Seasonal Synchrony of the Parasite *Perilitus coccinellae*[1] and Its Host *Coleomegilla maculata*[2]

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ABSTRACT

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Dormancy is significant in determining the seasonal interactions between the thelyotokous braconid parasite *Perilitus coccinellae* and its coccinellid host, *Coleomegilla maculata*. The parasite's autumnal diapause is maintained by short daylengths and it ends in 50% of the population by the winter solstice. Low temperatures are not required to terminate diapause. The autumnal-hibernal diapause of the host is maintained by short daylengths. By the end of Mar. the photoperiodic control of diapause ends in 50% of the beetles; subsequently temperature and availability of prey determine when oviposition begins. *P. coccinellae* parasitizes the overwintering *C. maculata* population twice: during Sept., before the beetles form overwintering aggregations, and again in spring after the beetles disperse.

The seasonal cycle of many temperate zone animals consists of a dormant phase, a period of growth and reproduction, and transitional phases which include diapause induction and postdiapause development. Among insects, the onset and termination of diapause synchronize the active and dormant phases to the appropriate seasons; thus, the timing of diapause induction and termination in insect parasites and their hosts is critical in determining the synchrony of the interacting species (see reviews by Askew 1971 and Fisher 1971). However with few exceptions (e.g., Schneiderman and Horowitz 1958, Vinogradova and Zinovjeva 1972) the factors that influence diapause in insect parasites are poorly known; such information is vital for understanding the population dynamics and co-evolution of host-parasite systems, and it is particularly important to biological control programs (see Tauber and Tauber 1976).

Perilitus coccinellae (Shrank), a thelyotokous braconid, parasitizes adults of many coccinellid species in the Holarctic (Hodek 1973); it overwinters as a 1st instar within the adult beetle (Balduf 1926, Hodek 1973). *Coleomegilla maculata* (DeGeer), a native coccinellid, overwinters as an adult in aggregated populations (Hagen 1962, Solbreck 1974). Our study examined hibernating populations of both host and parasite to determine factors controlling dormancy in the 2 species and the role of dormancy in their seasonal synchrony.

Because diapause is a dynamic state (Danilevsky 1965, Tauber and Tauber 1973a, 1976) we sampled periodically from field populations throughout dormancy so we could determine the role of naturally occurring environmental factors in diapause maintenance and postdiapause development.

Materials and Methods

Our procedures followed those outlined by Tauber and Tauber (1973a). We used adult *C. maculata* from the Ithaca, New York area from 2 overwintering populations near the edge of a corn field. We protected one of these aggregations (No. = ca. 600 beetles) with a screened cage. Based upon dissections, the sex ratio of *C. maculata* was approximately 60% females and 40% males. Each month (Oct.–Apr. 1975–1976 and Sept.–May 1976–1977), we took a sample from the overwintering populations. Individuals were divided equally among 6 photoperiodic conditions (Table 1). There were 6–10 beetles in each ½-pint cage; the beetles were provided with a cotton-plugged water vial, a Wheast®-protein mixture (Tauber and Tauber 1975), and an excess daily supply of live aphids (pea aphids, *Acyrthosiphon pisum* (Harris), and green peach aphids, *Myzus persicae* (Sulzer)). We tested for the requirement of chilling in diapause termination by beginning the sampling in the early fall, prior to the occurrence of low temperatures in the field (Tables 2 and 4).

Individuals were checked daily. We used the emergence of *P. coccinellae* from *C. maculata* and the initiation of oviposition of fertile eggs by *C. maculata* as criteria for diapause termination. Thus, our measurement for diapause duration in both species includes the period of postdiapause development.

The mean ± SD number of days were calculated for *P. coccinellae* emergence from its host for each photoperiodic condition of each monthly sample. Initiation of oviposition within 30 days of the sample date was used as an index of diapause termination in *C. maculata* (see details in Results section).

Results

Perilitus coccinellae

Under L:D 16:8 diapausing *P. coccinellae* emerged from their hosts relatively quickly (Tables 1 and 2). At shorter daylengths one portion of the population generally emerged within the time range observed under L:D 16:8, and a second portion emerged considerably later than those observed under L:D 16:8. Therefore in analyzing our data for each monthly sample we used the range of emergence times observed under L:D 16:8 as the standard for comparison with the emergence times under other photoperiods.

1975–1976 Experiments.—Under L:D 16:8 and 14:10, 97% of all parasites in the Oct. sample emerged within ca. 20 days of the sample date (Table 1). Under shorter daylengths (L:D 12:12, 10:14, and 9:15) emergence times were generally longer. In the Nov. sample, 50% of the population under constant daylengths of 12 or less emerged within the period observed under L:D

[1] Hymenoptera: Braconidae.

[2] Coleoptera: Coccinellidae. Received for publication July 26, 1978.

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Table 1.—Mean number of days ± SD for *P. coccinellae* to emerge from its host after transfer from outdoors to various photoperiods (1975–76). No. in parentheses = no. of parasites, A = emergence within the range obtained under L:D 16:8, B = emergence time longer than that observed under L:D 16:8.

Sample date (% parasitism)		Photoperiod (L:D) 16:8	14:10	12:12	10:14	9:15	Natural
Oct. 22 [34]	A	19±2(19)	20±2 (9)			25(1)	25(1)
	B		53(1)	81±56 (7)	124±62 (6)	112±50 (9)	109±43(12)
Nov. 21 [49]	A	13±2(12)	14±2(18)	12± 2 (8)	14± 5 (7)	12± 2 (6)	15± 3 (3)
	B		24(1)	74±38 (6)	146±54 (7)	102±56 (8)	73±56(11)
Dec. 22 [47]	A	13±1(17)	12±3(18)	13± 3(11)	17± 5 (6)	15± 5(16)	15± 1(10)
	B			142±53 (4)	119±25 (3)		
Jan. 22 [42]	A	13±2(13)	12±2(13)	13± 2(13)	13± 1(10)	12± 1(11)	14± 2(15)
	B			75(1)			
Feb. 21 [48]	A	13±1(34)	11±2(23)	11± 2(23)	13± 2(23)	11± 1(22)	15± 2(18)
Mar. 20 [44]	A	12±3(24)	11±2(21)	11± 2(21)	12± 1(21)	11± 1(19)	13± 2(25)
Apr. 21 [34]	A	8±2(20)	6±1(10)	7± 2(19)	8± 2(18)	8± 2(11)	9± 2(23)

Temp: Constant photoperiods = 24°±1°C; natural photoperiods = 23°±2°C.

Table 2.—Mean number of days ± SD for *P. coccinellae* to emerge from its host after transfer from outdoors to various photoperiods (1976–77). No. in parentheses = no. of parasites, A = emergence within the range obtained under L:D 16:8, B = emergence time longer than that observed under L:D 16:8.

Sample date (% parasitism)		Photoperiod (L:D) 16:8	14:10	12:12	10:14	9:15	Natural
Sept. 22 [27]	A	26±5(20)				35± 8 (2)	
	B		95±37(15)	171±73(15)	164±44(11)	189±70 (6)	181±34(10)
Oct. 21 [31]	A	19±3(20)	24± 6 (7)	25(1)	26(1)	23± 7 (2)	
	B		88±36 (8)	138±55(14)	156±66(13)	157±80(12)	127±36(14)
Nov. 22 [47]	A	16±2(30)	21± 5(33)	16± 4 (2)	19± 2 (5)	22± 2 (3)	19± 3 (7)
	B		118± 1 (2)	134±54(14)	117±50(11)	142±92(13)	120±40(20)
Dec. 22 [54]	A	12±2(31)	13± 3(30)	12± 3(13)	15± 4(19)	13± 3(17)	15± 2(12)
	B			87±46 (7)	113±71(10)	135±62 (6)	99±29(16)
Jan. 21 [51]	A	13±2(34)	13± 2(32)	13± 2(22)	14± 3(17)	14± 3(21)	16± 2(17)
	B			119(1)	152(1)	120(1)	102±10 (6)
Feb. 21 [63]	A	13±2(24)	13± 2(34)	12± 1(34)	13± 2(34)	13± 2(36)	13± 2(20)
	B				71(1)		68± 5 (3)
Mar. 21 [50]	A	11±2(23)	11± 2(29)	11± 2(24)	11± 2(29)	10± 1(23)	11± 2(23)
Apr. 21 [35]	A	7±2(14)	7± 2 (8)	8± 3(16)	7± 2(17)	7± 3(15)	7± 2(14)
May 20 [7]	A	2±1 (4)	3(1)	2± 1 (3)		2± 1 (3)	3± 2 (2)

Temp: Constant photoperiods = 24°±1°C; natural photoperiod = 23°±2°C.

16:8 (13±2 days). Similarly, between Dec. and Jan. the percentage of the population that emerged within 13±2 days increased from 83 to 97% (Table 1). In the Feb. sample, all individuals emerged within ca. 13 days. The emergence time was similar for Feb. and Mar., but it was shorter in the Apr. sample (Table 1).

P. coccinellae transferred into natural daylengths (at 23°±2°C) in Oct. and Nov. responded similarly to individuals transferred to constant short daylengths (e.g., L:D 10:14, 9:15). Within each sample from Jan. to Mar., the time to exit under natural photoperiods was generally equivalent to that under constant daylengths. Outdoors, parasites emerged (from hosts that had been provided with prey) beginning Apr. 21 and ending May 30 (median date - May 12).

1976–1977 Experiments.—In the Sept. sample, only 4% of the parasites under constant daylengths of 14 h or less, emerged within the time period (26±5 days) observed at L:D 16:8. In the Oct. sample 47% of the individuals at L:D 14:10 emerged within the time period

observed under L:D 16:8 (19±3 days); under shorter daylengths 9% of the population emerged within this 19-day period (Table 2). Ninety-seven % of the parasites under L:D 16:8 and 14:10, in the Nov. sample, emerged within ca. 20 days of the sample date. By the 3rd week of Dec., 68% of the population under constant daylengths of 12 h or less emerged within the time observed at L:D 16:8 (12±2 days). All of the parasites under constant daylengths, except 3 in Jan. and one in Feb., emerged within 13±2 days (Table 2). The emergence time was similar in Jan., Feb., and Mar., but it was shorter in the Apr. and May samples (Table 2).

From Sept. to Feb., *P. coccinellae* transferred into natural daylengths (23°±2°C) responded similarly to individuals under all constant short daylengths. From Mar. to May emergence times under natural conditions were not different from those under constant photoperiods. Outdoors, *P. coccinellae* emerged (from hosts that had been provided with prey) from May 18 to 21 (median date - May 19).

Coleomegilla maculata

The initiation of oviposition by *C. maculata* females occurred either within 30 days of the sample date or after 45 days from the sample date; therefore in analyzing the data, we used the 30-day period to classify the state of diapause in the beetles. In all cases the percentage of oviposition was based upon the number of unparasitized females in each condition. Under short daylengths approximately 90% of the beetles from the autumn samples survived for over 200 days but the females did not oviposit (Table 3).

1975–1976 Experiments.—In Oct., 89 and 50% of the *C. maculata* females under L:D 16:8 and 14:10 conditions, respectively, oviposited within 30 days; the remaining females under these photoperiods did not oviposit (Table 3). Under shorter daylengths none of the females oviposited within 30 days, but a small percentage did so within 45–200 days. In the Nov. sample at daylengths of 14 h or less, a high percentage of the females survived for 200 days but did not oviposit. Those females that oviposited in each of the constant photoperiods (except L:D 9:15) did so within 30 days of the sample date. Subsequently, from Dec. through Apr., the percentage of females ovipositing under all constant photoperiods generally increased (from 55 to 82%), and all of the females that oviposited, did so within 30 days of the sample date (Table 3).

C. maculata females transferred into natural daylengths (at 23±2°C) in Oct. and Nov. did not initiate oviposition until after 120 days; ca. 50% oviposited by day 200. Under natural photoperiods, 10 and 25% of the females from the Dec. and Jan. samples, respectively, began ovipositing within 30 days (Table 3). In the Feb. sample there was a slight decrease in the percentage (15%) of the females ovipositing within 30 days; however 91 and 71% of the females in the Mar. and Apr. samples, respectively, oviposited within this period. By the end of Mar., females oviposited within 30 days or not at all.

Two groups of 50 *C. maculata* adults, that remained in outdoors cages, were provided with aphid prey beginning Mar. 20 and Apr. 21, respectively. The females in the group initially fed in Mar. oviposited within an avg of 54 days (median date - May 13) (range: Apr. 21–June 25); ($\bar{x}$ max temp = 18°C, $\bar{x}$ min temp = 5.5°C).[3] Females in the group initially fed in Apr. oviposited within an average of 48 days (median date - June 8) (range: May 28–July 4); ($\bar{x}$ max temp = 20°C, $\bar{x}$ min temp = 9°C).[3]

1976–1977 Experiments.—Forty-three percent of the females placed in L:D 16:8 during Sept. oviposited within 30 days; at the other photoperiods no oviposition was observed within this period. In Oct., 92 and 33% of the females under L:D 16:8 and L:D 14:10, respectively, (Table 4), oviposited within 30 days. No oviposition occurred at L:D 9:15, and the few females that initiated oviposition under L:D 12:12 and L:D 10:14 did

[3] Monthly Meteorological Summary, Division of Atmospheric Sciences, Cornell University.

Table 3.—Percentage oviposition by *C. maculata* after transfer from outdoors to various photoperiods (1975–76)*† (no. of ♀ in each condition = 17–33).

Sample date	Preoviposition period (days)	Photoperiod (L:D)					
		16:8	14:10	12:12	10:14	9:15	Natural
Oct. 22	<30	89%	50%	0%	0%	0%	0%
	45–200	0%	0%	7%	12%	11%	46%
Nov. 21	<30	100%	30%	29%	12%	0%	0%
	45–200	0%	0%	0%	0%	9%	57%
Dec. 22	<30	100%	100%	25%	44%	9%	10%
	45–200	0%	0%	0%	0%	0%	90%
Jan. 22	<30	100%	100%	18%	11%	15%	25%
	45–200	0%	0%	0%	0%	0%	25%
Feb. 21	<30	100%	86%	70%	41%	79%	15%
	45–200	0%	0%	0%	0%	0%	30%
Mar. 20	<30	100%	65%	95%	57%	53%	91%
	45–200	0%	0%	0%	0%	0%	0%
Apr. 21	<30	100%	100%	63%	62%	83%	71%
	45–200	0%	0%	0%	0%	0%	0%

* % remaining = females that did not oviposit; most survived >200 days.
† Temp: Constant photoperiods = 24°±1°C; natural photoperiod = 23°±2°C.

Table 4.—Percentage oviposition by *C. maculata* after transfer from outdoors to various photoperiods (1976–77)*† (no. of ♀ in each condition = 20–41).

Sample date	Preoviposition period (days)	Photoperiod (L:D) 16:8	14:10	12:12	10:14	9:15	Natural
Sept. 22	<30	43%	0%	0%	0%	0%	0%
	45–200	29%	52%	6%	0%	33%	60%
Oct. 21	<30	92%	33%	0%	0%	0%	0%
	45–200	0%	21%	12%	35%	0%	64%
Nov. 22	<30	69%	40%	0%	0%	15%	0%
	45–200	0%	30%	7%	25%	0%	20%
Dec. 22	<30	59%	71%	0%	0%	0%	0%
	45–200	0%	0%	0%	0%	0%	28%
Jan. 21	<30	62%	50%	21%	0%	11%	7%
	45–200	0%	29%	0%	14%	0%	21%
Feb. 21	<30	67%	79%	50%	46%	43%	33%
	45–200	4%	0%	0%	0%	7%	13%
Mar. 21	<30	68%	80%	20%	18%	0%	47%
	45–200	0%	20%	0%	0%	0%	11%
Apr. 21	<30	86%	85%	67%	44%	61%	63%
	45–200	0%	0%	0%	0%	0%	11%
May. 20	<30	78%	100%	71%	76%	68%	94%
	45–200	5%	0%	0%	0%	0%	0%

* % remaining = females that did not oviposit; most survived >200 days
† Temp: Constant photoperiods = 24°±1°C; natural photoperiod = 23°±2°C.

so after 45 days. Over 80% of the other beetles in short day survived more than 200 days without ovipositing (Table 4). In the Nov. sample 69% of the females at L:D 16:8 oviposited within 30 days; at L:D 14:10 40% oviposited within this period. In the Dec. and Jan. samples 59 and 70% of the females at L:D 16:8 and L:D 14:10 oviposited within 30 days of the sample dates. Most of the females from the Feb.–May samples that oviposited, did so within 30 days of their respective sample dates (Table 4).

In the samples from Sept. to Dec. none of the *C. maculata* females transferred into natural conditions oviposited within a month of the sample dates. Subsequently, the number of females ovipositing within 30 days under natural conditions increased from 7 in Jan. to 94% in May (Table 4).

Overwintering *C. maculata* females collected on May 16 and maintained outdoors with aphid prey, initiated oviposition within an avg of 10 days (median date - May 24) (range: May 18–June 13); ($\bar{x}$ max temp = 23°C, $\bar{x}$ min temp = 9°C).[3] Active females collected on 23 June and maintained on aphid prey oviposited within an avg of 7 days (median date - June 30) (range: June 28–July 2); ($\bar{x}$ max temp = 25°C, $\bar{x}$ min temp = 13°C).[3]

Discussion

Perilitus coccinellae

A comparison of *P. coccinellae's* long day and short day responses indicates that during Sept. and Oct. a high percentage of the parasite population is in diapause and that diapause is maintained by short daylengths (Tables 1 and 2). During the course of autumn the time to emerge under L:D 16:8 decreases (Table 2); this decline reflects the progression of diapause development. Prior to the winter solstice the photoperiodic maintenance of diapause ends in 50% of the population; by the end of Jan. the photoperiodic maintenance of diapause ends in all but a very small proportion of the population (Fig. 1). This photoperiodically controlled diapause ends

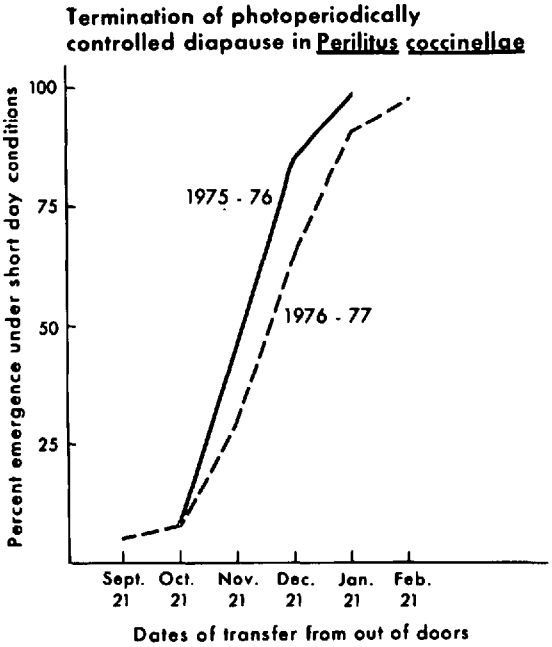

FIG. 1.—Percentage emergence within time range A under short day conditions for each monthly sample (data from L:D 12:12, 10:14, 9:15 and natural daylengths are combined). Percentages in 1975–76: Oct.-6, Nov.-43, Dec.-86, Jan.-98; in 1976–77: Sept.-5, Oct.-9, Nov.-26, Dec.-61, Jan.-89, Feb.-97. See Tables 1 and 2.

without an apparent terminating stimulus. Although long daylengths (e.g., L:D 16:8) can terminate diapause in *P. coccinellae* in the lab, they do not play a role in the termination of diapause in the field. Chilling is not necessary for diapause termination.

In our study the time required to emerge under long day conditions remained relatively constant from Dec. to Mar. Similarly, Hodek et al. (1977) recently showed that the time taken for *P. coccinellae* to emerge from another coccinellid host, *Coccinella septempunctata* (under L:D 18:6 and L:D 12:12, at 25°C), did not decrease between 2 sampling dates, Dec. and Mar. The emergence times were similar to those we observed. This constancy in emergence time probably occurs because the threshold temperature for postdiapause development is infrequently exceeded during the winter and thus there is little development. We conclude that the decrease in emergence time at all photoperiods in the Apr. sample indicates the occurrence of postdiapause development. We never found parasite cocoons in the overwintering aggregation, and we therefore conclude that parasite emergence occurs after the beetles disperse. This coincides with Solbreck's (1974) observation that *P. coccinellae* emerged from *C. maculata* that had dispersed from their overwintering sites.

Coleomegilla maculata

Characterization of diapause for *C. maculata* is more difficult than for its parasite because of (1) the variability in the responses of the females, and (2) the low numbers of females that oviposited under short daylengths in the autumn samples.

From *C. maculata's* photoperiodic responses we deduce that during early autumn (Sept. and Oct.) diapause is maintained by daylength. Because of the differing responses to natural and short daylengths, decreasing daylengths may be more effective in maintaining diapause than constant short daylengths (Tables 3 and 4). Between Dec. and Jan. the photoperiodic control of diapause begins to end. By late Mar. the photoperiodic control of diapause has ended in over 50% of the population.

Parker et al. (1977) examined the seasonal activity of *C. maculata* in Vermont by periodically monitoring respiration rates. They observed a low respiration rate from late Aug. to the end of the following May and concluded that this interval corresponds to the period of diapause in the population. In contrast, our experiments, which were designed to establish the relationship between photoperiod and diapause, show that the photoperiodic maintenance of diapause ends in Mar. From these 2 studies we conclude that a factor or factors other than photoperiod influence the maintenance of diapause from Mar. until May. Diet could serve as such a factor (see Hagen (1962) for an extensive review). Previously, Tauber and Tauber (1973b), working with another predacious species, showed that diet can act to maintain diapause after photoperiodic control ceases.

In a study of *C. maculata's* vernal dispersal, Solbreck (1974) found that in early winter, short daylengths retard flight. However, beetles tested in Mar. and Apr. did not show this response to short daylengths. Thus, both reproductive diapause and flight inhibition in *C. maculata* are influenced by short daylengths during autumn and early winter; the beetles lose this photoperiodic response by spring. Solbreck (1974) also demonstrated that spring temperatures above 15°C regulate the maturation of flight behavior and the dispersal of *C. maculata* from overwintering sites. From our data and from that of Solbreck (1974) and Parker et al. (1977) it appears that dispersal occurs prior to the time reproductive diapause ends in most individuals.

Seasonal Synchrony

Maslennikova (1968) categorized the types of interactions between insect hosts and their internal parasites in the regulation of diapause: (1) independent responses of host and parasite to environmental diapause-regulating factors, (2) simultaneous dependence of parasite on

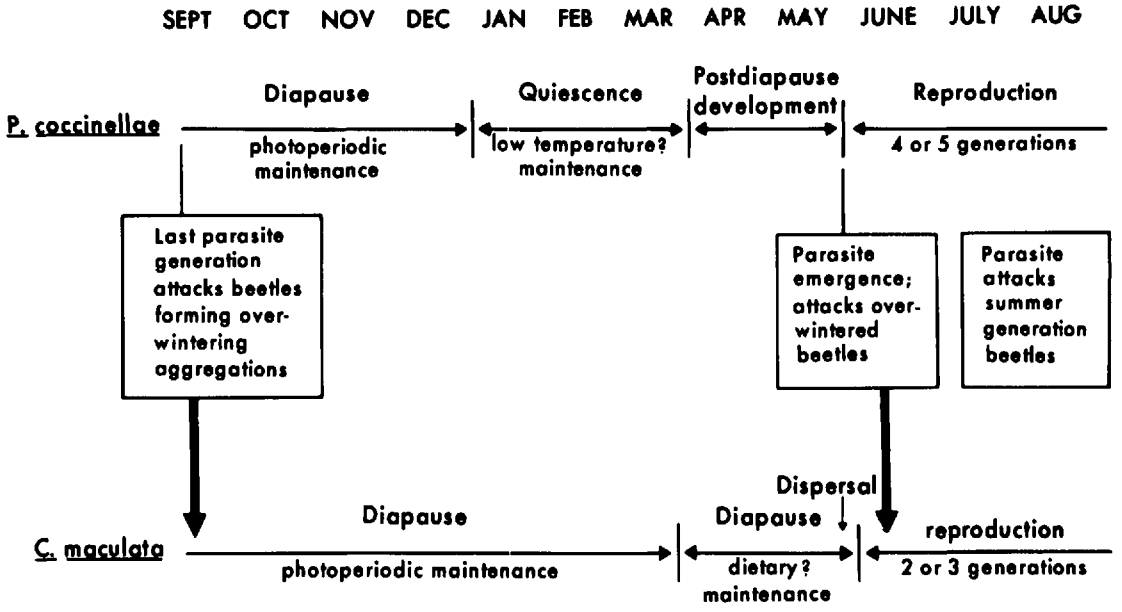

FIG. 2.—Seasonal synchrony of the parasite *Perilitus coccinellae* and its host *Coleomegilla maculata*.

host and environmental factors, and (3) dependence of parasite on host's physiological state. A comparison of the diapause characteristics of *P. coccinellae* and *C. maculata* from the Ithaca, N.Y., area shows that (1) diapause in both species is a dynamic state (i.e., diapause development continues throughout autumn), (2) both species respond to autumnal daylengths, (3) there is at least a 3-mo difference in the median date of diapause termination in the 2 species (Fig. 2), (4) both *P. coccinellae* and its host *C. maculata* respond independently to photoperiod during diapause maintenance. Thus during autumn they fit Maslennikova's 1st type of interaction.

Previously we showed that the beetle produces 2–3 generations/year and that the parasite produces 4 or 5 generations/year; summer temperatures govern the number of generations of *P. coccinellae*, while diet is very likely the limiting factor for *C. maculata* (Obrycki and Tauber 1978). By examining diapause maintenance and termination in *P. coccinellae* and *C. maculata*, and by determining the species' thermal requirements for development, we are able to predict much of their seasonal synchrony. From our data we conclude that *P. coccinellae* parasitizes the overwintering *C. maculata* population twice (Fig. 2): 1st, during Sept. before the beetles form their overwintering aggregations and 2nd, in spring after the beetles disperse.

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REFERENCES CITED

Askew, R. R. 1971. Parasitic Insects. American Elsevier, New York 316 pp.

Balduf, W. V. 1926. The bionomics of *Dinocampus coccinellae* Shrank. Ann. Entomol. Soc. Am. 19: 465–89.

Danilevsky, A. S. 1965. Photoperiodism and Seasonal Development of Insects. (English trans.) Oliver and Boyd, London. 282 pp.

Fisher, R. C. 1971. Aspects of the physiology of endoparasitic Hymenoptera. Biol. Rev. 46: 243–78.

Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. Annu. Rev. Entomol. 7: 289–326.

Hodek, I. 1973. Biology of Coccinellidae. Junk, The Hague, Academia, Prague 260 pp.

Hodek, I., G. Iperti, and F. Rolley. 1977. Activation of hibernating *Coccinella septempunctata* (Coleoptera) and *Perilitus coccinellae* (Hymenoptera) and the photoperiodic response after diapause. Entomol. Exp. Appl. 21: 275–86.

Maslennikova, V. A. 1968. Control of seasonal development in parasitic insects. P. 129–52. *In* A. S. Danilevsky, [ed.] The Photoperiodic Adaptations in Insects and Acari. Leningrad State Univ. (In Russian, English abstract).

Obrycki, J. J., and M. J. Tauber. 1978. Thermal requirements for the development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera: Braconidae). Can. Entomol. 110: 407–12.

Parker, B. L., M. E. Whalon, and M. Warshaw. 1977. Respiration and parasitism in *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). Ann. Entomol. Soc. Am. 70: 984–7.

Schneiderman, H. A., and J. Horowitz. 1958. The induction and termination of facultative diapause in chalcid wasps *Mormoniella vitripennis* (Walker) and *Tritneptis klugii* (Ratzeburg). J. Exp. Biol. 35: 520–51.

Solbreck, C. 1974. Maturation of post-hibernation flight behaviour in the coccinellid *Coleomegilla maculata* (DeGeer). Oecologia 17: 265–75.

Tauber, M. J., and C. A. Tauber. 1973a. Quantitative response to day length during diapause in insects. Nature. 244: 296–7.

1973b. Nutritional and photoperiodic control of the seasonal reproductive cycle in *Chrysopa mohave*. J. Insect. Physiol. 19: 729–36.

1975. Criteria for selecting *Chrysopa carnea* biotypes for biological control: adult dietary requirements. Can. Entomol. 107: 589–95.

1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Annu. Rev. Entomol. 21: 81–107.

Vinogradova, E. B., and K. B. Zinovjeva. 1972. Experimental investigation of the seasonal aspect of the relationship between blowflies and their parasites. J. Insect Physiol. 18: 1629–38.