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ABSTRACT   The intensity of diapause has a distinct seasonal pattern in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). During August, temperature and photoperiod only slightly affected the very intense diapause in field populations. By summer's end, diapause intensity diminishes, but photoperiod and temperature maintain diapause. Subsequently, the beetles lose their responsiveness to photoperiod at high temperatures (approximately 20°C), but at low temperatures (18–15°C) the beetles remain photoperiodically sensitive after emerging from the soil and initiating oviposition in the spring. Mated females that overwinter can lay fertile eggs without mating in the spring. Populations from climatically different areas in New York state (Riverhead, Long Island and Freeville, Upstate New York) have similar thermal thresholds (approximately 12°C) for reproductive development after dormancy. However, the Riverhead population has a less intense diapause and lower thermal requirements for initiating oviposition ($K = 135$ HDD$_{12}$ [heat-degree days]) than the Freeville population ($K = 213$ HDD$_{12}$). This diversity results in large differences in the timing of vernal emergence and oviposition at the two sites. The results suggest that natural selection acts on both the timing of emergence and oviposition after dormancy and on the variation in the occurrence of the events.

KEY WORDS   Insecta, diapause termination, phenology, photoperiod

EVOLUTIONARY ANALYSES of life histories generally are undertaken from demographic or genetic viewpoints; seldom do they include physiological considerations. However, physiological processes are the vital connection between the ecological expression of life history traits that determine fitness, and the components of population genetics that constitute heritability and genetic covariances (Stearns 1983, Tauber & Tauber 1986). When physiological aspects are neglected, life history studies offer an incomplete and static view of the dynamic interactions between populations, organisms, and the environment.

Seasonality is a primary environmental variable that influences the expression of life history traits. The environmental cues that regulate reproduction, development, migration, and dormancy, and the physiological responses to these cues change with seasons. Thus, comparative studies of the ecophysiological interactions between organisms and their seasonal environments give a vital dimension to the understanding of evolutionary processes.

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is an excellent subject for ecophysiological investigations of how life histories evolve. The seasonal cycle of the species is well studied; skillful workers have clarified the physiological and endocrine bases for many of its life history functions (e.g., de Kort et al. 1980, de Kort 1981, Briers et al. 1982). Much of the physiological work with the Colorado potato beetle has been undertaken with a strong ecological perspective (see Arnoldi 1966, de Kort et al. 1980, de Wilde & Hsiao 1981, Hsiao 1981).

Our paper focuses on the physiological interface between ecology and genetics by evaluating interpopulation and intrapopulation differences in the seasonal responses to the factors that regulate dormancy and oviposition in the field. Our study involved two populations of *L. decemlineata*—one from Upstate New York (Freeville, Tompkins County; latitude: 42°27′N) and one from Long Island, New York (Riverhead, Suffolk County; latitude: 40°58′N). The upstate locality is about 300 km inland from the one on Long Island. Upstate, the climate is cooler, the soils are heavier (Rhineland silt loam, as opposed to sandy loam on Riverhead), and the growing season is shorter than on Long Island. The population of Colorado potato beetle at Freeville is mostly univoltine, with some bivoltinism; on Long Island, however, a large portion of the population produces a second generation (M. J. Tauber et al. 1988).

We asked the following questions: What is the seasonal pattern of response to diapause-maintain-

ing stimuli? What is the intrapopulation and interpopulation variation in the ecophysiological status of beetles during diapause? What variability in responses underlies reproductive development leading to emergence and reproduction by overwintered beetles?

Materials and Methods

Once induced, dormancy typically is divided into two physiologically distinct periods: diapause maintenance (during which token stimuli act to prevent development and reproduction, even if environmental conditions are favorable) and postdiapause development (during which favorable conditions promote developmental and reproductive processes) (Tauber et al. 1986). Because these physiological states are not easily recognized in living beetles, we used oviposition as a sign of diapause termination, therefore, our findings pertain largely to females. We defined the "preoviposition period" as the time (days) from field sample (or removal from cold conditions) to the initiation of oviposition; this period includes diapause development and postdiapause development.

In our tests, beetles were maintained in cages (0.24 liter) and continuously provided with bouquets of fresh *Solanum tuberosum* (cv. Katahdin) foliage. Temperatures fluctuated ±0.5°C of the designated constant temperature. Reference specimens from each population are deposited in the Cornell University Insect Collection (Lot # 1158).

Diapause Maintenance. We collected many adult *L. decemlineata* (second summer generation) at the end of summer and overwintered them in outdoor screen cages (75 by 60 by 90 cm) that were dug into the soil to a depth of 30 cm. Foliage from field-grown 'Katahdin' plants was provided until the beetles had burrowed into the soil.

At regular intervals from late summer through early spring, we transferred beetles from the field to a variety of photoperiodic and thermal conditions in the laboratory (Tables 1–4). The experiments were conducted over two years on the Freeville and the Riverhead populations, 1982–1983 and 1983–1984.

Postdormancy Reproduction. To determine the thermal requirements for reproduction after dormancy, we collected adults in mid (1983) or late (1982) summer (Freeville), or we reared and maintained adults under diapause-inducing conditions in the laboratory (Riverhead). After two weeks at 23.9°C, the beetles were transferred through a series of decreasing temperatures (21, 18, 16, 10, and 5°C) at 2-wk intervals under a photoperiod of 10:14 (L:D). Beetles had continuous access to 'Katahdin' foliage until the temperature reached 5°C. After approximately 3 mo at 5°C (without food), paired adults were moved to a range of temperatures (Table 5) under a photoperiod of 10:14 or 16:8 and held to determine the preoviposition periods.

To find out if overwintered females must mate before ovipositing fertile eggs in spring, we ran two tests (Table 6). From the population at Freeville, we collected diapausing beetles in summer and overwintered them in the laboratory (as described above). When females were transferred from 5°C (10:14 photoperiod) to 24°C (16:8 photoperiod), half were isolated in individual cages and half were paired with males. All received fresh potato foliage daily, and the incidence of fertile oviposition and the preoviposition periods were recorded. We conducted a similar test on the Riverhead population, except that beetles were overwintered under natural conditions. Females were transferred from the field to 21.1 or 24°C (16:8 photoperiod) in January and April 1984.

To analyze the relationship between temperature and development, we used the reciprocal of the developmental times (medians) and then fitted a regression line to the data from each population using the least-squares method. We estimated the lower thermal threshold, t, for each population by extrapolating the regression line through the x-axis (temperature). We then derived K (heat-degree days, HDD) from the equation, $K = 1/y(x - t)$, in which y = mean developmental rate and x = temperature (°C).

Postdormancy Emergence Under Field Conditions. In late summer, beetles were collected and placed into outdoor cages (180 by 180 by 180 cm). They were provided field-grown 'Katahdin' foliage until they had burrowed into the soil. The cages were removed in late autumn and screened emergence traps were placed over the sites in early spring before emergence began. The traps were checked at least every two days. Soil temperatures were recorded from a depth of approximately 12 cm (Freeville) and 15 cm (Riverhead) (Table 7).

Ecophysiological Responses of Overwintered Beetles. To determine the responses of emerged beetles to diapause inducing conditions, we collected beetles that had overwintered under natural conditions at Freeville. The beetles were paired in cages (0.24 liter) and were continuously provided fresh 'Katahdin' foliage. In 1983, the beetles were exposed to a variety of temperatures under one photoperiod (16:8 photoperiod) (Table 8). In 1984, two temperatures and two photoperiods were tested (Table 8). For comparison, we examined the response of first-generation, summer beetles to long daylengths and high (23.9°C) temperatures.

Results

Diapause Maintenance — Freeville (1982–1983 and 1983–1984). (Tables 1 and 2). In the sample from mid-August, diapause duration was similar across all photoperiods and temperatures; under all conditions the mean time to oviposition was greater than 140 d. At all temperatures (especially the low temperatures), long daylength (16:8

Table 1. Responses to photoperiod and temperature by overwintering *L. decemlineata* from Freeville, N.Y., 1982–1983

	Photoperiod (L:D) and temperature (°C)									
	16:8 23.9	16:8 21.1	16:8 18.3	16:8 15.6	14:10 23.9	12:12 23.9	10:14 23.9	10:14 21.1	10:14 18.3	10:14 15.6
19 Sept.[a]										
% oviposition	100	83.3	100	62.5	71.4	28.6	66.7	85.7	16.7	14.3
n	(9)	(6)	(7)	(8)	(7)	(7)	(9)	(7)	(6)	(7)
Preoviposition period[b]	33.3 ± 3.8	110.2 ± 31.2	132.9 ± 33.8	224.6 ± 58.4	198.4 ± 55.9	152.0 ± 39.6	194.8 ± 28.6	185.8 ± 19.7	232	265
	29–40 (9)	70–146 (5)	82–175 (7)	168–305 (5)	146–263 (5)	124–180 (2)	170–251 (6)	169–225 (6)	—(1)	—(1)
10 Dec.										
% oviposition	100	100	100	66.7	100	100	50	75	50	25
n	(4)	(5)	(4)	(3)	(4)	(3)	(4)	(4)	(4)	(4)
Preoviposition period[b]	22.3 ± 9.7	24.6 ± 5.1	59.5 ± 13.2	56.0 ± 22.6	36.8 ± 10.5	32.3 ± 4.7	51.5 ± 37.5	108.7 ± 29.6	89.5 ± 17.7	271
	13–33 (4)	19–31 (5)	45–73 (4)	40–72 (2)	25–47 (4)	27–36 (3)	25–78 (2)	83–141 (3)	77–102 (2)	—(1)
11 Jan.										
% oviposition	100	80	100	100	100	100	50	40	66.7	25
n	(4)	(5)	(4)	(5)	(4)	(3)	(4)	(5)	(3)	(4)
Preoviposition period[b]	13.8 ± 1.9	26.8 ± 1.2	47.8 ± 3.4	61.4 ± 14.6	30.5 ± 11.1	31.7 ± 17.5	24.0 ± 19.8	5.5 ± 12.0	120.0 ± 49.5	108
	11–15 (4)	14–38 (4)	45–52 (4)	50–83 (5)	17–43 (4)	17–51 (3)	10–38 (2)	47–64 (2)	85–155 (2)	—(1)
25 Feb.										
% oviposition	100	—	—	100	—	—	100	—	—	—
n	(5)			(2)			(5)			
Preoviposition period[b]	15.4 ± 5.1	—	—	51.0 ± 25.5	—	—	22.0 ± 5.1	—	—	—
	10–21 (5)			33–69 (2)			14–28 (5)			

[a] 19 September sample held at 16:8 photoperiod, 26.7°C: 100% oviposition in 30.2 ± 7.3 d (range, 18–39; n = 7).
[b] Preoviposition period: mean ± SD days, followed by the range and number of ovipositing females in parentheses.

Table 2. Responses to photoperiod and temperature by overwintering *L. decemlineata* from Freeville, N.Y., 1983–1984

	Photoperiod (L:D) and temperature (°C)									
	16:8 23.9	16:8 21.1	16:8 18.3	16:8 15.6	14:10 23.9	12:12 23.9	10:14 23.9	10:14 21.1	10:14 18.3	10:14 15.6
19 Aug.										
% oviposition	71.4	85.7	66.7	50	40	33.3	66.7	66.7	12.5	11.1
n	(7)	(7)	(6)	(6)	(5)	(9)	(6)	(9)	(8)	(9)
Preoviposition period[a]	189 ± 129.6, 87–341 (5)	211.3 ± 66.2, 150–335 (6)	186.0 ± 39.4, 156–241 (4)	206 ± 44, 167–254 (3)	185.5 ± 88.4, 123–248 (2)	146.3 ± 49.0, 98–196 (3)	192.8 ± 30.0, 156–229 (4)	211.2 ± 38.0, 158–266 (6)	242, —(1)	172 (1)
21 Sept.										
% oviposition	100	72.3	50	0	12.5	0	60	83.3	0	16.7
n	(9)	(11)	(8)	(9)	(8)	(5)	(10)	(6)	(9)	(6)
Preoviposition period[a]	61.4 ± 19.9, 39–104 (9)	119.4 ± 48.8, 80–226 (8)	143.8 ± 25.3, 107–165 (4)	—	224, —(1)	—	150.5 ± 46.7, 94–215 (6)	188.0 ± 41.5, 121–225 (5)	—	215 (1)
20 Oct.										
% oviposition	100	87.5	85.7	45.5	75	71.4	55.6	87.5	50	25
n	(10)	(8)	(7)	(11)	(4)	(7)	(9)	(8)	(4)	(8)
Preoviposition period[a]	47.4 ± 26.8, 18–92 (10)	102.4 ± 99.9, 34–299 (7)	115.7 ± 48.8, 44–183 (6)	94.8 ± 28.0, 52–130 (5)	97.7 ± 81.3, 26–186 (3)	70.4 ± 32.2, 41–114 (5)	68.6 ± 26.0, 40–103 (5)	120.0 ± 66.7, 36–204 (7)	192.5 ± 3.5, 190–195 (2)	123.5 ± 21.9, 108–139 (2)
22 Nov.										
% oviposition	100	100	83.3	75	88.9	66.7	40	55.6	0	28.6
n	(8)	(7)	(6)	(8)	(9)	(6)	(5)	(9)	(8)	(7)
Preoviposition period[a]	38.9 ± 25.6, 15–94 (8)	44.9 ± 10.6, 27–57 (7)	63.0 ± 11.4, 56–83 (5)	89.3 ± 26.0, 59–122 (6)	45.6 ± 22.1, 12–76 (8)	46.0 ± 33.5, 8–78 (4)	57.5 ± 6.4, 53–62 (2)	55.2 ± 48.5, 15–139 (5)	—	112.0 ± 24.0, 95–129 (2)
5 Jan.										
% oviposition	100	100	100	22.2	100	87.5	50	80	9.1	14.3
n	(8)	(7)	(8)	(9)	(6)	(8)	(8)	(10)	(11)	(7)
Preoviposition period[a]	22.5 ± 5.8, 15–32 (8)	40.5 ± 18.8, 22–222 (6)	61.6 ± 20.4, 39–99 (8)	85.0 ± 26.9, 66–104 (2)	33.8 ± 14.9, 19–61 (6)	27.4 ± 7.5, 17–37 (7)	69.3 ± 14.1, 56–89 (4)	71.6 ± 11.9, 59–99 (8)	85, —(1)	176 —(1)
21 Feb.										
% oviposition	100	100	83.3	60	100	80	100	100	25	14.3
n	(5)	(7)	(6)	(5)	(6)	(5)	(3)	(7)	(8)	(7)
Preoviposition period[a]	21.2 ± 3.5, 18–27 (5)	31.0 ± 11.5, 22–48 (5)	26.4 ± 6.2, 18–34 (5)	73.3 ± 40.3, 27–100 (3)	29.3 ± 14.5, 13–53 (6)	30.0 ± 8.1, 23–41 (4)	28.0 ± 16.5, 17–47 (3)	31.4 ± 12.7, 20–52 (7)	47.0 ± 21.2, 32–62 (2)	77 (1)
11 Apr.										
% oviposition	100	100	100	25	100	66.7	80	66.7	22.2	11.1
n	(6)	(7)	(5)	(8)	(6)	(9)	(5)	(6)	(9)	(9)
Preoviposition period[a]	15.7 ± 5.8, 11–26 (6)	26.1 ± 10.6, 15–44 (7)	19.5 ± 2.1, 17–22 (4)	40.0 ± 9.9, 33–47 (2)	22.7 ± 17.2, 12–57 (6)	23.7 ± 8.6, 15–40 (6)	16.5 ± 2.1, 14–19 (4)	25.8 ± 15.9, 13–49 (4)	27.0 ± 19.8, 22–82 (2)	47 (1)

[a] Preoviposition period: mean ± SD days, followed by the range and number of ovipositing females in parentheses.

Table 3. Responses to photoperiod and temperature by *L. decemlineata* from Riverhead, Long Island, N.Y., 1982–1983

	16:8 / 26.7	16:8 / 23.9	16:8 / 21.1	16:8 / 18.3	16:8 / 15.6	14:10 / 23.9	12:12 / 23.9	10:14 / 23.9	10:14 / 21.1	10:14 / 18.3	10:14 / 15.6
19 Sept.											
% oviposition	73	91	82	73	55	27	18	27	27	27	9
n	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(11)
Preoviposition period[a]	68.8 ± 40.3 (8); 35–150	88.5 ± 6.20 (10); 36–239	92.5 ± 28.3 (9); 55–125	133.5 ± 24.2 (8); 111–173	176.5 ± 29.1 (6); 150–233	202.3 ± 73.3 (3); 136–281	161.0 ± 31.1 (2); 139–183	146.0 ± 27.4 (3); 125–177	196.3 ± 40.0 (3); 168–234	213.3 ± 40.5 (3); 168–246	269 (1)
23 Oct.											
% oviposition	67	100	55	83	50	36	55	36	46	9	0
n	(12)	(11)	(11)	(12)	(12)	(11)	(11)	(11)	(11)	(11)	(12)
Preoviposition period[a]	18.8 ± 5.51 (8); 11–34	45.6 ± 32.7 (11); 16–132	33.8 ± 9.6 (6); 20–90	63.4 ± 26.6 (10); 23–90	116.0 ± 28.4 (6); 96–171	73.0 ± 74.0 (4); 34–184	94.3 ± 33.1 (6); 69–159	131.3 ± 61.1 (4); 76–201	161.4 ± 72.3 (5); 48–241	192 (1)	—
7 Dec.											
% oviposition	100	46	82	82	75	64	64	46	33	75	23
n	(10)	(11)	(11)	(11)	(12)	(11)	(11)	(11)	(12)	(12)	(13)
Preoviposition period[a]	14.1 ± 4.4 (10); 10–20	13.2 ± 4.1 (5); 10–20	21.3 ± 4.0 (9); 13–27	49.7 ± 15.7 (9); 27–72	56.8 ± 8.3 (7); 45–72	36.3 ± 12.0 (7); 24–55	39.7 ± 13.7 (7); 24–62	31.8 ± 3.4 (5); 27–36	95.5 ± 33.1 (4); 76–145	119.3 ± 52.2 (4); 55–204	150.3 ± 23.0 (3); 128–174
11 Jan.											
% oviposition	91	100	82	73	73	75	46	36	55	25	25
n	(11)	(11)	(11)	(11)	(11)	(12)	(11)	(11)	(11)	(12)	(12)
Preoviposition period[a]	12.0 ± 2.3 (10); 9–17	16.8 ± 5.7 (11); 10–29	38.7 ± 26.0 (9); 20–106	45.5 ± 22.6 (8); 32–100	72.3 ± 3.7 (8); 39–148	22.8 ± 18.8 (9); 11–72	24.6 ± 9.1 (5); 15–39	31.3 ± 14.6 (4); 18–48	53.2 ± 24.1 (6); 26–95	82.0 ± 32.4 (3); 53–117	125.7 ± 17.0 (3); 113–145
6 Feb.											
% oviposition	100	92	75	83	83	83	83	92	58	42	33
n	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
Preoviposition period[a]	12.1 ± 3.6 (12); 9–21	14.4 ± 2.4 (11); 10–18	21.1 ± 3.4 (9); 16–26	28.2 ± 6.5 (10); 19–39	67.2 ± 45.6 (10); 30–179	15.5 ± 4.0 (10); 11–22	17.2 ± 5.2 (10); 13–30	12.7 ± 3.1 (11); 9–17	29.6 ± 6.9 (7); 18–37	55.6 ± 27.7 (5); 21–93	97.0 ± 24.5 (4); 75–127
21 Mar.[b]											
% oviposition	100	100	100	71	93	—	100	83	92	29	8
n	(13)	(13)	(7)	(14)	(14)	—	(12)	(12)	(12)	(14)	(13)
Preoviposition period[a]	11.0 ± 2.0 (13); 8–16	12.4 ± 2.1 (13); 9–16	16.6 ± 3.7 (11); 13–24	24.6 ± 5.1 (10); 20–38	44.8 ± 21.1 (13); 29–87	—	14.9 ± 6.9 (12); 9–32	13.9 ± 3.4 (12); 10–22	35.3 ± 23.4 (11); 14–83	46.0 ± 19.2 (4); 30–71	60 (1)
27 Apr.											
% oviposition	86	86	100	100	100	—	—	—	100	100	63
n	(7)	(7)	(7)	(7)	(7)	—	—	—	(7)	(7)	(8)
Preoviposition period[a]	7.2 ± 1.9 (7); 5–10	20.0 ± 25.8 (6); 7–78	14.3 ± 4.8 (7); 9–23	15.0 ± 2.4 (5); 12–18	41.7 ± 33.0 (7); 20–114	—	—	—	24.4 ± 22.1 (7); 10–72	25.0 ± 13.0 (4); 14–43	47.4 ± 2.9 (5); 43–50

[a] Preoviposition period: mean ± SD days, followed by the range and number of ovipositing females in parentheses.

[b] 21 March sample held at 12:12 photoperiod, 15.6°C: 61.5% oviposition in 85.9 ± 48.7 d (range, 29–171, n = 13). 21 March sample held at 14:10 photoperiod, 15.6°C: 76.9% oviposition in 43.1 ± 14.6 d (range, 20–60; n = 13).

Table 4. Responses to photoperiod and temperature by overwintering *L. decemlineata* from Riverhead, Long Island, N.Y., 1983–1984

	Photoperiod (L:D) and temperature (°C)						
	16:8 23.9	16:8 21.1	16:8 18.3	13:11 21.1	10:14 23.9	10:14 21.1	10:14 18.3
29 Aug.							
% oviposition	71.4	57.1	67.9	7.1	21.4	28.6	7.1
n	(28)	(28)	(28)	(28)	(28)	(28)	(28)
Preoviposition period[a]	72.3 ± 84.8	86.2 ± 32.5	203.1 ± 39.9	277.0 ± 62.2	171.0 ± 19.4	225.3 ± 33.3	242.0 ± 2.8
	8–238 (20)	11–282 (16)	74–264 (19)	233–321 (2)	140–189 (6)	156–268 (8)	240–244 (2)
30 Oct.							
% oviposition	69.6	50.0	60.7	7.1	21.4	21.4	7.1
n	(56)	(28)	(28)	(28)	(28)	(28)	(28)
Preoviposition period[a]	38.8 ± 30.7	63.3 ± 54.1	118.4 ± 51.4	210.5 ± 4.9	180.5 ± 38.6	187.8 ± 31.3	145.0 ± 93.3
	12–101 (39)	21–203 (14)	23–212 (17)	207–214 (2)	99–206 (6)	126–213 (6)	79–211 (2)
21 Nov.[b]							
% oviposition	64.3	67.9	71.4	—	14.3	42.9	0
n	(28)	(28)	(14)		(14)	(14)	(14)
Preoviposition period[a]	18.9 ± 8.0	29.1 ± 13.1	53.7 ± 35.9	—	44.5 ± 7.8	64.5 ± 26.7	—
	11–46 (18)	17–75 (19)	30–153 (10)	—	39–50 (2)	23–92 (6)	—
23 Jan.							
% oviposition	72.7	90.9	63.6	72.7	72.7	36.4	36.4
n	(22)	(11)	(11)	(11)	(11)	(11)	(11)
Preoviposition period[a]	11.2 ± 2.3	21.4 ± 20.8	56.2 ± 26.1	36.6 ± 26.9	77.5 ± 86.9	29.5 ± 20.3	79.0 ± 18.7
	9–17 (16)	11–77 (10)	24–91 (7)	11–93 (8)	14–273 (8)	11–49 (4)	53–97 (4)
9 Apr.							
% oviposition	83.3	83.3	83.3	—	83.3	100	100
n	(6)	(6)	(6)		(6)	(6)	(6)
Preoviposition period[a]	9.0 ± 0.7	11.6 ± 1.1	21.2 ± 3.8	—	9.2 ± 1.3	12.0 ± 1.4	34.2 ± 22.6
	8–10 (5)	10–13 (5)	17–27 (5)	—	7–10 (5)	10–14 (6)	18–68 (6)

[a] Preoviposition period: mean ± SD days, followed by the range and number of ovipositing females in parentheses.
[b] 21 November sample held at 14:10 photoperiod, 23.9°C yielded 71.4% oviposition ($n = 14$) in 18.5 ± 5.3 d (range, 7–24; $n = 10$).

photoperiod) elicited a greater incidence of oviposition than did shorter daylengths (Table 2).

In September and October, a photoperiod of 16:8 (at 23.9°C) resulted in 100% reproduction, and at this temperature, oviposition occurred faster in 16:8 than in the other photoperiods (Tables 1 and 2). In most samples held at temperatures below 23.9°C, the 16:8 photoperiod also increased the incidence of oviposition and shortened the preoviposition period.

In November, the 16:8 photoperiod at 21.1°C showed an increased incidence of oviposition and a decreased time to oviposition; photoperiods of 14:10 and 12:12 also showed a decrease in the preoviposition period. At temperatures below 23.9°C, the incidence of oviposition was greater and the time to oviposition was shorter at long daylengths (16:8 photoperiod) than at short (10:14) ones.

By December and January (at 23.9°C), the effect of daylength on the incidence of oviposition was diminished; only the samples held at short daylengths (12:12 photoperiod, January; 10:14 photoperiod, December and January) had less than 100% oviposition. At temperatures below 23.9°C, photoperiod influenced the incidence of oviposition and the time to oviposition.

In February (at 23.9 and 21.1°C), the incidence of oviposition was high and the preoviposition periods short under all photoperiods. Short daylengths

continued to retard diapause development at 18.3 and 15.6°C.

In the sample from April, short daylengths appeared to diminish the incidence of oviposition at 23.9 and 21.1°C, but the time for first oviposition was not affected. The beetles held at 18.3 and 15.6°C remained sensitive to short daylengths.

Table 5. Geographical variation in thermal requirements for oviposition by *L. decemlineata* overwintered under low temperature (5°C)[a]

Temperature (°C)	Preoviposition period (d)		n ♀♀
	Mean ± SD	Range	
Freeville, N.Y.			
18.3	39.2 ± 20.1	21–79	13
21.0	29.6 ± 14.5	14–79	25
23.9	22.7 ± 10.3	10–54	27
26.7	15.2 ± 3.9	9–23	19
Riverhead, Long Island, N.Y.			
15.6	38.1 ± 14.4	28–70	8
18.3	27.4 ± 9.3	16–40	5
21.0	20.3 ± 12.5	10–64	20
23.9	10.6 ± 1.9	7–13	7
26.7	16.8 ± 15.4	7–46	6

[a] Results at 10:14 and 16:8 photoperiod did not differ significantly; therefore when both photoperiods were tested (Freeville: 21.0 and 23.9°C; Riverhead: 21.0°C), both sets of data are included. All other data points are from 16:8 photoperiod.

Table 6. Influence of males on fertile oviposition by field-collected *L. decemlineata* females after overwintering under laboratory (5°C) or natural conditions

	Unpaired ♀♀		♀♀ with ♂♂	
	% fertile oviposition (n)	Preoviposition period[a]	% fertile oviposition (n)	Preoviposition period[a]
Freeville, N.Y.				
Collected in summer and overwintered in laboratory; tested in April	86 (7)	17.7 ± 7.1 (6)	100 (13)	25.1 ± 11.6 (13)
Riverhead, N.Y.				
Collected and tested in January; 21.1°C	100 (8)	19.9 ± 8.6 (8)	100 (10)	21.4 ± 20.8 (10)
Collected and tested in January; 24.0°C	100 (9)	11.1 ± 3.5 (9)	100 (16)	11.2± 2.3 (16)
Collected and tested in April; 21.1°C	83 (6)	13.2 ± 3.3 (6)	100 (5)	11.6 ± 1.1 (5)
Collected and tested in April; 24.0°C	100 (6)	8.0 ± 1.4 (4)	100 (5)	9.0 ± 0.7 (5)

[a] Preoviposition period is mean ± SD days; number of females is in parentheses.

Variation in the duration of diapause under all conditions was high throughout the overwintering seasons. This is evident in the wide range of preoviposition periods (Tables 1 and 2).

Diapause Maintenance—Riverhead (1982–1983 and 1983–1984). (Tables 3 and 4). In August and September, the incidence of oviposition was very low under short daylengths and the preoviposition periods were very long (Tables 3 and 4). During October, there was a slight increase in percentage oviposition; long daylengths and high temperatures shortened the preoviposition period.

During November and December, temperature did not have a major influence on the incidence of oviposition at long daylengths, but it did influence

influence the preoviposition period. Daylength influenced the incidence and the duration of the preoviposition period at all temperatures.

As the season progressed from January through March, the duration of the preoviposition period decreased under all conditions (with a few exceptions). Short daylengths, especially at the low temperatures, tended to decrease the incidence of preoviposition and increase the time for first oviposition.

By April, a high percentage of the beetles in all conditions oviposited, and the duration of the preoviposition period generally was inversely related to temperature. Under all conditions, variation in the duration of diapause was high throughout the overwintering period. Even in the April samples, a few beetles exhibited very long preoviposition periods under warm, long-day conditions (Tables 3 and 4).

Postdormancy Reproduction. In artificially overwintered beetles, the duration of the preovi-

Table 7. Summary of *L. decemlineata* emergence after overwintering at two localities in New York

	% emergence				
	1	10	50	90	99
Freeville					
1983					
HDD$_{12}$[a]	84	148	227	404	447
Julian date[b]	145	158	166	178	182
n = 90					
1984					
HDD$_{12}$[a]	160	241	278	406	507
Julian date[b]	161	168	171	184	194
n = 29					
Riverhead					
1984					
HDD$_{12}$[a]	1	1	4	19	30
Julian date[b]	120	126	136	147	156
n = 86					
1985					
HDD$_{12}$[a]	6	24	37	96	161
Julian date[b]	112	121	131	145	158
n = 1,037					

[a] Heat-degree days$_{12}$ are based on soil temperatures at 15 cm (Riverhead) and 12 cm (Freeville).

[b] Julian date 145 = 25 May 1983, 161 = 9 June 1984, 120 = 29 April 1984, 112 = 22 April 1985.

Table 8. Reproductive responses to *L. decemlineata* females from Freeville, N.Y., to photoperiod and temperature during spring and summer

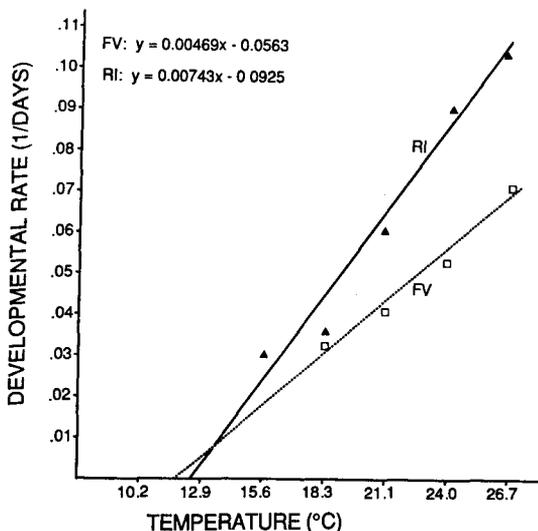| Collection date and condition in laboratory	% oviposition	% diapause	n pairs
26 May to 4 June 1983			
16:8[a] (29.4°C)	100	0	12
16:8 (26.7°C)	100	0	10
16:8 (23.9°C)	92	8	12
16:8 (21.1°C)	100	0	12
16:8 (18.3°C)	92	8	12
16:8 (16.5°C)	91	9	11
4 June to 6 June 1984			
16:8 (23.9°C)	100	0	20
10:14 (23.9°C)	100	0	20
16:8 (15.6°C)	86	14	15
10:14 (15.6°C)	33	67	15
7 August 1984			
16:8 (23.9°C)	0	100	10

[a] Photoperiod (L:D).

Fig. 1. Thermal requirements for oviposition by overwintered *L. decemlineata* adults (16:8 photoperiod). FV = Freeville, N.Y., $t = 12°C$, $K = 213$ HDD; RI = Riverhead, Long Island, N.Y., $t = 12.5°C$, $K = 134$ HDD.

position period decreased with increasing temperatures (Table 5). Daylength did not influence the duration of the preoviposition period (Student's t test: Freeville, 21°C: $t = 1.14$, $P = 0.27$; 24°C: $t = 1.13$, $P = 0.27$; Riverhead, 21.1°C: $t = 0.92$, $P = 0.38$).

The rate of reproductive development (one per preoviposition period) in females from Freeville and Riverhead increased linearly with increasing temperature (Fig. 1). The thermal thresholds for reproductive development were similar in the two populations (Freeville, $t = 12.0°C$ and Riverhead, $t = 12.5°C$); however, the number of heat-degree days (K) required for oviposition differed markedly (Freeville: $K = 213$ HDD and Riverhead: $K = 135$ HDD).

Overwintered females that were isolated from males oviposited fertile eggs as frequently and within similar preoviposition periods as did paired females (Table 6). This was true whether the females were overwintered under laboratory or field conditions (Freeville, $t = -1.435$, df = 17) (Riverhead, January, 24°C, $t = -0.067$, df = 23; April, 24°C, $t = -1.394$, df = 7; January, 21.1°C, $t = -0.194$, df = 16; April, 21.1°C, $t = 1.000$, df = 9).

Postdiapause Emergence Under Field Conditions. At Freeville, overwintered beetles began postdiapause emergence on 25 May in 1983 and on 9 June in 1984, and median emergence occurred after 227 and 278 HDD_{12} had accumulated (soil temperature at 12 cm). In both years, emergence extended approximately 35 d. The range of heat accumulation over which 10–90% emergence occurred was 256 HDD_{12} in 1983 and 165 HDD_{12} in 1984 (Table 7). Beetles emerged much earlier (in calendar date and in physiological time) at Riverhead than Free-

ville (Table 7). Emergence began on 29 April in 1984 and on 22 April in 1985 at Riverhead, and it required only 4 and 37 HDD_{12} (soil temperature at 15 cm) for median emergence. Emergence at Riverhead extended over about 36–46 d, but the period covering 10–90% emergence involved a much smaller range of HDD_{12} (18 in 1984 and 72 in 1985) than at Freeville.

Ecophysiological Responses of Overwintered Beetles. Naturally overwintered and emerged beetles generally had a high incidence of oviposition under conditions of long daylengths (16:8 photoperiod) and high or low temperatures (15.6–29.4°C). Under short daylengths, the incidence of oviposition was substantial only at high (23.9°C) temperatures (Table 8). However, the incidence of oviposition was greatly reduced when overwintered beetles were exposed to short daylengths and low temperature (15.6°C). Field-collected beetles from the first summer generation all entered diapause under long daylength and high temperature.

Discussion

Leptinotarsa decemlineata have a very intense diapause (as measured by the duration of the preoviposition period) in mid-August. At this time, diapause is only slightly affected by either photoperiod or temperature (Table 2). By mid-September, diapause intensity diminishes greatly, and photoperiod and temperature interact to maintain diapause (Tables 1 and 2). The intensity of diapause continues to decrease at a high rate until the end of October; subsequently, the relatively constant preoviposition period indicated that the rate of decline in diapause intensity is considerably slower. At high temperatures, responsiveness to photoperiod disappears by February; i.e., the percentage of oviposition and the time to oviposition at 23.9°C are similar across all photoperiods. However, the beetles remain responsive to photoperiod at low temperatures throughout dormancy (Tables 1, 2, and 8).

Our results indicate that most females enter dormancy after mating and are able to initiate fertile oviposition without mating again in spring (Table 6). This is consistent with previous reports (Minder & Kozarzhevskaya 1966).

Unlike many insects studied (Tauber & Tauber 1976), the Colorado potato beetle does not have a discrete break between the diapause and postdiapause periods. The intensity of diapause and the responses to photoperiod and temperature gradually change as the overwintering period progresses, but overwintered beetles continue to respond to photoperiod at low temperatures even after emergence (Table 8). This agrees with the findings of de Wilde and his coworkers that diapausing and nondiapausing Colorado potato beetles require long-day conditions to sustain oviposition (see de Kort et al. 1980). It also agrees with previous work indicating that imaginal diapause in some species,

including the Colorado potato beetle, is not an all-or-none, but a graded response (Tauber & Tauber 1976, Hodek 1983). In *L. decemlineata* sensitivity to photoperiod does not appear to be lost, but the range of temperatures over which it is expressed becomes restricted (Tables 1–4).

Overall, the seasonal progression of diapause in beetles from Freeville and Riverhead was similar (compare Tables 1 and 2 with 3 and 4). The primary difference between the two populations lies in the intensity (duration) of diapause. Because our samples at Riverhead did not begin until late August, we do not know how intense diapause was before this time. However, in subsequent samples, beetles from Riverhead generally showed a much shorter preoviposition period (less intense diapause) than those from Freeville.

The two populations from New York also differed in their postdormancy thermal requirements for reproduction (Table 5; Fig. 1). The pattern of the variation is rare, but not unknown among insects studied to date (see Tauber et al. 1987). The two populations had equivalent thermal thresholds ($t = \sim 12°C$) for reproductive development, but the Freeville population required 60% more heat-degree days for oviposition ($HDD_{12} = 213$ for Freeville and 135 for Riverhead). A similar type of variation (approximately equal t values and large differences in K values) was found for postdiapause development by *Ostrinia nubilalis* Hübner from two climatically different areas of Alberta, Canada (Lee & Spence 1987). Just as with the Colorado potato beetle, heat requirements for completion of development were lower for the *O. nubilalis* population associated with the milder climate.

The differences in ecophysiological responses (depth of diapause and thermal requirements for development after dormancy) between the two populations were reflected in their patterns of emergence in the field. At Riverhead, median emergence occurred much earlier (in calendar date and physiological time) than at Freeville—after only 4 (1984) and 37 (1985) HDD_{12} had accumulated, in comparison with the 227 (1983) and 278 (1984) HDD_{12} for median emergence at Freeville (Table 7). It is important to recognize this type of interpopulation variation and to include it in phenological models designed to predict emergence. Because of the intrinsic differences that can occur among geographic populations, a model that accurately predicts emergence by overwintered beetles in New Jersey (Lashomb et al. 1984) does not describe emergence at either Freeville or Riverhead.

The *L. decemlineata* from Riverhead presented us with an intriguing anomaly. Females that had overwintered in the laboratory required approximately 135 HDD_{12} to emerge from the substrate (vermiculite) and to initiate oviposition. In contrast, median emergence in the field required only 4 (1984) and 37 (1985) HDD_{12}. The thermal responses and behavior of beetles in the soil may vary

as the overwintering period progresses (Minder & Kozarzhevskaya 1966). Either of these, or other, factors could have caused the discrepancies between predicted and actual times of emergence.

Adaptive Significance. The patterns of response we obtained are in keeping with two important aspects of the phenology of the Colorado potato beetle. First, the critical photoperiod for diapause induction, the thermal requirements for nondiapause reproduction, the thermal influence on diapause induction, the intensity of diapause, and the thermal requirements for postdormancy oviposition vary between the two populations in New York state, in what appears to be an adaptive manner (C. A. Tauber et al. 1988, M. J. Tauber et al. 1988). Mild temperatures and sandy soil allow early planting of potatoes at the coastal (Riverhead) site; this favors early emergence and a high incidence of bivoltinism in the Colorado potato beetle. In turn, these traits may result in selection for a less intense diapause and reduced thermal requirements for reproduction, both after dormancy and during the summer (C. A. Tauber et al. 1988, M. J. Tauber et al. 1988).

At the cooler, inland site (Freeville), where the soils are heavy and moisture-laden, and potatoes are planted one month later than on Long Island, the situation is reversed. Spring emergence occurs late, and there is a high incidence of univoltinism. These traits favor an intense diapause and high thermal requirements for reproduction in both overwintered and summer beetles.

Second, intrapopulation variability plays an important role in the phenological adaptation of the beetle. This is true for the induction of diapause during the summer (C. A. Tauber et al. 1988, M. J. Tauber et al. 1988), and it also holds for overwintered beetles. The beetles have considerable intrapopulation variation in their patterns of spring emergence (Table 7), and in the physiological responses that control emergence. Diapause intensity and the thermal requirements for oviposition are very variable among individuals (i.e., range of variation on Tables 1–5). In addition, there are geographical differences in the variability in the physiological responses. The approximately 35-d spread in vernal emergence at Freeville occurs over a range of 165 to 256 HDD_{12}; at Riverhead a larger spread in emergence time (36–46 d) is achieved within a range of only 18 to 72 HDD_{12}. Thus, it appears that selection acts not only on the timing of emergence after dormancy, but also on the variability in the response patterns that control the range of variation in emergence.

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