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ORIGINAL ARTICLE

Diet of adult ladybird beetle host modifies the postdiapause development of the parasitoid *Dinocampus coccinellae* (Hymenoptera: Braconidae)

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Abstract. Our study showed that under natural conditions the rate and speed of postdiapause emergence by overwintering larvae of the endoparasitic wasp, *Dinocampus coccinellae* (Schrank) is enhanced when its ladybird beetle host *Coleomegilla maculata* (DeGeer) receives a nutritious (proteinaceous) diet during late winter and early spring. Living aphid prey provided during April and May yielded the fastest rates of *D. coccinellae* postdiapause development, followed by an artificial protein/carbohydrate diet and flowering (pollen-producing) heads of dandelion. *D. coccinellae* development was slowest when hosts received only sugar water or water alone. These results indicate that there is an interaction during late dormancy between host diet and subsequent parasitoid performance. From these studies we conclude that the initiation of feeding by *C. maculata* hosts, whether on prey or nutritious plant-based substances, during early spring may play an important role in the timing and success of postdiapause larval development and emergence by the parasitoid *D. coccinellae*. This interaction appears to be an adaptive feature that synchronizes the completion of the parasitoid's postdiapause development with the feeding and occurrence of potential ladybird beetle (*C. maculata*) hosts in spring. Thus, we conclude that at this point in their life cycles, the developmental success of both the host and the parasitoid are interdependent. It appears that the presence and utilization of aphid prey and/or a rich pollen source early in the spring season could have both positive and negative effects on the local population of ladybird beetle hosts.

INTRODUCTION

Following the termination of hibernal diapause, free-living temperate zone insects typically undergo a period of postdiapause development, which generally is responsive to growth- and development-enhancing environmental factors (e.g. temperature, moisture, food), but not to diapause-inducing or maintaining stimuli such as photoperiod (Nechols et al., 1980; Tauber et al., 1986; Denlinger, 2022, 2023). Similarly, the period of postdiapause development and emergence of overwintered endoparasitoids from their hosts has been shown to be influenced by development-enhancing physical factors, and under laboratory conditions, by the internal state and behavior of their host, e.g., the host's consumption of prey or plant materials (e.g., pollen or nectar) (Tauber et al., 1983, 1986; Fei et al., 2023). Thus, it is likely that the vernal diet of the host species may influence the seasonal timing of endoparasitoid postdiapause development, but to our knowledge, such an effect has not been examined in field populations of parasitoids that overwinter within predatory insect hosts.

The braconid *Dinocampus coccinellae* (Schrank) (previously *Perilitus coccinellae*) (Hymenoptera: Braconidae) parasitizes several coccinellid species throughout the world (Ceryngier et al., 2012, 2023; Knapp et al., 2019; Vansant et al., 2019; Sethuraman et al., 2022; Fei et al., 2023; Ricupero et al., 2023; Mendoza-Arroyo & del-Val, 2024). A common host for this parasitoid in North America is the ladybird beetle *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), a species distributed primarily east of the Rocky Mountains (Gordon, 1985; Hesler & Brust, 2024; GBIF, 2025; Lost Ladybug Project, 2025). Adult *C. maculata* overwinter in aggregations, commonly at the base of prominent trees or bushes in woody areas adjacent to open fields (Hodek, 2012). Typically, in early spring, the overwintered ladybird adults feed on a range of prey and non-prey items (Lundgren et al., 2005; Lund-

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* Deceased.

gren, 2009; Hodek & Evans, 2012), including pollen from early blooming flowers, especially dandelions (*Taraxacum officinale*) (Asterales: Asteraceae). As a result, the physiological and seasonal interactions between the overwintered host and parasitoid are of considerable interest.

Like many of its ladybird beetle hosts, the parasitoid *Dinocampus coccinellae* may have multiple generations per year. It overwinters as mature eggs or first instars within hibernating adult ladybird beetle hosts (Balduf, 1926; Parker et al., 1977; Ceryngier et al., 2012). First instars feed on host tissues, but later instars consume teratocytes, cells derived from the parasitoid egg that contribute to the growth and development of the parasitoid within the ladybeetle host (Sluss, 1968; Ceryngier et al., 2012; Strand, 2014; Fei et al., 2023). Mature parasitoid larvae exit through the abdominal tergites of their adult beetle hosts and immediately spin silken cocoons; the silk of the cocoon typically entwines the legs of the beetle and binds it to the silken covered cocoon (Balduf, 1926; Wright & Laing, 1979; Ceryngier et al., 2012). Laboratory and field studies have elucidated the effects of host diet (aphids and pollen) on aspects of fitness expressed by *D. coccinellae* parasitizing *C. maculata* adults and also on the survival of the parasitized beetle hosts (Maure et al., 2016), but none have examined the effects of host feeding on the development of the overwintering parasitoids.

Our previous studies of *C. maculata* / *D. coccinellae* interactions showed that: (1) autumnal-hibernal diapause of *D. coccinellae* within *C. maculata* hosts is maintained by short daylengths during autumn and ends in approximately 50% of the parasitoid population in December. By the end of January, diapause (responsiveness to photoperiod) has ended in over 95% of *D. coccinellae*. (2) Overwintering *C. maculata* adults and *D. coccinellae* immatures within their hosts respond independently to photoperiod. (3) The accumulation of 185°C days above a thermal threshold of 9°C is required for completion of postdiapause preimaginal development of *D. coccinellae* within *C. maculata* hosts that have been provided with live aphid prey. (4) When aphid prey are available, the thermal requirements for complete nondiapause development (oviposition to adult eclosion) are greater for *D. coccinellae* (395°C days > 9.8°C) than its ladybird beetle host *C. maculata* (236°C Days > 11.3°C) (Obrycki & Tauber, 1978, 1979; Tauber et al., 1983).

The objective of our current study was to examine the effect of the diet of adult hosts (*C. maculata*) on the postdiapause preimaginal development of *D. coccinellae* under field conditions. Specifically we asked: (1) Does the diet (prey based or plant based, protein or sucrose based) of overwintering *C. maculata* hosts affect the incidence and speed of successful postdiapause development of the parasitoid *D. coccinellae*? (2) If so, is the effect present over the entire postdiapause period (winter and early spring season), or only during specific times within the period?

MATERIAL AND METHODS

Host diet and photoperiod – parasitoid postdiapause development

Overwintering *C. maculata* adults were sampled from an aggregation in Ithaca, New York (approx. 42.4°N, 76.5°W) on 16 December 1978, 7 February 1979, and 31 March 1979 (Table 1). To confirm the diapause status of the host beetles and the parasitoids throughout this overwintering period, tests were conducted under both long and short daylengths. Thus, on each sample date 90 adults were placed under 16L : 8D, 24°C and 90 were maintained at 10L : 14D, 24°C. For each photoperiod, 30 adults were fed daily a mixture of live pea aphids (*Acyrthosiphon pisum*) (Harris) and green peach aphids (*Myzus persicae*) (Sulzer) (Hemiptera: Aphididae) and water, 30 were fed a Wheast-protein-carbohydrate diet [mixture of Wheast, protein hydrolysate of yeast, sugar, and honey (volumetric ratio 1 : 1 : 1 : 1)] (Tauber & Tauber, 1975) and water, and 30 received sugar water (6 g of sugar dissolved in 200 ml of water) in a cotton plugged glass vial. The cages of *C. maculata* hosts were checked daily for *D. coccinellae* larvae exiting from hosts and spinning a cocoon. Postdiapause preimaginal development (days from sample date to larval *D. coccinellae* exit from a *C. maculata* host), was recorded for each photoperiod and diet treatment. Under the Wheast-protein-carbohydrate diet and the sugar water treatments, some emerging *D. coccinellae* larvae were consumed by other *C. maculata* adults in the cages before the parasitoid larva could completely spin a cocoon and pupate. When this occurred, the number of days for *D. coccinellae* exit was estimated based on the remnants of the *D. coccinellae* larva and the behavior of the parasitized *C. maculata* (lack of movement and legs entwined with some silk from the partially formed *D. coccinellae* cocoon).

Statistical analysis

For each sample, the mean number of days from the sample to *D. coccinellae* exit from the *C. maculata* hosts over all photoperiod/host diet treatments were analyzed using a two-way ANOVA (JMP 17.0). Because photoperiod was not a significant factor influencing postdiapause development in the December 1978 and February 1979 samples, data from the two photoperiods were combined to compare days to exit from the hosts at each diet treatment using the Tukey-Kramer HSD test for multiple mean comparisons (JMP 17.0).

Effect of host diet on rates of parasitoid postdiapause development

Overwintering *C. maculata* adults were sampled on 6 March 1980, 22 March 1981, 21 April 1981, and 14 May 1981 from an aggregation in Ithaca, New York (Table 2). Beetles from the 6 March 1980 sample were maintained at 16L : 8D, 24°C; all samples in 1981 were placed into 16L : 8D, 22°C. In the 6 March 1980 and 22 March 1981 samples, one group of *C. maculata* was fed a mixture of live *A. pisum* and *M. persicae* and water, one group was fed the Wheast-protein-carbohydrate diet and water, one group received sugar water (6 g of sugar dissolved in 200 ml of water), and the final group of *C. maculata* adults was maintained on water only. In the April and May 1981 samples, a diet treatment consisting of heads of fresh dandelion producing pollen + H_2O was added; the sugar H_2O treatment was dropped in the May sample. The beetles from all samples were checked daily for exit of *D. coccinellae* larvae from hosts.

Statistical analysis

For each sample date a one-way ANOVA was used to analyze the effects of host diet treatment on the number of days for *D.*

Table 1. Influence of host diet on the rate and incidence of postdiapause emergence of the overwintering parasitoid *Dinocampus coccinellae* from its adult ladybird host (*Coleomegilla maculata*). Samples of adult *C. maculata* were taken from field populations in Ithaca, Tompkins County, New York on 16 Dec 1978, 7 Feb 1979, and 31 March 1979.

	Host diet			
	Aphids + H_2O	Wheast diet[2] + H_2O	Sugar H_2O	
Sample date 16 Dec 1978				
16L : 8D				
Days to emergence	15.9 ± 1.9	19.7 ± 1.6	22.2 ± 2.7	F = 17.85, df = 5, 81, P < 0.0001
N (n) [%][1]	30 (18) [60%]	30 (19) [63%]	30 (13) [43%]	Photoperiod: P = 0.3152
10L : 14D				
Days to emergence	17.0 ± 2.8	18.0 ± 1.6	21.2 ± 2.8	Diet: P < 0.0001
N (n) [%]	30 (15) [50%]	30 (9) [30%]	30 (13) [43%]	LD*Diet: P = 0.048
Tukey-Kramer HSD[3]	C	B	A	
Sample date 7 Feb 1979				
16L : 8D				
Days to emergence	14.6 ± 1.4	19.2 ± 3.3	20.9 ± 6.2	F = 10.24, df = 5,59, P < 0.0001
N (n) [%]	30 (13) [43%]	30 (14) [47%]	30 (8) [27%]	LD: P = 0.507
10L : 14D				
Days to emergence	13.6 ± 0.7	16.1 ± 2.2	23.0 ± 6.2	Diet: P < 0.0001
N (n) [%]	30 (11) [37%]	30 (8) [27%]	30 (11) [37%]	LD*Diet P = 0.111
Tukey-Kramer HSD[3]	C	B	A	
Sample date 31 March 1979				
16L : 8D				
Days to emergence	11.5 ± 2.1	12.8 ± 2.8	15.7 ± 4.7	F = 6.49, df = 5, 70, P < 0.0001
N (n) [%]	30 (15) [50%]	30 (16) [53%]	30 (9) [30%]	LD: P < 0.001
10L : 14D				
Days to emergence	9.8 ± 0.5	11.7 ± 1.9	12.5 ± 1.6	Diet: P < 0.0001
N (n) [%]	30 (12) [40%]	30 (16) [53%]	30 (8) [27%]	LD*Diet P = 0.39

[1] N = number of adult *C. maculata* tested, (n) = number of *D. coccinellae* exiting from a *C. maculata* host, [%] = No. of *D. coccinellae* exiting from host / No. of *C. maculata* at each treatment (× 100); an indicator of the effect of host diet on the percentage preimaginal survival of *D. coccinellae*. [2] Wheast-protein-carbohydrate diet [mixture of Wheast, protein hydrolysate of yeast, sugar, and honey (volumetric ratio 1 : 1 : 1 : 1)]. [3] Data from the two photoperiods were combined to compare values at the diet treatments using Tukey-Kramer HSD (JMP 17.0) when photoperiod was not a significant factor influencing postdiapause development in the December 1978 and February 1979 samples. Different letters indicate significant differences among means within a row (Tukey-Kramer HSD; JMP 17.0).

coccinellae larvae to exit from *C. maculata* hosts (JMP 17.0). When the ANOVA indicated significant differences among diet treatments, data from each diet treatment within each sample date were compared (Tukey-Kramer HSD, JMP 17.0).

Influence of host diet under field conditions

Adult C. *maculata* (120) were collected from an overwintering aggregation in Ithaca, New York, on 3, 15, and 30 April 1979 and maintained in a 1 m^3 outdoor cage covered with metal window screening in a shaded location under a canopy of trees and bushes (Table 3). Forty adults on each sample date were fed daily a mixture of *A. pisum* and *M. persicae* with water, 40 were maintained on the Wheast-protein-carbohydrate diet with water, and 40 received sugar water. Daily maximum and minimum temperatures within the outdoor cage (Table S1) and larval *D. coccinellae* exit from *C. maculata* were recorded.

Statistical analysis

For these data, the number days from when we began feeding *C. maculata* hosts to the date *D. coccinellae* larvae exited from the *C. maculata* hosts in the field were analyzed using a two-way ANOVA (JMP 17.0) (Table 3).

Effect of host diet on percentage emergence of *Dinocampus coccinellae*

For all experiments (Tables 1, 2, 3), the effect of host diet on the percentage emergence of *D. coccinellae* was assessed by dividing the number of *D. coccinellae* exiting from hosts by the number of *C. maculata* adults maintained at each diet treatment (× 100). The percentage emergence of *D. coccinellae* provides an indication of preimaginal survival assuming that approximately equal numbers of parasitized *C. maculata* hosts were randomly assigned to each diet treatment. The values observed when *C. maculata* adults were fed live aphids was used as the basis of comparison for the other diet treatments within that sample.

RESULTS

Effects of host diet and photoperiod on parasitoid postdiapause preimaginal development

As expected, photoperiod (16L : 8D versus 10L : 14D) did not have a significant effect on *D. coccinellae* postdiapause larval emergence from *C. maculata* hosts sampled on 16 December 1978. However, diet and the interaction between host diet and photoperiod were significant in that sample, with diet having the strongest effect (Table 1). The preimaginal developmental time of *D. coccinellae* larvae was shortest (16–17 days) when hosts were fed an aphid diet, longest (21–22 days) when they were fed the sugar H_2O diet, and intermediate on the Wheast-protein-carbohydrate diet. A similar, but not identical pattern of response was observed in the 7 February 1979 sample. Host diet had a significant effect on *D. coccinellae* developmental time, and again, photoperiod had no significant effect. Also, in this sample, there was no significant interaction between host diet and photoperiod. At the end of March 1979, host diet continued to have a significant effect on postdiapause development of *D. coccinellae*, but in this sample, there was a significant effect of photoperiod (Table 1). However,

Table 2. Time for postdiapause preimaginal development of the parasitoid *Dinocampus coccinellae* (days from sample date to *D. coccinellae* larval exit from host) and percentage emergence of *D. coccinellae* within *Coleomegilla maculata* hosts fed different diets. Samples taken during 1980–1981 from Ithaca, Tompkins County, New York populations of *C. maculata*.

Sample date	Host (adult *Coleomegilla maculata*) diet treatments					Oneway ANOVA (F; df; P)
	Aphids + H_2O	Wheast diet[1] + H_2O	Sugar H_2O	Dandelion + H_2O	H_2O	
6 March 1980[2]						
Mean ± SD[3]	12.7 ± 1.5 (B)	14.3 ± 2.0 (A)	14.3 ± 1.9 (A)	Not tested	17[4]	F = 9.08; 2, 92;
N sampled (n) [%][5]	80 (40) [50%]	70 (37) [53%]	70 (17) [24%]		70 (1) [1%]	P < 0.0003
22 March 1981[6]						
Mean ± SD	15.5 ± 2.5 (B)	18.2 ± 3.2 (AB)	18.0 ± 2.7 (AB)	Not tested	20.8 ± 5.9 (A)	F = 3.05; 3,33;
N sampled (n) [%]	30 (11) [37%]	30 (12) [40%]	30 (8) [27%]		30 (6) [20%]	P < 0.042
21 April 1981						
Mean ± SD	11.4 ± 1.0 (B)	14.7 ± 3.5 (AB)	11.0 ± 2.8 (B)	13.6 ± 2.5 (AB)	17.5 ± 3.5 (A)	F = 5.56; 4.29;
N (n) [%]	30 (15) [50%]	14 (3) [21%]	14 (2) [14%]	30 (12) [40%]	15 (2) [13%]	P < 0.0019
14 May 1981						
Mean ± SD	9.3 ± 2.1	8.1 ± 2.3	Not tested	11.6 ± 3.0	–	F = 3.16; 2,14;
N (n) [%]	30 (3) [10%]	30 (9) [30%]		20 (5) [25%]	10 (0)	P = 0.074

[1] Wheast-protein-carbohydrate diet [mixture of Wheast, protein hydrolysate of yeast, sugar, and honey (volumetric ratio 1 : 1 : 1 : 1)]. [2] Data previously reported in review chapter by Tauber et al. (1983); beetles maintained at 16L : 8D, 24°C. [3] Means followed by different letters within a row are significantly different, (Tukey-Kramer HSD, JMP 17.0). [4] One *D. coccinellae* emerged from *C. maculata* adults provided H_2O only; not included in ANOVA. [5] N = number of adult *C. maculata* placed into each diet condition, (n) = number of *D. coccinellae* exiting from a *C. maculata* host, [%] = No. of *D. coccinellae* exiting from host / No. of *C. maculata* at each treatment (× 100); an indicator of the effect of host diet on the preimaginal survival of *D. coccinellae*. [6] Beetles from all samples in 1981 were maintained at 16L : 8D, 22°C.

unlike what would be expected (longer development times under the shorter daylength), the pattern of variation was reversed, and remains unexplained.

The percentage of *C. maculata* hosts that yielded *D. coccinellae* larvae ranged from 30% to 63% in the December 1978 sample (Table 1). Similarly, in the February 1979 sample, the percentage of *D. coccinellae* exiting from hosts ranged from 27% to 47%; and in March 1979 the range was from 27% to 53% (Table 1). Based on overall results from the three sample dates, the percentage emergence of *D. coccinellae* showed no consistent seasonal pattern of variation in response to photoperiod or host diet.

Effect of host diet on parasitoid postdiapause development

At all sample dates, except 14 May 1981, the diet provided to the *C. maculata* hosts had a significant effect on *D. coccinellae* postdiapause preimaginal development (Table 2). In the March 1980 sample, *D. coccinellae* larvae emerged sooner when their *C. maculata* hosts were fed aphid prey (a mixture of *A. pisum* and *M. persicae*) than when they received the Wheast-protein-carbohydrate diet or sugar H_2O only (Table 2). In March 1981, *D. coccinellae* postdiapause preimaginal development also was quicker when the host diet was aphids, than when the hosts were provided water only. Parasitoid preimaginal developmental times, when hosts were provided the Wheast-protein-carbohydrate diet or sugar H_2O, were intermediate between the aphid diet and water only treatment (Table 2). A similar pattern was observed in April 1981. The parasitoids developed more quickly when their hosts were fed the aphid diet compared to water only; intermediate values were observed when hosts were provided the Wheast-protein-carbohydrate diet or dandelion heads (Table 2). Postdiapause development times for the two individuals that exited hosts provided sugar water in April 1981 were also shorter than for those that received water only. A reduction in the parasitoid postdiapause development times for all dietary treatments was observed in the April and May 1981 samples compared to values in the March 1981 sample (Table 2). By the middle of May, the host diet did not have a significant effect on postdiapause preimaginal development of *D. coccinellae* larvae.

The aphid and Wheast-protein-carbohydrate host diets yielded similar levels of preimaginal emergence of *D. coccinellae* in both the March 1980 and 1981 samples (Table 2). Also, there were similarities between the two diets (aphids versus a Wheast-protein-carbohydrate mixture) in these two years. In both years, emergence when the host diet consisted only of sugar water was relatively low, and it was < 20% when *C. maculata* hosts were maintained on water only (Table 2). In April 1981, the percentage of *D. coccinellae* larvae exiting hosts tended to be low in the water only treatment, but higher on the aphid host diet (Table 2). In the May 1981 sample, no parasitoids exited hosts in the water treatment, and only 10% of hosts yielded parasitoids in the aphid diet treatment (Table 2).

Influence of host diet under field conditions

Both the date (beginning, middle, and end of April) at which feeding of *C. maculata* adults started in an outdoor field cage and the diet treatment that they received had significant effects on the postdiapause development of the *D. coccinellae* parasitoids that they hosted (Table 3). For each test date, exit of *D. coccinellae* larvae from *C. maculata* hosts occurred earliest when *C. maculata* were fed the aphid diet (*A. pisum* and *M. persicae*) (Table 3). And, for each of the three diet treatments, the mean number of days for *D. coccinellae* to exit from *C. maculata* hosts declined over the April 3 to April 30 test period (Table 3).

Table 3. Influence of host diet on postdiapause development of *Dinocampus coccinellae* under field conditions. Samples of *Coleomegilla maculata* adult hosts were collected from overwintering sites in Ithaca, Tompkins County, New York; feeding of overwintering beetles in outdoor cages started on three dates 3, 15, and 30 April 1979.

Date initial feeding	Host diet		
	Aphids [1]	Wheast diet [2]	Sugar H_2O
	Treatments included water		
3 April 1979			
Mean ± SD days [3]	34.9 ± 2.6	38.4 ± 2.6	48.3 ± 5.6
Median date [4]	11 May	15 May	25 May
No. parasitoids	14	8	4
Est. % survival [5]	35%	20%	10%
15 April 1979			
Mean ± SD days	27.7 ± 3.5	32.5 ± 3.9	30.4 ± 3.0
Median date	12 May	17 May	16 May
No. parasitoids	19	13	14
Est. % survival	48%	33%	35%
30 April 1979			
Mean ± SD days	18.1 ± 3.2	23.8 ± 6.5	24.4 ± 7.5
Median date	19 May	21 May	21 May
No. parasitoids	19	16	15
Est. % survival	48%	40%	38%

Twoway ANOVA: F = 35.01, df = 8,113, P < 0.0001; Start date P < 0.0001; Host diet P < 0.0001; Start date*Host diet P < 0.0054. [1] 17 May (*A. pisum*) and (*M. persicae*). [2] Wheast-protein-carbohydrate diet [mixture of Wheast, protein hydrolysate of yeast, sugar, and honey (volumetric ratio 1:1:1:1)]. [3] Mean number of days from initiation of feeding to parasitoid exit from host. [4] Median date of parasitoid exit from host. [5] Est. % survival [%] = No. of *D. coccinellae* exiting from host / No. of *C. maculata* at each treatment (× 100); an indicator of the effect of host diet on the percentage preimaginal survival of *D. coccinellae*.

DISCUSSION

Previous studies of the seasonal interaction of the parasitoid *Dinocampus coccinellae* and its host *Coleomegilla maculata* documented that the photoperiodically maintained diapause in this parasitoid largely ends by late January (Obrycki & Tauber, 1979). Following the termination of diapause, the rate of postdiapause development by *D. coccinellae* is correlated with temperatures > 9°C. The studies conducted to determine this temperature-development relationship were carried out with *C. maculata* hosts that had a daily supply of live aphids (*A. pisum* and *M. persicae*) (Tauber et al., 1983). However, after leaving overwintering sites in the spring, parasitized and unparasitized adult *C. maculata* may, or may not, find prey, and this variable in the hosts' life cycle may have important, but until now, unknown effects on the survival and development of the parasitoid.

Our results show that the type of food and the timing of feeding by *C. maculata* hosts during spring could play an important role in the completion of postdiapause preimaginal development and the exit of *D. coccinellae* larvae from their hosts. In our late winter and early spring samples, postdiapause development of *D. coccinellae* was fastest when *C. maculata* hosts were provided live aphid prey, compared to when hosts were provided a Wheast-protein-carbohydrate diet, sugar water, or water (Table 1). In later spring samples, no consistent host diet effect was observed in the postdiapause development of *D. coccinellae*. Such a seasonal pattern of responsiveness by *D. coccinellae* may indicate that host feeding provides a nutritional benefit that specifically enhances the rate of postdiapause development, or it may reflect the presence of a trigger or stimulus that activates the parasitoid to complete postdiapause development, once feeding has been initiated by its host.

In the present experiments (Table 1) and in our previous studies of the seasonal synchrony between *D. coccinellae* and *C. maculata* (Obrycki & Tauber, 1979), we observed that the parasitoid had relatively consistent postdiapause developmental times from winter (December) to early spring (end of March), when temperatures are generally below the thermal threshold for postdiapause development (9°C). Previously, Hodek et al. (1977) reported a stable pattern of mean and median exit times from December and March samples of *D. coccinellae* overwintering within the ladybird beetle *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). Later in the season (between March and May), we observed declines in postdiapause development times of *D. coccinellae* indicating the likelihood that postdiapause development had proceeded during that period, perhaps when temperatures were greater than the threshold for postdiapause development (> 9°C) and notably when *C. maculata* hosts may or may not have been actively feeding.

Studies have shown that when they are within ladybird beetle hosts, *D. coccinellae* larvae induce the production of teratocytes, cells derived from the parasitoid egg; these cells absorb amino acids from the host and provide nutrition for the developing parasitoid larva (Sluss, 1968; Kadono-Okuda et al., 1995; Okuda & Kadono-Okuda, 1995; Ceryngier et al., 2012; Strand, 2014; Fei et al., 2023). In a study of the interaction of *D. coccinellae* within diapausing *Coccinella septempunctata*, Kadono-Okuda et al. (1995) documented that teratocytes remained relatively small within diapausing *C. septempunctata* hosts, but following the termination of diapause in host beetles, the teratocytes increased in size. Based on our results, we suggest that these enlarged teratocytes may provide nutrition for the developing postdiapause *D. coccinellae* larvae prior to the initiation of feeding by *C. maculata* hosts.

Tauber et al. (1983) outlined three types of seasonal adaptations that specifically apply to the synchronization of parasitoid life cycles with those of their hosts: (1) regulation of their own or their hosts developmental rates, including during diapause and/or postdiapause development, (2) use of alternate hosts and/or life stages of a single host species, and (3) the ability to parasitize at a new trophic level (hyperparasitism or autoparasitism). *Dinocampus coccinellae* has evolved several mechanisms illustrating the first two categories, underlying its seasonal synchrony with the ladybird beetle host *C. maculata*. The general diapause characteristic of *D. coccinellae* overwintering within its host is adaptive for both protection from winter conditions and for bringing the parasitoid into temporal and spatial synchrony with its host. We propose that the diet-modified temperature regulation of *D. coccinellae* postdiapause development also is an adaptive feature that synchronizes parasitoid spring activity with the feeding and occurrence of potential ladybird beetle (*C. maculata*) hosts. Following parasitoid emergence in spring, i.e., during the reproductive season (late spring through autumn), thermal requirements for development most likely have a major role in determining the number of generations (3–4 in upstate New York) of *D. coccinellae* (Obrycki & Tauber, 1978). During this period the parasitoid may not only utilize adults of various coccinellid species as hosts, but they may also parasitize coccinellid immature stages (Obrycki et al., 1985).

Maturation of *C. maculata* and their vernal flight from overwintering sites require temperatures > 15°C. (Solbreck, 1974). However, postdiapause development and emergence of *D. coccinellae* can commence at temperatures > 9°C. (Tauber et al., 1983). As a result, the vernal appearance of the parasitoid appears to be adapted to the sustained seasonal availability of overwintering or overwintered adult ladybeetles as potential hosts. Thus, we propose that the overwintering population of the ladybeetle is subject to parasitoid attack both before and after aggregating at the overwintering site and also after vernal dispersal.

One aspect of the seasonal interaction between *D. coccinellae* and *C. maculata* that requires further examination is the possible effect of parasitism on the timing of dispersal of *C. maculata* hosts from overwintering sites. In a similar braconid parasitoid-adult Coleoptera host relationship, Wylie (1982) observed that parasitized flea beetles emerged earlier from overwintering sites than non-parasitized adults, and he concluded that this enhanced host activity provided the emerging parasitoids greater access to non-parasitized hosts in the spring. Based on a study of an overwintering population of females of the ladybird beetle *Coccinella septempunctata* in the Czech Republic, that were parasitized by *D. coccinellae*, Ceryngier et al. (2004) speculated that parasitization might alter the rate of diapause and postdiapause development in host females. Our tests here did not address the above interesting questions directly, but the results indicate that host diet may be an important component to consider in further investigations.

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Table S1. Daily maximum/minimum temperatures at ground level in a shaded outdoor field cage. Study of host diet influence on postdiapause development of *Dinocampus coccinellae* within *Coleomegilla maculata* hosts. Days for *D. coccinellae* to exit from hosts presented in Table 3.

Date (1979)	Max °C	Min °C
April 5	4	2
April 6	5	–3
April 7	2	–4
April 8	4	–5
April 9	1	–1
April 10	2	–1
April 11	9	–5
April 12	8	0
April 13	10	–1
April 14	8	0
April 15	5	5
April 16	No data	
April 17	5	2
April 18	8	1
April 19	10	–2
April 20	12	–2
April 21	18	–2
April 22	20	10
April 23	20	2
April 24	24	4
April 25	24	15
April 26	17	16
April 27	No data	
April 28	20	5
April 29	9	3
April 30	15	0
May 1	8	4
May 2	11	–1
May 3	18	3
May 4	17	6
May 5	No data	
May 6	18	3
May 7	21	6
May 8	32	13
May 9	30	17
May 10	30	16
May 11	28	19
May 12	29	16
May 13	28	11
May 14	19	14
May 15	19	14
May 16	21	10
May 17	16	10
May 18	23	6
May 19	23	13
May 20	No data	
May 21	26	14
May 22	18	9
May 23	15	7
May 24	16	11
May 25	14	10
May 26	14	9
May 27	15	8
May 28	13	9
May 29	14	9
May 30	15	10
May 31	16	8