

Environmental Control of the Seasonal Life Cycle of *Adalia bipunctata* (Coleoptera: Coccinellidae)¹

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ABSTRACT *Adalia bipunctata* L. has low developmental thresholds (t) for postdiapause and non-diapause development that adapt it to activity early in the season. Postdiapause reproductive development leading to oviposition requires an accumulation of 87 degree-days (K) above a relatively low developmental threshold temperature (t) of 6.8°C. Overwintering adults disperse and initiate oviposition during early to mid-May. The linearly derived (t) and (K) values of 263 ± 9.0 degree-days above 9.0°C for preimaginal development and daily maximum-minimum temperatures from outdoors accurately predicted outdoor developmental rates. Preimaginal development outdoors during June and July required 269 ± 12 degree-days above 9.0°C under conditions of excess prey. In the field, there are two to three generations per year in the Ithaca, N.Y., area. The critical photoperiod for diapause induction in the Ithaca, N.Y., (~42°N) population lies between LD 13:11 and LD 14:10 (23°C). Short daylengths maintain diapause, and during autumn the duration of diapause is quantitatively related to photoperiod. Diapause completion does not require chilling; during winter-early spring, photoperiod may exert some influence on the timing of diapause termination.

Adalia bipunctata L., a primarily aphidophagous coccinellid, generally occurs in arboreal habitats throughout the Holarctic and is one of the most common coccinellids in orchards (Putman 1964, Hodek 1973). In this paper we use a combination of field and laboratory studies to examine the influence of temperature and photoperiod on its seasonal development. We determined the critical photoperiod for diapause induction, the role of temperature and photoperiod in diapause maintenance, the effect of temperature on postdiapause development, and the influence of naturally fluctuating temperatures on preimaginal development.

This report is part of a series on the predacious coccinellids of New York State in which we examine responses to key environmental factors that influence seasonal development (Obrycki and Tauber 1978, 1979, 1981, 1982). Such studies allow prediction of seasonal development and reproduction and are a prerequisite for understanding the population dynamics of these beneficial species and their prey (see Tauber and Tauber 1976, 1978).

Materials and Methods

Diapause Induction

We collected *A. bipunctata* adults from the Ithaca, N.Y., area, maintained them under LD 16:8, $21 \pm 1^\circ\text{C}$, and provided them with a standard diet of water, a Wheat-protein mixture, and a daily supply of aphids—*Acyrtosiphon pisum* (Harris) (pea aphids) and *Myzus persicae* (Sulzer) (green peach aphids). F₁ individuals from these field-collected adults were used to determine the critical photoperiod for diapause induction.

Larvae were fed *A. pisum* and reared at $23 \pm 1^\circ\text{C}$ under a range of constant photoperiods (Table 1). Adults were maintained at the larval photoperiods and fed the standard diet. We considered diapause to be averted in beetles that oviposited within 14 days of emergence. The

remainder of the beetles were kept to determine the duration of diapause; they had access to the standard diet.

Diapause Maintenance and Termination

Our procedures followed those outlined by Tauber and Tauber (1973). The overwintering population consisted of adults collected or reared outdoors during late summer and early fall. These individuals were sheltered in a 1-m³ screen cage and provided with the standard diet until October when the beetles stopped feeding.

We took samples from the overwintering population in October, December, March, and May and distributed individuals among several photoperiods (Table 2). After sampling, we provided all adults with the standard diet and checked individuals daily for the initiation of oviposition. Our measure of diapause duration (the pre-oviposition period) includes the period of postdiapause development.

To establish whether chilling is required for diapause termination, we began sampling diapausing adults in early fall, before the occurrence of low temperatures in the field.

Postdiapause Development

As egg sources for the postdiapause development study, we used field-collected *A. bipunctata* females that oviposited under LD 16:8 and LD 14:10 ($23 \pm 1^\circ\text{C}$). Larvae were reared on *A. pisum* in individual vials under diapause-inducing conditions (LD 10:14 at $24 \pm 1^\circ\text{C}$). Upon emergence, adults were maintained at LD 10:14 at 24°C for 2 weeks and then moved through a sequence of decreasing temperatures, all at LD 10:14 (15.6°C, 1 week; 10°C, 1 week; 5.6°C, 12 to 20 weeks). In all conditions, the adults were provided the standard diet.

After 12, 13, and 20 weeks at 5.6°C (LD 10:14), groups of *A. bipunctata* were distributed into seven constant temperatures (10 to 26.7°C) (LD 16:8). We gave the adults the standard diet and recorded the dates of

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Table 1.—Induction and duration of reproductive diapause in *A. bipunctata* under a series of constant photoperiods (23 ± 1°C)

Photoperiod (L:D)	Preoviposition period ($\bar{x} \pm SD$) (days)	% Diapause	No. of ovipositing females
16:8	8.4 ± 2.2	0	18
15:9	8.9 ± 2.3	0	11
14:10 ^a	(A) 10.4 ± 2.4 (B) 26.7 ± 6.4	46	7 6
13:11	61.8 ± 16.2	100	13
12:12	98.5 ± 8.2	100	11
10:14	113.3 ± 18.1	100	11

^aGroup A females oviposited in about the same time as observed at LD 16:8 and 15:9—no diapause; group B females took substantially longer to oviposit—weak diapause.

first oviposition. The relationship between temperature and the rate of postdiapause development leading to oviposition was analyzed using linear regression to determine *t* and *K* values (Obrycki and Tauber 1978, 1981).

Thermal Requirements for Development Outdoors

Previously, we had established the *t* and *K* values for nondiapause development in *A. bipunctata* (Obrycki and Tauber 1981). To determine the accuracy of these values for predicting development under fluctuating field temperatures, we reared individual larvae outdoors in a 1-m³ screen cage during June and July 1980. The larvae were fed *A. pisum* daily and developmental times for the total life cycle were recorded. Daily maximum and minimum temperatures within the screen cage were also monitored. Calculation of heat accumulations above *t* = 9.0°C (Obrycki and Tauber 1981) were by the method of Baskerville and Emin (1969).

Results

Diapause Induction

The preoviposition periods under LD 16:8 and LD 15:9 averaged 8 to 9 days (Table 1). At LD 14:10, 7 of 13 females oviposited within an average of 10 days (group A), whereas the remaining 6 females oviposited in ca. 27 days (group B, Table 1). Under short photoperiods, the duration of diapause was inversely related to daylength; the preoviposition period increased from 62 to 113 days as the photoperiod decreased from LD 13:11 to LD 10:14.

Diapause Maintenance and Termination

A. bipunctata females transferred from the field to LD 16:8 and LD 14:10 in October initiated oviposition within ca. 15 days (Table 2). Under LD 12:12, one-third of the females oviposited within a mean of 75 days; the remaining females survived for ca. 200 days but did not oviposit. At LD 10:14, one-fifth of the females oviposited within an average of 145 days; most of the remaining females survived for ca. 200 days without oviposition. Thus, in October there was an inverse relationship between daylength and the time required to initiate oviposition (Table 2).

In the December sample, most females under LD 14:10 oviposited within 14 days. Under LD 12:12 and LD 10:14, oviposition occurred either within 30 days (group A, Table 2) or after a much longer period (e.g., over 90 days) (group B, Table 2).

By March, females initiated oviposition within an average of 12 days under all photoperiodic conditions tested (Table 2). There was a small but significant ($\alpha = 0.05$; Behrens-Fisher multiple comparison test; Welch's approximate *t* solution, Games and Howell [1976]) difference between the mean lengths of the preoviposition periods at LD 14:10 and the shorter daylengths of LD

Table 2.—Mean number of days (± SD) for *A. bipunctata* females to initiate oviposition after transfer from outdoors to various photoperiods (1979–1980)^a

Sample date	Photoperiod (L:D)				Natural
	16:8	14:10	12:12	10:14	
22 Oct.	14.6 ± 1.6 ^b (9/9)	12.3 ± 3.3 (8/10)	75 ± 8.4 (3/9)	144.5 ± 34.6 (2/10)	116 ± 37 (4/10)
22 Dec.	A —	10.8 ± 1.8 (10/11)	20.8 ± 7.7 (7/13)	18.0 ± 5.3 (3/10)	21.5 ± 4.9 (2/10)
	B —	—	117 (1/6)	97.0 ± 10.8 (3/7)	61.3 ± 30.3 (3/8)
7 Mar.	—	7.0 ± 1.7 (6/8)	10.8 ± 3.1 (8/12)	12.0 ± 4.3 (8/11)	12.6 ± 2.7 (7/8)
21 May	—	2.8 ± 1.3 (7/8)	2.5 ± 1.0 (6/6)	2.4 ± 1.0 (7/9)	3.0 ± 1.2 ^c (4/4)

^aNumbers in parentheses indicate number of ovipositing females per total number of females in each condition. Temperature under constant daylengths = 23 ± 1°C; temperature under natural daylengths = 23 ± 2°C.

^bLD 16:8 used only in October sample.

^cNatural condition maintained outdoors.

Table 3.—Postdiapause reproductive development (days; mean of replicate means \pm SE) of *A. bipunctata* under constant temperatures ($\pm 1^\circ\text{C}$; LD 16:8)

Determination	Temp ($^\circ\text{C}$)						
	10	12.8	15.6	18.3	21.1	24	26.7
Preoviposition period ($\bar{x} \pm \text{SE}$; days)	24.9 \pm 3.4	15.3 \pm 3.7	11.0 \pm 2.2	8.0 \pm 1.9	6.0 \pm 1.3	5.0 \pm 0.8	4.5 \pm 0.5
Range (days)	21–33	11–21	6–16	4–13	4–10	3–7	3–7
No. of females in each replicate	13, 8	12, 7	13, 11, 7	15, 7, 9	18, 7, 8	14, 10, 9	16, 11, 7

12:12 and LD 10:14 (Table 2). In May, females oviposited within 3 days of the sample date at all photoperiods.

Under natural daylengths, the *A. bipunctata* that were sampled in October required ca. 116 days to begin oviposition. In the December sample, oviposition under natural daylengths was similar to that observed at LD 12:12 and LD 10:14; one portion of the females (group A) oviposited within ca. 22 days, whereas the rest (group B) averaged 61 days. In the March and May samples, oviposition under natural daylengths was similar to that under constant photoperiods (Table 2).

Postdiapause Development

Between 10 and 26.7 $^\circ\text{C}$, there was a direct relationship between temperature and the rate of postdiapause development leading to oviposition (Table 3). The analysis of variance (ANOVA) test for linearity indicated that the postdiapause developmental rates were linearly related to the temperatures examined. The t value for postdiapause development of *A. bipunctata* is 6.8 \pm 1.0 $^\circ\text{C}$; the thermal constant (K) is 86.5 \pm 3.3 degree-days (Fig. 1).

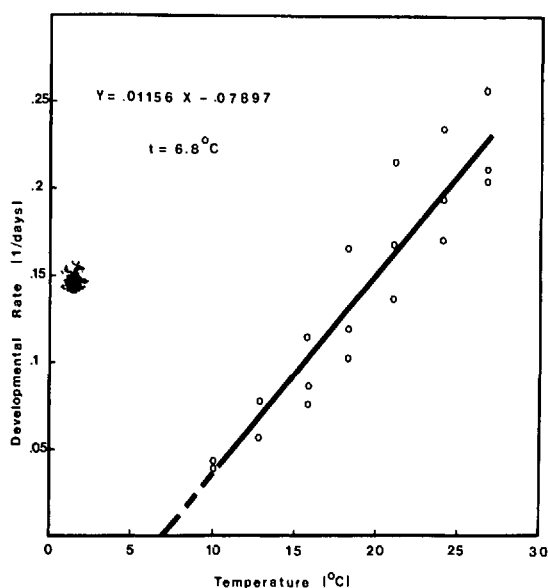


FIG. 1.—Rate of postdiapause reproductive development leading to oviposition by *A. bipunctata*. Intercept on the temperature axis (6.8 $^\circ\text{C}$) is the lower theoretical threshold temperature for development (t); open circles represent replicate mean developmental rates.

Nondiapause Development Outdoors

In the outdoor rearings adults emerged within 269 \pm 12 degree-days above the t value of 9.0 $^\circ\text{C}$ (Fig. 2). During these rearings (June to mid-July), daily temperatures generally fluctuated within the linear portion (15.6 to 29.4 $^\circ\text{C}$) of the temperature-developmental rate curve (Obrycki and Tauber 1981).

Discussion

Diapause Induction

At 23 $^\circ\text{C}$, the critical photoperiod for diapause induction (>50% diapause) in the Ithaca population of *A. bipunctata* falls between LD 13:11 and LD 14:10. Thus, *A. bipunctata* has the type I response of Beck (1980); exposure to long daylengths averts diapause. At LD 14:10, half of the females (Table 1, group A) had a preoviposition period of 10 days, indicating no diapause. The remaining females (Group B) oviposited in 27 days; this indicates that LD 14:10 induces a weak diapause in ca. 50% of the females.

Leaving aside the possible influence of temperature, diet, and other factors on diapause induction, we can estimate that, in the Ithaca area, diapause is induced no later than mid-September, when daylengths (including

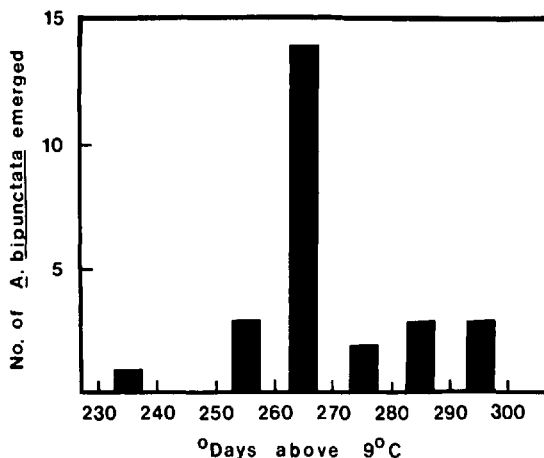


FIG. 2.—*A. bipunctata* development under field temperatures with excess aphid prey during June and July 1980. The number of adults emerging at 10-degree-day intervals above a developmental threshold of $t = 9.0^\circ\text{C}$. The mean number of degree-days \pm SD = 269 \pm 12 ($n = 26$).

civil twilight) decrease from LD 14:10 to LD 13:11 (Fig. 3).

Diapause Maintenance and Termination

An analysis of *A. bipunctata*'s photoperiodic responses in October (Table 2) indicates that (1) long daylengths can terminate diapause in the laboratory, (2) short daylengths (LD 12:12 and LD 10:14) maintain diapause, and (3) chilling is not required for diapause termination. *A. bipunctata*'s quantitative response to photoperiod (Tables 1 and 2) suggests that decreasing autumnal daylengths play a role in diapause maintenance, much as they do in *Chrysopa carnea* Stephens (Tauber and Tauber 1973).

By the third week of December, the response to photoperiod had diminished substantially; under short day (LD 12:12 and LD 10:14), only a proportion of the December sample remained in a long diapause. However, there still is a relatively large, although not significant ($\alpha = 0.05$; Behrens-Fisher statistic, Games and Howell [1976]) difference in the responses to long day (LD 14:10) and short day (LD 12:12 and LD 10:14). Thus, the beetles still appear to be very sensitive to diapause-maintaining photoperiods at this time.

In March, all oviposition occurred within a relatively short period after sampling. However, the beetles oviposited significantly ($\alpha = 0.05$) sooner under LD 14:10 than under short photoperiods (Table 2). This difference was small, but because of it we hesitate to conclude that sensitivity to photoperiod had ceased by the March sample. Whether daylength plays a major role in timing diapause termination in late winter through early spring is open to further study.

Between the March and May samples, the preoviposition period decreased substantially, and in May, photoperiod had no effect on oviposition. This indicates that postdiapause development had occurred by May and that it is probably not affected by daylength (Fig. 3).

Thermal Requirements for Postdiapause Development

Responses to environmental factors during the post diapause period may be subject to different selection pressures from those during the nondiapause period (Tauber and Tauber 1976). This situation appears to be the case with *A. bipunctata*, because the threshold temperature for postdiapause development ($6.8 \pm 1.0^\circ\text{C}$) is lower than that for nondiapause development ($9.0 \pm 0.9^\circ\text{C}$) (Obrycki and Tauber 1981). The low *t* value for postdiapause development provides an explanation for field observations that *A. bipunctata* is the first of a group of aphidophagous coccinellid species to become active in the spring (Hodek 1960, Obrycki and Tauber, unpublished data).

To predict the initiation of oviposition by overwintered *A. bipunctata* populations in the field, we used Baskerville and Emin's (1969) method to calculate degree-days above our *t* value of 6.8°C . We used the daily maximum and minimum temperatures² from 1 March for each of 3 years (1978, 1979, and 1980), and we predicted that postdiapause oviposition in *A. bipunctata* would begin by 12 May, 26 April, and 28 April, respectively. Generally, *A. bipunctata* initiate oviposition between 10 and 20 May in the Ithaca area (Obrycki and Tauber, unpublished data). Thus, our laboratory-derived *t* and *K* values slightly underestimate the duration of the postdiapause period in the field. We propose that the availability of prey may influence the timing of postdiapause oviposition in spring, either through an effect on diapause termination, as in *Coleomegilla maculata* DeGeer (Obrycki and Tauber 1979), or through an effect on postdiapause development.

Seasonal Activity

A. bipunctata's low *t* value for postdiapause (6.8°C) and nondiapause (9.0°C) development adapts it to ear-

²Monthly Meteorological Summary, Division of Atmospheric Sciences, Cornell University.

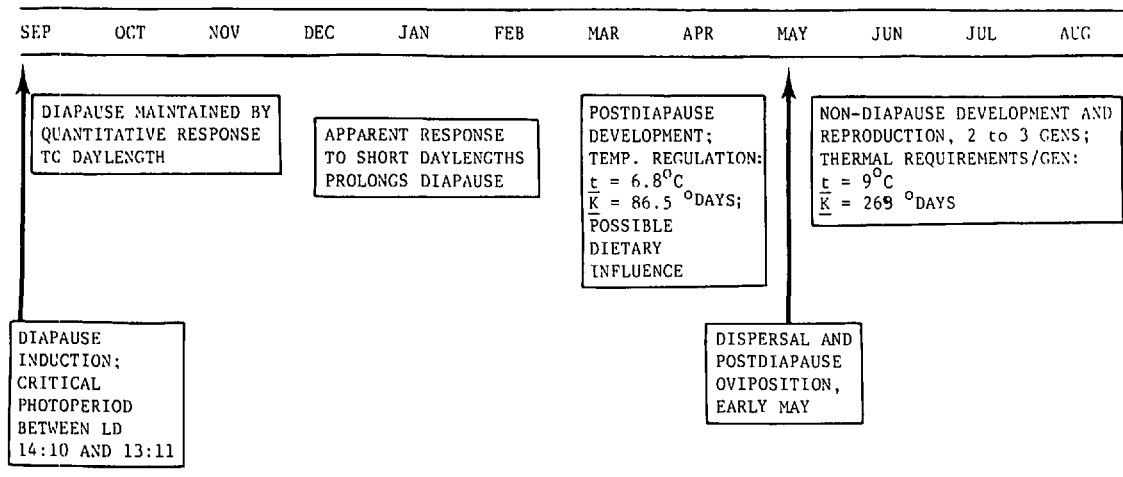


FIG. 3.—Seasonal life cycle of *A. bipunctata*.

lier and faster development in spring and early summer, when temperatures are near the developmental thresholds, than four other coccinellids that have been studied (*Coccinella septempunctata* L., *C. transversoguttata richardsoni* Brown, *Coleomegilla maculata*, and *Hippodamia convergens* Guérin-Méneville) (see Obyrcki and Tauber 1981, 1982). However, later in the season, when temperatures are high and consistently above the threshold values, *A. bipunctata* develops more slowly than the other four species, because of its large *K* value (269 degree-days) (Obyrcki and Tauber 1981).

Based solely upon thermal requirements, Obyrcki and Tauber (1981) predicted that *A. bipunctata* would produce three to four generations in the Ithaca area; actually, two to three generations are observed (Fig. 3) (Obyrcki and Tauber, unpublished data). Because our laboratory-derived *K* value of 263 ± 9.0 degree-days (Obyrcki and Tauber 1981) is very similar to the *K* value (269 ± 12 degree-days) for development outdoors, we propose that the difference in the number of generations may result from variation in the amount and kind of prey available in the field.

Food has been shown to have several effects on *A. bipunctata*, including reduction in the annual number of generations (Putman 1964), regulation of the preoviposition period and fecundity (Hariri 1966), and influence on larval development and survival (Blackman 1967). From our studies, we propose that temperature determines the maximum developmental rate of *A. bipunctata*, whereas food (availability and type) determines the actual number of generations produced.

Food also affects voltinism in some coccinellids by influencing aestival diapause (Hagen 1962, McMullen 1967). This is not the case for *A. bipunctata*, but it is possible that prey availability may influence the timing of autumnal diapause induction.

Biological Control

A major adaptation of entomophagous species is their seasonal synchrony with their hosts or prey (see Tauber and Tauber 1976, 1978). Many aphid predators and parasites have higher thermal requirements for development (high *t* and *K* values) than their aphid hosts or prey (Campbell and Mackauer 1975, Obyrcki and Tauber 1982). This difference allows the host or prey to complete a generation faster than the beneficial species. In contrast, Neuenschwander (1975, 1976) determined that the hemerobiid *Hemerobius pacificus* Banks develops and reproduces at lower temperatures than its aphid prey. He proposed that this predator could be used as a biological control agent early in the season when low temperatures prevent the use of other predators or parasites. A similar statement can be made for *A. bipunctata*. Although its temperature thresholds for development are not as low as *H. pacificus*, they are lower than the other coccinellids we have examined (Obyrcki and Tauber 1981, 1982).

A. bipunctata's arboreal habitat association also adapts it as an early-season predator of aphids. Many aphid species begin their development during early spring on

trees and shrubs, before moving to annual plants (see Blackman 1974). For example, *M. persicae* populations occur early in the spring on peach trees. Tamaki (1973) observed that *C. transversoguttata richardsoni* and *H. convergens* were the two principal coccinellids preying upon *M. persicae* in Washington. Under such circumstances, the activity of *A. bipunctata* should be promoted. The role of *A. bipunctata* as an early-season predator of filbert aphids in Oregon is currently under investigation.

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