* = 10°C (hatch to adult eclosion); these values are close to the calculated values for both populations (Table 2). Calculations were by the method of Allen (1976) without bias correction. Use of a linear model for predicting development under field conditions is justified, because outdoor temperatures rarely exceed those at which the beetles develop at optimal rates under constant temperatures.

Results

Preimaginal Development at Constant Temperatures. Between 15.6 and 29.4°C, developmental rates (Table 1) were positively related to

temperature (e.g., total development for Riverhead, $r^2 = 0.974$; for Freeville, $r^2 = 0.988$). At all temperatures, the variation around the mean developmental time was relatively small for both populations, with the Riverhead population showing slight, but statistically significant, more variation (average coefficient of variation for complete development over all temperatures for Freeville: *V* = 6.99; for Riverhead: *V* = 8.97; two-way ANOVA, with arcsine transformation *F* = 8.86; *df* = 1, 5, *P* = 0.025–0.05).

The developmental times for the Freeville population were generally slightly shorter than those for the Riverhead population (Table 1), and the *t* values for each developmental stage were generally similar for the two populations (Table 2). The lowest *t* in both cases occurred in the egg and fourth instar. *K* values were generally similar for both populations, especially for total development. Total development (egg to adult emergence) in the Freeville and Riverhead populations required 470 DD above 9.1°C and 463 DD above 9.8°C, respectively. Analysis of variance showed no significant differences between the temperature/developmental rate regression lines (slopes or intercepts) for the two populations (Fig. 1).

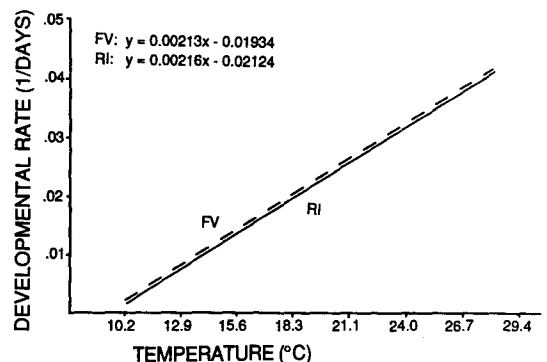


Fig. 1. Relationship between temperature and developmental rate (egg to adult) in two populations of Colorado potato beetles from New York. FV = Freeville, Upstate New York; RI = Riverhead, Long Island. There are no significant differences between the two regression lines (slope: *F* = 0.09, *P* = 0.766; intercept: *F* = 0.61, *P* = 0.441).

Table 3. Larval and pupal mortality of Colorado potato beetles at constant temperatures (16:8 photoperiod)

	Temperature (°C)					
	15.6	18.3	21.1	23.9	26.7	29.4
	Freeville					
Percentage mortality (mean ± SD) ^a	59 ± 7	23 ± 5	26 ± 10	13 ± 7	22 ± 25	41 ± 25
Total number	125	108	112	92	94	93
Stage-specific mortality ^b						
Instar I	29	7	4	0	0	5
Instar II	2	2	3	0	1	1
Instar III	7	2	2	2	0	2
Instar IV	21	4	6	7	12	33
Pupa	20	9	11	5	11	5
	Riverhead, Long Island					
Percentage mortality (mean ± SD) ^a	76 ± 19	43 ± 13	31 ± 28	24 ± 12	13 ± 9	21 ± 8
Total number	96	91	97	89	83	88
Stage-specific mortality ^b						
Instar I	60	34	25	15	8	5
Instar II	16	7	11	5	1	6
Instar III	13	0	0	4	0	3
Instar IV	21	9	2	1	3	7
Pupa	0	0	0	2	0	3

^a Three experiments combined.

^b Percentage dying of those entering stage.

Mortality. The highest mortality (59%) for individuals from the Freeville population was at 15.6°C; the first instar, fourth instar, and pupal stage were the most severely affected by low temperature (Table 3). Mortality was lower (13–26%) at higher temperatures (18.3–26.7°C), and then increased again to 41%, at 29.4°C. The majority of the deaths at the higher temperatures occurred during the late immature stages (fourth instars and pupae).

Mortality at 15.6°C was higher in the Riverhead population (76%) than in the Freeville population. The majority of the deaths at 15.6°C occurred during the first stadium, but there were also many deaths in the fourth stadium. Mortality decreased to 13% as temperatures increased to 26.7°C (Table 3). At 29.4°C, mortality increased slightly to 21%.

Reproduction under Constant Temperatures. Temperature strongly influenced reproduction in both populations (Table 4). In the Freeville population, the percentage of females that oviposited ranged from 0 to 25.7% at temperatures below 22°C. At 23.9°C, the incidence of oviposition increased abruptly, and it remained high at the higher temperatures. A greater percentage of females from the Riverhead population oviposited at low temperatures than from the Freeville population, and the temperature-related increase in the incidence of oviposition was less abrupt than in the Freeville population.

There was no fertile oviposition in either population at 15.6°C, although some females from the Long Island population developed and deposited infertile eggs at this temperature. Females from the Freeville population also laid no fertile eggs at 18.3°C.

The preoviposition periods of the fertile females were positively related to temperature (Freeville:

$r^2 = 0.950$; Riverhead: $r^2 = 0.914$). Freeville females had a higher thermal threshold for oviposition than those from Riverhead (Table 2), and the slopes and *y*-intercepts of their regression lines differ significantly (slope: $F = 5.69$, $P = 0.026$; intercept: $F = 6.40$, $P = 0.019$). The rates of oviposition during the first week of fertile oviposition were similar in both populations (Table 4).

Photoperiodic Effects on Development. There were significant differences in the mean developmental times under the various photoperiods (ANOVA; Experiment 1: $F = 8.52$, $P \leq 0.0001$; Experiment 2: $F = 10.78$, $P \leq 0.0001$; Experiment 3: $F = 12.55$, $P \leq 0.0001$) (Table 5). Although the differences did not exceed 4 d, development tended to accelerate as daylengths decreased from 16:8 to 14:10 photoperiods.

Development in the Field. At Freeville, our outdoor rearings began at various times between the end of May and the beginning of July, and they continued until the end of August. In all three years, the rates of development in the field were much faster than those predicted from our rearings in the laboratory (Table 6A). The deviation from predicted values occurred across all life stages, including the sessile egg and pupal stages. In general, development was increasingly faster than predicted as the season progressed (correlation coefficient [accumulated degree-days on date of oviposition versus deviation of actual from predicted developmental time, three years combined]: $r = -0.76$; $df = 21$; $P < 0.01$).

Our rearings at Riverhead began in mid-July in 1982 and in late May in 1983 and 1984; they extended through the end of August or the beginning of September. In 1982 the rates of development in the field were slower than predicted (Table 6B). In 1983 and 1984 the rates of development were

consistently faster than predicted, but there was no correlation between heat accumulation on the day of oviposition and the amount of deviation from predicted rates of development ($r = 0.05$; $df = 14$; $P > 0.05$, data from 1983 and 1984 combined; data from 1982 not available). All stages, including the egg and pupa, contributed to the deviation in all years.

Our outdoor rearings in all years and at both localities were marked by large variability among individuals, even those from a single egg mass (Table 6). However, the difference in variability between the laboratory and outdoor rearings was significant only for the Riverhead population (Table 6; mean \pm SD coefficient of variation across all rearings at Freeville: $V = 11.94 \pm 8.65$, $t = -1.38$, $df = 27$, $P > 0.05$; at Riverhead: $V = 56.48 \pm 42.28$, $t = -2.71$, $df = 22$, $P = < 0.001$). For the Freeville population, the coefficient of variation decreased significantly as the season progressed; the correlation was significant at the minimal level (Freeville: $r = -0.45$, $df = 21$, $P = 0.01-0.05$; Riverhead: $r = 0.482$, $df = 14$, $P > 0.05$).

Discussion

Variation in the Thermal Regulation of Development—This Study. We chose to study populations from Riverhead and Freeville, N.Y., because both the climate and the phenology of the Colorado potato beetle differ at these two localities. Riverhead is on the eastern edge of Long Island, near the coast. The soils are sandy and well drained, and the area has a relatively long, warm growing season. A relatively high proportion of the beetles at Riverhead produces two generations every year (Tauber et al. 1988a). Freeville, which is situated in Upstate New York, approximately 300 km west-northwest and inland of Riverhead, has a cooler and shorter growing season and relatively poorly drained soils. Potatoes are planted and harvested about a month later at Freeville than at Riverhead. Most of the Colorado potato beetles at Freeville are univoltine; a small proportion produces a second generation per year. Both voltinism and climate can affect the evolution of thermal responses in insects (e.g., Masaki 1978, Taylor 1981). Therefore, we expected that if the Colorado potato beetle had undergone geographical divergence in its developmental responses to temperature, the differences between these two populations would be large.

The two populations differed slightly in their responses to temperature, and their relative responses coincided with the temperature conditions of the two localities. Development generally was faster in the Freeville than in the Riverhead population (Table 1); this variation probably resulted from the overall lower thermal threshold for development in the Freeville population (Table 2). However, the differences between the populations were small enough that the regression lines (temperature compared with developmental rate) did

Table 4. Reproduction under constant temperatures by Colorado potato beetles (16:8 photoperiod)

	Temperature (°C)					
	15.6	18.3	21.1	23.9	26.7	29.4
No. and (%) ovipositing	0 (0)	1 (3.2)	9 (25.7)	32 (100)	29 (85.3)	23 (100)
No. and (%) ovipositing fertile eggs	0 (0)	0 (0)	8 (22.9)	26 (81.3)	25 (73.5)	16 (69.6)
Total pairs	16	31	35	32	34	23
Preoviposition period (mean \pm SD days) fertile ♀♀ (no.)	—	—	16.6 \pm 4.3 (8)	8.5 \pm 3.2 (26)	6.6 \pm 2.0 (25)	5.2 \pm 0.7 (16)
No. (mean \pm SD) of eggs/d during week 1 of fertile oviposition (no. pairs)	—	—	21.8 \pm 15.8 (8)	32.4 \pm 10.6 (26)	42.4 \pm 18.5 (28)	54.0 \pm 18.9 (17)
Riverhead, Long Island						
No. and (%) ovipositing	2 (25)	9 (42.9)	24 (85.7)	23 (92.0)	30 (96.8)	28 (96.6)
No. and (%) ovipositing fertile eggs	0 (0)	4 (19.0)	17 (60.7)	23 (92.0)	29 (93.5)	23 (79.3)
Total pairs	8	21	28	25	31	29
Preoviposition period (mean \pm SD days) fertile ♀♀ (no.)	—	17.0 \pm 4.2 (4)	13.1 \pm 1.8 (17)	8.0 \pm 1.1 (23)	6.9 \pm 1.3 (29)	5.0 \pm 0.7 (23)
No. (mean \pm SD) of eggs/d during week 1 of fertile oviposition (no. pairs)	—	16.7 \pm 3.0 (4)	19.7 \pm 7.9 (17)	37.5 \pm 12.4 (23)	45.8 \pm 14.6 (29)	48.4 \pm 12.5 (23)

Table 5. Photoperiodic effects on mean \pm SD (no. of individuals) preimaginal developmental time (oviposition to adult eclosion) of Colorado potato beetle from Riverhead, Long Island (23.9°C) (data from Lansky [1984])

	Photoperiod (L:D)					
	10:14	12:12	13:11	14:10	15:9	16:8
Exp 1	31.5 \pm 3.2 (34)	29.5 \pm 2.6 (37)	29.6 \pm 1.6 (34)	30.2 \pm 4.6 (33)	31.6 \pm 2.5 (35)	33.4 \pm 3.0 (36)
Exp 2	30.9 \pm 1.7 (32)	29.5 \pm 1.8 (25)	32.1 \pm 1.7 (22)	30.6 \pm 1.3 (26)	31.4 \pm 2.4 (19)	33.5 \pm 3.2 (26)
Exp 3	30.2 \pm 2.1 (30)	30.3 \pm 2.9 (31)	30.1 \pm 1.6 (30)	29.3 \pm 1.5 (32)	33.4 \pm 2.8 (27)	32.0 \pm 2.5 (26)

not differ significantly between the two populations. It is of interest that the developmental times of beetles from Riverhead were somewhat more variable, both in the field and under constant temperatures, than those from Freeville. Immatures from the Freeville population also suffered less mortality at low temperatures than the Riverhead population, and the trend was reversed at the higher temperatures.

The above suggests that evolutionary modification of the developmental responses of preimaginal stages to temperature constitutes an important feature in the adaptation of the beetle to the climate of new geographical areas. However, the diversification of preimaginal developmental responses to temperature is not nearly as profound as the geographical differences in reproductive responses to photoperiod and temperature (Tauber et al. 1988a,b). This is not unlike other insects in which diapause plays a major role in regulating the seasonal cycle (see Ritland & Scriber 1985, Tauber et al. 1987).

Variation in the Thermal Regulation of Development—Comparisons Among Studies. Including our study, the thermal requirements for development of seven populations of the Colorado potato beetle have been extensively examined under laboratory conditions—two from Europe (de Wilde 1948, Chlodny 1975), four from northeastern United States (Ferro et al. 1985, Logan et al. 1985, Groden & Casagrande 1986, this study), and one from midwestern United States (Walgenbach & Wyman 1984). These investigations consistently show a direct relationship between temperature and the rate of development for all stages. Nevertheless, considerable variation exists among the studies in the developmental times reported for the various stages, including the nonfeeding egg and pupal stages.

At temperatures around 15.5°C, the range of developmental times for the egg extended from 10.7 d (15°C) to 14.5 d (15.7°C) (Walgenbach & Wyman 1984, Ferro et al. 1985, Logan et al. 1985; Table 1, this paper). Somewhat smaller, but still substantial, variation occurred at temperatures around 20°C (6.2 d at 20°C to 8.0 d at 21°C) (de Wilde 1948, Walgenbach & Wyman 1984, Ferro et al. 1985, Logan et al. 1985; Table 1, this paper). At temperatures near 26°C, developmental times ranged between 4.3 d (26.7°C) and 6.2 d (26°C) (de Wilde 1948; Table 1, this paper).

Among all the studies, the variation in the developmental times was relatively small for first and

second instars, but was large for the third instar. In most instances, development of the third instar at 15.5°C required between 6.3 and 7.5 d (Walgenbach & Wyman 1984, Logan et al. 1985; Table 1, this paper). In contrast, development of third instars from Massachusetts required only 2.8 d (15°C) (Ferro et al. 1985). At temperatures near 20°C, development of the third instar required from 2.5 d (20°C) to 4.2 d (21.1°C). Again, the larvae from Massachusetts developed the fastest.

We suspect that the studies also differ in the developmental times for fourth instars. Direct comparisons were not possible because most of the workers reported their data in different ways. For example, we calculated the developmental time of the fourth instar from ecdysis to ecdysis; thus the free-living and prepupal period of the fourth instar are combined. In contrast, Ferro et al. (1985) combined the prepupal period of the fourth instar with the pupal stage. It was not clear how Logan et al. (1985) handled the prepupal period of the fourth instar, and de Wilde (1948), Walgenbach & Wyman (1984), and Groden & Casagrande (1986) reported all three periods separately. Comparisons of the combined free-living and prepupal fourth instar and the pupal stage illustrate large variation among the studies. Generally, development was fastest in the study from Massachusetts (Ferro et al. 1985); at 15°C, it was 10.4 d faster, and at 24°C it was 3 d faster than in our study.

At first glance, the disparity in preimaginal developmental rates among the reports suggests geographical variation among populations. However, except in our comparative study of two populations, experimental conditions differed sufficiently to preclude this conclusion. For example, the variety of potato foliage provided to the beetles and the treatment of foliage varied among the tests; radiant heat was excluded in some studies, not others. All of these factors influence preimaginal development in the Colorado potato beetle (Hsiao 1978, May 1982, Dimock & Tingey 1985, Wright et al. 1985, Groden & Casagrande 1986, Hare 1987). Furthermore, factors such as photoperiod, the dates that the parental stocks were collected in the field, and the duration that the parental stocks were maintained in the laboratory, probably differed among the studies. All of these factors were held constant in our study.

Photoperiod and Development. In nature, larvae develop in daylengths that range between 16:8 and 14:10. At these photoperiods, developmental rates generally increase slightly as daylengths de-

Table 6. Deviation of Colorado potato beetle development from predicted values over three seasons and at two localities in New York

Date of oviposition	Accumulated DD ₁₀ on date of oviposition ^a	Deviation from expected values		
		DD ₁₀	Days	n
A. Freeville				
1982				
2 July	405.2	-110.8 ± 20.6	-14.4 ± 2.0	17
7 July	446.6	-134.9 ± 11.8	-19.6 ± 1.1	5
9 July	470.3	-114.8 ± 16.5	-17.6 ± 2.5	18
1 August	717.9	-149.1 ± 21.9	-46.7 ± 2.1	3
5 August	759.0	-162.6 ± 10.6	-45.0 ± 1.2	4
6 August	766.7	-152.8 ± 7.2	-41.3 ± 2.3	3
12 August	820.0	-163.4 ± 4.9	< -40	6
1983				
31 May	120.2	-103.3 ± 2.8	-10.3 ± 0.6	3
3 June	127.9	-77.7 ± 22.9	-6.8 ± 2.1	4
4 June	133.5	-102.8 ± 9.9	-9.4 ± 1.1	5
6 June	146.4	-90.1 ± 20.6	-8.0 ± 1.7	5
10 June	164.9	-97.5 ± 7.2	-7.6 ± 0.5	5
11 June	173.2	-89.8 ± 6.6	-8.8 ± 0.5	5
12 June	181.7	-93.2 ± 7.8	-9.2 ± 0.8	5
13 June	192.3	-99.0 ± 13.2	-10.0 ± 1.0	5
14 June	204.2	-69.9 ± 12.6	-7.7 ± 1.2	3
27 July	656.1	-110.7 ± 18.9	-11.2 ± 1.8	10
30 July	698.6	-114.7 ± 11.6	-12.9 ± 1.8	6
3 August	748.7	-105.2 ± 7.7	-14.8 ± 1.0	5
4 August	762.0	-128.8 ± 5.0	-20.8 ± 0.4	6
5 August	773.5	-123.5 ± 7.0	-22.8 ± 0.5	27
6 August	786.6	-123.9 ± 5.9	-22.2 ± 0.5	5
1984				
11 June	216.0	-122.4 ± 44.5	-8.5 ± 4.4	30
B. Riverhead, Long Island				
1982				
17 July	627.9	38.5 ± 44.5	3.0 ± 3.6	20
18 July	647.5	46.3 ± 44.3	3.2 ± 3.8	19
1983				
26 May	173.8	-53.9 ± 50.9	-5.0 ± 4.2	2
1 June	191.3	-49.0 ± 18.0	-4.0 ± 1.3	8
4 June	209.8	-44.4 ± 42.2	-3.3 ± 3.1	3
5 June	217.3	-74.6 ± 27.7	-6.0 ± 2.0	4
7 June	233.5	-33.6 ± 19.4	-3.0 ± 1.4	2
9 June	248.0	-63.2 ± 14.1	-6.0 ± 1.0	3
11 June	260.5	-28.2 ± 42.5	-3.0 ± 3.6	3
13 June	285.0	-68.2 ± 14.5	-7.6 ± 1.1	5
5 July	308.5	-68.3 ± 19.9	-7.5 ± 1.9	4
14 July	601.3	-80.0 ± 6.9	-7.7 ± 0.6	3
17 July	644.2	-90.9 ± 31.5	-9.0 ± 2.6	3
1984				
24 May	152.0	-59.8 ± 6.5	-6.2 ± 0.8	5
26 May	164.5	-35.8 ± 34.9	-3.6 ± 2.7	12
8 June	250.4	-56.6 ± 39.3	-4.7 ± 3.2	10
9 June	267.4	-62.6 ± 23.3	-6.0 ± 2.0	4
2 August	857.4	-6.9 ± 40.8	-1.3 ± 4.9	26

Deviation = actual - expected; data are mean ± SD (no.). Expected values based on total development of 460 DD above $t = 10^{\circ}\text{C}$. Data from most dates represent individuals from a single egg mass.

^a DD accumulations began 1 March, except Riverhead 1982, which began 15 May.

crease. Thus, as the growing season comes to an end, the development of immatures accelerates. The slow development under very short daylength (10:14) remains unexplained; larvae do not encounter this photoperiod in nature.

Variation in Thermal Regulation of Reproduction. The Riverhead and Freeville populations also differed in their reproductive responses to temperature. Moreover, the pattern of geographical variation was the opposite from that expected from

the temperature conditions of the two localities. Although Freeville's climate is considerably cooler than Riverhead's, adults from the Riverhead population underwent reproductive development and initiated fertile oviposition at considerably lower temperatures than those from the Freeville population (Table 4).

Temperature and photoperiod influence the incidence and duration of oviposition in the Colorado potato beetle (e.g., de Kort et al. 1980; de Wilde

& Hsiao 1981; Tauber et al. 1988a,b). Our data suggest that the early schedule of potato planting and the essentially bivoltine nature of the Riverhead population provide significant selective pressure for reproduction under low temperature. Differences between the Riverhead and Freeville populations in their responses to diapause-inducing cues is discussed elsewhere (Tauber et al. 1988a,b).

Developmental Rates Under Field Conditions.

Comparison of laboratory-derived predictions of seasonal events with the timing of their occurrence under field conditions is a useful method for verifying phenological models and identifying factors that might add accuracy to the models. Given this, the literature and our study present some interesting contrasts.

Walgenbach & Wyman (1984) obtained relatively good correlation between their laboratory-derived predictions and observed rates of development under field conditions in Wisconsin. They found no need to adjust their predictions to include thermoregulation by the larvae. By contrast, Groden & Casagrande (1986) reported relatively good correlation between predicted and actual rates of larval growth after adjusting for thermoregulation with May's (1982) formula.

Our results differ from these two studies. There was substantial disagreement between the developmental rates predicted from our laboratory data and the actual developmental times in the field for the Freeville and Riverhead populations (Table 6). The discrepancy occurred across all stages (mobile and sessile), and therefore is not solely the result of thermoregulation by the larval stages. Our study also showed large variation in the developmental times among individuals under field conditions, especially at Riverhead. This variation was substantial even among individuals derived from a single egg mass (Table 6), and it suggests that phenological models for the Colorado potato beetle, like those for many insects (see Shaffer 1983), should attempt to quantify variation in developmental time. This will require additional studies to identify the genetic and environmental causes for the variation.

Although temperature is predominant in regulating development in the Colorado potato beetle, the discrepancies we observed strongly suggest that additional factors are important. Our experiments do not suggest that photoperiod alone plays a primary role in this function. We cannot exclude the interaction of photoperiod, temperature, and food quality or quantity as an influence on growth rates; such an effect was shown at the end of the season for the closely related milkweed leaf beetle, *Labidomera clivicolis* (Kirby) (Palmer 1982).

The linear model of heat accumulation that we used (Allen 1976) almost consistently underestimated developmental rates in the field. This suggests that inhibition of development by high temperature also was not the cause of the discrepancies between actual and predicted developmental times

as has been shown for other populations of the Colorado potato beetle (Ferro et al. 1985). Therefore, we propose that fluctuating temperatures may speed development; however, this does not explain the between-year variation of predicted and actual developmental rates, especially at Riverhead.

Given our findings and those in the literature, we conclude that current temperature-driven models are not adequate to describe rates of development or the variability in developmental rates of the Colorado potato beetle from diverse localities. Thus, complex environmental variables, such as fluctuating temperature, changing photoperiod, and changing food quality and quantity, should be considered for inclusion in the models—those focused on research, and those used for decision-making in pest management. Furthermore, careful consideration should be given to the cause and consequences of the large phenotypic variation in developmental rates expressed under field conditions. This variability, whether generated from genetic or environmental causes, may be a key factor in the evolution of the Colorado potato beetle's phenology.

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